Conservation of threatened natural habitats

Anthony V Hall (Editor)

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PREFACE

The aim of this book is to give a holistic setting to the conservation of plants and animals. Instead of concentrating on species alone, the aim is to spread the concern to the physical and biological features; including humanity that make up the habitat in which organisms live. All too often, it is not the species that is directly being destroyed, but its habitat. Lacking the essential support systems that the habitat once provided, the species then perishes as inevitably as if its individuals had been over-utilized into oblivion by a hungry humanity.

This is an important orientation for the thrust to provide conservators with a firm scientific backing for their claims to governments and land-owners for adequate funds to conserve their region's plant and animal life. It acts as a complement to two valuable texts: Conservation biology: an evolutionary-ecological perspective, by Soulé and Wilcox (eds 1980), and Conservation and evolution, by Frankel and Soulé (1981).

These books will help university faculties meet the growing need for courses in conservation biology, besides helping qualified conservators in their work. They will help biologists move into a field that is full of vital, virtually unresearched problems. For example, a basic factor in the planning of reserves is the amount of gene-flow needed between populations for their long-term variability and viability, yet there is very little experimental evidence to allow this to be assessed. This book is full of similar unanswered problems.

The urgency of making conservation biology take a strong place in academic curricula and research programmes is very great. The authors of every chapter in this book ring the alarm bells of dying ecosystems that are taking with them the support functions that make the Earth such a fine place for humanity and the other species that share the planet.

Conservation of plants, animals and their habitats must meet a dual function. It must provide long-term security for the ecosystems which are directly or indirectly exploited by humanity so as to meet the needs of human survival. It must also meet the moral obligation of humanity, as the super-dominant species on the Earth, to ensure an unchanged prospect of survival of the plants and animals sharing the Earth with us. The aim here is to allow species to flourish, or to stay as they are, or, like death, to go naturally extinct without being propelled thence by humanity. The trick to learn is how to integrate the development of comfortable habitats for humanity with those of the world's wild creatures, which in a sense are already 'developed' from the great, ancient natural forces of the biosphere. The integration of development for humanity with the needs of nature is a task of prime urgency.

This book has grown from the proceedings of the International Symposium on the Conservation of Threatened Natural Habitats held at the University of Cape Town in September 1980. The Symposium was followed by a Workshop to write a conservator's handbook, Conservation of Ecosystems: Theory and Practice (Siegfried and Davies eds 1982). The handbook is intended to give a step-by-step analysis of the actions needed by local conservation bodies. Both the Symposium and Workshop were convened by the South African National Programme for Environmental Sciences, a cooperative undertaking of scientists and administrators concerned with the study and solution of problems relating to the environment. The conference brought together workers with extended experience from over 100 countries and all continents. The papers presented in this volume benefitted from the critical review of a wide circle of peers. As such they provide a global perspective on many issues fundamental to the conservation, utilization and management of our planet's varied habitats.

The massive scope of the threatened-habitat problem is set out in the first chapter by Norman Myers, based upon his long experience with both developing and developed countries in many parts of the world. He shows the grim burdens of population growth that bedevil attempts at nature conservation in so many countries, and outlines the threats to habitats in a selection of biomes.

Chapter 2 carries a discussion on the objectives of habitat conservation in the light of practical obstacles, written by Robert Allen, a former staff member of the International Union for the Conservation of Nature and Natural Resources (IUCN), who gives valuable guidance based upon his knowledge of the 'World Conservation Strategy' (IUCN 1980a).

This is followed by a chapter by the conservation-biologist Michael Soulé, who precedes a contribution on genetic aspects with an account of three alternative scenarios for conservation, a strong reminder of the future linkages that the planning of nature reserves must take into account: futurology is a vital but insufficiently studied part of providing security for plants, animals and humanity.

In chapter 4, Daniel Botkin contributes his expertise on ecosystem modelling to show the vital importance of this approach for the management of endangered species. He uses an example of the links between geochemistry, chemical cycling, nutritional quality of vegetation, and the abundance of African large mammal life, to show the significance of ecosystem studies. The field he touches upon here is inadequately studied: even some of the most basic experiments still have to be carried out.

Theoretical aspects of management and selection of areas for conservation are discussed in the next two chapters. The first is by Jared Diamond, who was responsible for developing an important outlook on the maintenance of species diversity in the limited, island-like patches that are often all that is left for conservation today. Kenton Miller's approach to the principles of selecting habitats for conservation deserves wide attention: his account is based upon many years of experience of creating nature reserves in Latin America and the Caribbean. This part of the book is rounded off with an account of the rather different problems of marine conservation, and the techniques developed by the author, Carleton Ray, to identify and manage priority critical habitats.

The book closes with two case studies. In the African Great Lakes, Geoffrey Fryer takes us into the problems of conservation of a rich fish fauna in the face of exploitation, guided only by standing crop data for management that are at best difficult to get and at worst, somewhat misleading. Finally, S K Jain and R K Sastry describe the problems of plant conservation in India, stressing the critical values of plant life in supporting ecosystems and in helping cope with the hazards of soil erosion and siltation of vitally important water storage dams. In all the gloom of widespread pressures on plant life, a brighter note is struck in the well advanced programme to establish Biosphere Reserves in India so that its great variety of biomes may at least survive in representative areas.

Habitat conservation is a vitally important concept. Without proper attention to it, humanity and the other species sharing 'spaceship Earth' can expect a steady worsening in life standards. Will this book, with its distinguished authorship, succeed in getting all its readers to realize and act upon their global duties to Nature?

ACKNOWLEDGEMENTS

The idea of convening an international symposium and workshop on the topic of threatened habitats arose from the dilemma faced by South African conservationists confronted with the need to conserve nearly 2000 threatened plant species. Any strategy aimed at the species level has no chance of success in a floristically and faunistically rich country such as South Africa. Hence the need to define very clearly the concepts, objectives and strategies relevant to conserving habitats rather than species. The organization of the meeting fell to Brian Huntley, assisted by Roy Siegfried, Graham Noble, Douglas Hey and Tisha Greyling.

The production of the camera-ready copy of this volume was possible through the untiring efforts of Elma Mantle, Karen Esler, Pascal Chesselet, Enid Steer and Margie Jarman. To them my sincere thanks.

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TABLE OF CONTENTS

CHAPTER 4 The garden of the unicorn - the ecosystem context for the management of endangered species

Daniel B Botkin

CHAPTER 5 Management for maintenance of species diversity

Jared M Diamond

CHAPTER 6 Selecting terrestrial habitats for conservation

Kenton R Miller

CHAPTER 7 Conservation of marine habitats and their biota

G Carleton Ray

CHAPTER 8 The conservation and rational exploitation of the biota of Africa's Great Lakes

Geoffrey Fryer

CHAPTER 9 Safeguarding plant diversity in threatened natural habitats

S K Jain and A R K Sastry

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CHAPTER 1 PROBLEMS AND OPPORTUNITIES IN HABITAT CONSERVATION

Norman Myers

INTRODUCTION

The surface of the earth is undergoing man-imposed changes that match the upheavals of a Pleistocene glaciation. Indeed some observers consider that the broad-scale disruption of the planet's ecosystems is as great as virtually any evolutionary dislocations that have occurred through the geologic past, and whereas the upheavals of prehistory took millions of years to run their course, the current alterations are occurring within decades, within the twinkling of an evolutionary eye (Ehrlich et al 1977; Myers 1979, 1980, 1981a; Council on Environmental Quality 1980; Polunin 1980; Raven 1980; Soulé and Wilcox 1980).

Within the scope of this chapter, it is not possible to document the nature and extent of these changes of the earth's biomes. An exercise of that scale would need a book in itself. We must confine ourselves then, to a review of the situation in a selection of biomes from both the tropical and temperate zones, and from both the terrestrial and marine realms.

IMPACT OF HUMAN NUMBERS AND HUMAN EXPECTATIONS

Before we go on to look at these biomes, however, let us briefly review the key component of the entire conservation situation, namely the question of growing human numbers and growing human aspirations. It is due to human impact that wildlife habitats are declining on every side. It is reasonable to suppose that we are now losing one species with every day that goes by, and that we could witness the extinction of one million species, out of earth's stock of 5-10 million species, by the end of the century (Myers 1979). Of these many extinctions, only the merest handful will be due to 'natural' causes, as in the case of a monkey in Amazonia that, virtually undisturbed by human activities, is rapidly losing ground to fellow monkey species that are presumably more competitive.

According to recent reports by the United Nations Fund for Population Activities and by the World Bank, zero population growth will not be achieved on earth for another 130 years. True, the 1970s have revealed some encouraging signs of a decline in growth rates. India's growth rate is now well below 2 percent per year, and China's may well have sunk as low as 1 percent. Throughout Asia and Latin America, there is widespread evidence that growth rates are falling, often fast. But not yet fast enough to counter-balance the sudden upsurge in growth rates (not due to soaring birth rates but plunging death rates) during the 1950s and 1960s. Moreover, growth rates in black Africa are still trending upwards.

The overall result will be that, by the year 2110, global population is likely to have expanded to 10,5 billion, or 2½ times as many as the earth now supports (sic). (The projected total is based on 'reasonable expectations' for expansion of family planning programmes). Of the 10,5 billion, 9,1 billion will be living in today's developing nations; and the two regions with the greatest proportions of impoverished peasantry (the people who do most damage to natural environments), viz. southern Asia and black Africa, will account for 6,2 billion or 60 percent of humankind.

The first region that is expected to stabilize its population growth rate will be Europe, reaching zero growth rate by 2030, expanding from 484 million today to 540 million. The next region to stabilize will be North America, expanding from its present 249 million to 318 million by 2060. Oceania, with 23 million now, is expected to reach 41 million by 2070. Eastern Asia, including China, now totals 1059 million, and is projected to reach 1725 million by the year 2090. The Soviet Union, now totalling 265 million people, will reach 379 million before stabilizing by 2100; and at more or less the same point in time, Latin America, with 364 million people today, will reach 1200 million, and southern Asia, with 1405 million, will reach 4145 million. Last to stabilize will be Africa, now totalling 470 million and expected to reach 2193 million by the year 2110.

Let us break down these broad regional figures, and take a quick look at some individual countries. Kenya, with 17 million people today, and with one of the finest wildlife spectacles ever known on earth, is projected to reach 109 million by the year 2095. Ethiopia, with exceptionally differentiated topography, climates and habitats, and hence an extraordinarily diverse fauna and flora, now totals just over 30 million people, and is projected to expand (theoretically, at least) to 162 million by the year 2140. Madagascar, with 10 000 endemic plant species out of 250 000 plant species throughout the earth - a unique concentration of unique plant life - now totals 9,5 million people, and is projected to reach 45 million early in the 22nd century. Colombia, featuring more bird species than any other single nation, now contains 27 million, and is projected to reach 60 million in another 90 years' time. Philippines, with more tree species on a single mountain than in the whole of United States, and presumably with a similarly exceptional total of other plant species, and a complement of animal species, now totals 48 million, and is projected to reach 125 million. Indonesia, with its thousands of islands that suggest some spectacular levels of endemism (less than one tenth of its species are believed to have been catalogued by science), is now approaching 150 million people, and may well grow to 388 million before it reaches stabilization. Such is a summary selection of some countries that, through geographic accident, possess a disproportionate share of a global heritage in wildlife diversity.

Of course many of the projected figures will not work in practise. In virtually all the countries listed, death rates are no longer declining nearly so fast as they were, even though there is still plenty of 'slack' to take in before they eliminate major forms of disease. Whereas several of the countries listed were self-sufficient in food only 15 years ago, none is now in that fortunate position - and all are becoming increasingly dependent on increasingly scarce supplies of surplus food around the world. One must expect that these countries face a bleak outlook so far as their human populations are concerned.

One must also expect that hungry people do not always make best use of their living space. Impoverished peasants tend to make extensive, rather than intensive, use of their agricultural lands. Their cultivation techniques do not become ever-more efficient; instead they become ever-more wasteful of land resources. Lacking funds, the peasant cannot buy high-yielding seeds, fertilizer, pesticides, machinery and the other prerequisites of modern agriculture. Instead of being able to support himself and his family off as little as three hectares, he may find he needs twice as much. Result, the most fertile and best watered lands become over-crowded, and excess communities spill out into less suitable lands for cultivation - where the peasant may find that he needs twice as much land yet again to support his family. Upshot of this sorry prospect: as more people become poorer, they will tend to use much more land to eke out a minimum existence - and the additional land they require will be taken from wildlife habitats. Hence the main threat to wildlife in parks around the developing tropics (where 70 percent of all species occur) derives not from thousands of poachers with their poisoned arrows. Rather it derives from many millions of people with a far more formidable weapon in their hands, a digging hoe.

Some inhabitants of the planet do not meet the entire costs of their expansive lifestyles. For example, Americans, complaining for years about the mounting price of domestic beef, have been looking elsewhere for cheap supplies of hamburger meat. True, Americans have witnessed a three-fold increase in the price of hamburger meat in the second half of the 1970s, until this one item has become the most inflationary item in the weekly shopping basket. The American government fnally decided that it could take no single better initiative to counter inflation than to increase its imports of beef - and the least costly source has proven to be Central America. From southern Mexico to Panama, the amount of pasture-land and the numbers of cattle have increased two and a half times during the past 25 years. Almost all of the pasture-lands have been established by clearing away the primary forest of the region. If present deforestation trends persist, Central America will have virtually nothing left by the year 1990. Ironically, hardly any of the increased beef output has made its way into the stomachs of local citizens. In fact, the average Central American now consumes less beef than he did in 1955. Almost all the expanded output makes its way northwards into the United States, where it is seized upon, as 'reasonably priced' beef, by the hamburger chains and by the other fast-food enterprises. Hence the 'hamburger connection' between affluent life-styles in North America, and disappearing forests in Central America (Myers 1981c). Tragically, the loss of the forests and their wildlife will eventually impose a cost on the entire community around the world. Scientists have found that the forests of the region are so rich in their diverse floras and faunas that they offer unusual potential for anti-cancer materials among other drugs, start-point products for innovative industry, and rich gene reservoirs for the burgeoning activities of bio-engineering.

At the same time, there is a related constraint. It lies with growing human aspirations. Poor people in developing nations now learn, from community television centres, from glossy magazines published in Europe and North America, and from dozens of other 'media advances', that the 'good life' entails far more than they believed appropriate 20 years ago. Hence again an accelerating scramble for land: those who can sustain themselves adequately off their existing farms now feel that they would like to expand their lifestyle, so they look around for additional areas in which to grow their cash crops. Overall result, a sustained squeeze on the patches of wildlands that remain around our earth.

Thus it is not only the poorest of the poor who cause great damage to natural environments. Better-off people can generate problems - and it is the most affluent people on earth who match the very poorest in their growing pressures on wildlife living-space. The reader of this book is likely to be a developed-world citizen. Let him (or her) reflect that one American or Swiss or Swede, or two Britishers or two Japanese, consume, in terms of vegetable food (crop plant growth, some of which reaches human stomachs via livestock) at least 10-15 times as much as a Ugandan or a Bangladeshi; and in terms of energy, he accounts for 50 times as much. Similar disproportionate figures can be quoted for key natural resources. If we look at 'global accountancy' figures, we find that there is still enough of everything to meet the needs of the present human community - enough food, enough energy, enough fibre, enough raw materials of every sort, and enough living space for both humankind and wildlife. All depends on how the resources are shared out.

A similar tale can be told of deforestation in Indonesia and Cameroon, among other countries. Forests are being felled in order to supply hardwood timber to meet marketplace demand in advanced nations. Hardwoods are required for parquet floors, weekend yachts, and other prequisites of the 'good life'. Moreover, much of the timber harvesting is conducted by giant corporations that are based in the developed world, such as Georgia Pacific of the United States, Mitsubishi of Japan and Bruynzeel of Netherlands. Again we might well ask, 'Whose hand is on the chainsaw at work in tropical forests?' And we might further ask whether the developed world citizen is paying a proper price for his hamburger meat and hardwood products: the price tag at his local restaurant or luxury-goods store does not reflect all the costs that go into the production of the items in question, notably the environmental costs of deforestation.

Our aim should be to 'internalize' the 'externality costs' that are not reflected today in international trade patterns. At the same time, we can try to become increasingly self-reliant, with each nation, and each human community, trying to work its own material salvation. As an example of national self-reliance, China offers a sound illustration. In 1949, under the old regime, China comprised half a billion people. They were mostly ill-fed, diseased, uneducated, poorly housed, and living in a land whose forests and soil cover and water stocks were declining year by year. Today China has twice as many people, virtually all of whom are adequately fed and housed and employed and educated, and they live in a land whose forests and soil cover and water stocks are increasing. China is one of the few countries where wildlife, generally speaking, is making a come-back (Myers 1976). China's wildlife had reached all but the brink of extinction, and any change must have been an improvement (if not final doom). But China's experience indicates that, if we all accept a basic rule of life in the global village, viz. that we must accept 'mutual coercion mutually agreed on', then we can all get by - and by 'all', we mean all of humankind, plus the millions of fellow species that have shared the one-earth home with us for many millennia, and that now face the prospect of being elbowed off the planet in a matter of a few decades.

This review of the population question is necessarily confined to a mere summary. Every reader will know where to find further information. Indeed every reader will have already heard much of the issue. But it does no harm for us to be reminded, once again, of the central challenge that faces wildlife supporters in whatever part of the world.

THREATENED HABITATS IN A SELECTION OF BIOMES

Tropical moist forests

Tropical moist forests form a green band of vegetation running around the equator, and extending some ten degrees of latitude north and south. Biologically speaking, these forests are the richest ecosystems on Earth, containing, within their total extent of less than 10 percent of the planet's land surface, some 40-50 percent of earth's estimated 5-10 million species (Council of Environmental Quality 1980; Myers 1980b and c; Raven 1980; USA Interagency Task-Force on Tropical Forests 1980).

Yet this biome is less known than any other. We now know more about certain sectors of the moon's surface than about the heartlands of many tropical forests. In 1972, the Tasaday tribe was discovered in a Philippines rain forest, separated from the outside world by a mere 24 km of forest, and apparently isolated since Neolithic time.

Moreover, these forests are being disrupted and depleted more rapidly than any other biome. If present land-use trends and exploitation patterns persist (and they are likely to accelerate), large sections of the forests will become markedly modified, if not fundamentally transformed, within the next 3 to 5 decades. Some authoritative observers believe that by the end of the century, many of these forests will have been reduced to degraded remnants, if not eliminated altogether (USA Interagency Task-Force on Tropical Forests 1980; Raven 1980).

There are three main agents at work. One is the timber harvester, extracting specialist hardwoods to meet market-place demands primarily from developed nations of the rich temperate world, whose consumption of tropical timber has increased fifteen times during the past three decades. Another agent is the cattle rancher, especially in Latin America, who clears away the forest completely in order to establish grasslands. Forest zone ranches in Brazilian Amazonia now cover at least 100 000 km^2 and other large forest tracts have been similarly converted in Colombia, Peru and Bolivia. In Central America, the number of cattle and the amount of pasture-land have increased 2½ times from 1950 to 1981; almost all the additional beef is despatched to the United States, where most of it makes its way into the hamburger and frankfurter trade in response to booming demand for 'cheap' beef. The third agent, and by far the most widespread, is the forest farmer - meaning not only the shifting cultivator of a traditional type, but the squatter-style peasant who, landless elsewhere, now penetrates deep into the forest zones that have hitherto remained beyond the pressures of these growing hordes of 'spontaneous settlers'. Altogether these forest farmers are now estimated to total at least 150 million persons, occupying some two million km^2 of tropical moist forests (out of a total extent of some nine million km^2) and eliminating perhaps 200 000 km^2 of forest each year, conceivably much more.

These various figures are prepared through order-of-magnitude reckonings. They are rough and ready calculations, presented only as a best judgement assessment within a broad range of possible estimates. As a general conclusion, however, we can realistically assert that these three agents, in conjunction with other agents such as the fuelwood gatherer, the plantation man who grows rubber and oil palm trees, and other persons who wish to convert primary forest to other purposes, are accounting for 260 000 km^2 per year.

In short, we could be losing around 700 km^2 of tropical moist forest, or an area as large as Vermont or Wales, each day. This works out to a figure of 50 ha per minute - to be compared with a figure of 20 ha per minute derived from earlier estimates by FAO in the mid-1970s.

A conversion rate of 260 000 km^2 per year means, in theory, that the entire biome of roughly nine million km^2 will become subject to gross disruption, if not outright destruction, within only 35 years. Of course the rate of conversion is likely to accelerate in many areas, and to decline in a few: the pattern is highly differentiated - with all that implies for conservation planning.

Virtually all lowland forests of Southeast Asia seem likely to become heavily logged by the year 2000 at the latest, many of them by 1990. Little could remain of Central America's moist forests within another 10 years, quite probably less - and the same for West Africa. By contrast, much of Central Africa, namely Zaire, Gabon and Congo, feature low human densities and abundant mineral resources, which means that these countries perceive little incentive to liquidate their 'forest capital' in order to finance economic development. The upshot is that large expanses of little-disturbed forest could remain in the Zaire Basin by the end of the century. Similarly the western portion of Brazilian Amazonia, because of its remoteness and exceptionally humid climate (making conventional agriculture extremely difficult), may undergo only moderate change.

This brief review of exploitation patterns overtaking tropical moist forests points up a pervasive conclusion with regard to the degradation of natural environments around the earth. We all - citizens of both the rich and consumerist temperate zones and the developing and populous developing tropics - have a hand in the process, ie not only people on the spot but also persons in far-off lands who, by virtue of their lifestyles, generate market-place demand for products from eg tropical forests. To this extent, everybody's hand is on the chainsaw at work in tropical forests.

Furthermore, we shall all lose if tropical forests continue to be depleted. By our actions, we are precipitating not only an end to future supplies of hardwood timber for the global community, but we are causing the demise of unique ecosystems, species communities and gene reservoirs that could serve the utilitarian needs of society into the indefinite future.

Beyond these considerations, there could be even broader and more critical repercussions arising from the progressive degradation of tropical moist forests. The process could trigger profound climatic changes. Widespread burning of the forests by small-scale farmers and large-scale ranchers is possibly contributing to a build-up of carbon dioxide in the earth's atmosphere (though it now appears, according to latest scientific evidence, that it makes little or no difference to oxygen stocks). While tropical moist forests obviously have a huge capacity to soak up carbon dioxide through photosynthesis, it is now thought that widespread burning means they are probably serving as a net source of carbon dioxide. If carbon dioxide continues to increase in the global atmosphere, the 'greenhouse effect' will cause the earth's temperature to rise - and one result will be warmer and drier weather in the North American grain-growing region, with all that implies for the world's capacity to feed itself (Bryson and Murray 1977; Degens 1979; Stumm 1977; Woodwell et al 1979).

Wetlands

Of much smaller extent than tropical moist forests, while often virtually as rich and diverse in biological terms, wetlands face as many pervasive and immediate threats as do tropical moist forests (Chapman 1977; Council on Environmental Quality 1980, Ehrlich et al 1977; Myers 1979). A good share of the planetary spectrum of species like a lot of water in their environments. Amphibians, for example, are highly dependent on water: their young must live in this element entirely during their first stages of life, while an adult cannot be separated from moisture for long. This means that amphibians are unable to move beyond a limited range of habitats; and in turn, it means that, like other wetland-dwellers, amphibians cannot survive man's interference with their life-support systems to the extent that many birds, insects and other animal groups generally can tolerate. Moreover frogs, toads, salamanders and others do not like to spawn in rivers or large lakes, but prefer still, slack waters of ponds and marshes - precisely the areas that man mostly readily modifies or eliminates.

By consequence, wetland dwellers - including not only amphibians but molluscs and several other major categories of species - are especially susceptible to drainage projects, water impoundments and other manipulations of hydrological systems. In many parts of the world, notably developed regions, wetlands are disappearing faster than any other type of environment. Man exploits 'unproductive' zones such as marshes by draining them to make them arable, or by covering them with industrial plants, housing estates, highways and the like. In the United States, for example, the state of Wisconsin once had over 31 000 km^2 of wetlands, now only around 6500 km^2. Of all threatened groups of vertebrate species in the United States, amphibians could well be in greatest trouble; of 2000 inland snail species, at least 400 are considered to be threatened to varying degree, while almost half of all the region's molluscs are either endangered or extinct (one snail used to range from Iowa to southern Ontario, but now it survives only under the spray of the Chittenago Falls in Madison County, New York State). In Great Britain, almost all amphibians are threatened, including even the common frog in many areas.

Despite their bleak outlook, however, wetland dwellers do not receive a fraction of the publicity accorded to mammals and birds. For every thousand nature-lovers who are concerned about the tiger and the peregrine falcon, it would be surprising to find one who is likely to have heard of the Houston toad, let alone to care about its fate.

Coastal zones

Generally as rich in biological terms, and generally as threatened through human activities, are coastal zones (Chapman 1977; Council on Environmental Quality 1980; Ehrlich et al 1977; Goldberg 1976; Myers 1979, Wood and Johannes 1975). These ecosystems include salt marshes and mangrove communities, estuaries and coral reefs - some of the most diverse ecosystems on earth. For example, intertidal salt marshes are an exceptionally fertile part of coastal estuarine ecosystems, recycling mineral and organic nutrients entering the marsh environment from both terrestrial and off-shore sources. So productive are they in terms of plant growth, that certain salt marshes yield as much as ten tonnes of organic material per acre per year. Salt marshes likewise provide a habitat for a broad array of fish, shellfish, wildfowl and mammals: many fish species make transient use of marshes for feeding, for over-winter stays, and as nurseries, during critical phases of their annual life-cycles, while hundreds of species of ducks, geese and other waterfowl visit coastal ecosystems as resting stations and as feeding grounds during their migratory travels.

Similarly tropical coral reefs, along with tropical mangrove communities, are among the richest ecosystems on earth. Indeed their habitats are frequently comparable in complexity and diversity to tropical rain forests. They provide food and shelter for around one third of all kinds of fish and for very large numbers of invertebrate species (Connell 1978; Ehrlich 1975). Acccording to the Food and Agriculture Organization, between one half and three-quarters of commercial marine fish species depend upon estuarine ecosystems during part or all of their life-cycles. At least half of marine life forms directly utilized by humans occur in coastal waters, while nearly all the remainder derive from coastal and oceanic upwellings.

Yet coastal-zone ecosystems not only constitute a 'crossroads' for several interrelated and major ecosystems, of both terrestrial and oceanic realms. They also serve as the sites of many major human activities. This means that coastal-zone ecosystems can undergo greater degradation, and at a faster rate, than virtually any other ecological zone on earth. They suffer from sedimentation and siltation from land sources, also from pollution from far-inland sites, as well as pollution from coastal industries. Moreover, it is precisely these zones that support some of the densest human populations on earth. Of the United States' populace, for example, one third lives and works in regions surrounding estuaries; and of the ten largest metropolitan areas in the world, seven border existing or former estuarine regions, viz New York, Tokyo, London, Shanghai, Buenos Aires, Osaka and Los Angeles. Of the 50-plus cities that are projected to grow to more than five million people each by the year 2000, half are located on estuaries. As a measure of the sea-derived pollution that may overtake these ecosystems, marine transportation systems are projected to increase by as much as seven times by the year 2000, which will mean a great expansion of port facilities along coastlines, plus secondary economic activities and human settlements in coastal zones.

To gain an idea of the disruptive land-use patterns that are overtaking coastal zones, let us briefly review the recent experience of the United States. According to a National Estuary Study of the Department of the Interior in 1970, the United States suffers an annual loss of estuarine environments of almost half of one percent per year and, small as this amount sounds, it has led to an accumulative impact between 1950 and 1980 of almost 400 000 km^2. Not counting Alaska and Hawaii, the (48) United States feature just over 8 million km^2 of estuarine waters, of which 6 million are classified as commercial shellfish waters - and 1,6 million of these are now closed, because of pollution, to shellfishing. A recent report from the Fish and Wildlife Service in Washington DC estimates that almost one quarter of the country's estuaries have become severely degraded, and another 50 percent moderately so, through pollution from oil refineries and other industrial complexes along coastlines. In 1929, USA fishermen landed 41 million kg of oysters, in 1975 only 25 million; the Chesapeake Bay region outside Washington DC produced 53 million kg of oysters per year at the end of the last century, now less than one fifth as much. Along the USA coastline from Maine south to Florida and westwards as far as Texas, fisheries losses caused by pollution are now put at USA $55 million per year. One wonders how high this bill will grow when the damages are assessed for the 530 million litre oil spill in 1979-80 off the Mexican coastline.

As for coastal ecosystems of the tropics, many coral reefs and mangrove communities have been degraded or destroyed along extensive sectors of coasts of the Americas, Africa, east and west Malaysia, Philippines, Indonesia, Vietnam, east and west India, east and south Australia, and south Thailand (UNESCO 1978). Overly-destructive dredging operations have damaged or eliminated coral reefs in the Virgin Islands, Micronesia, Seychelles, Puerto Rico, the Bahamas, Hawaii and Florida (Chapman 1977).

Semi arid and arid zones

The drylands of the earth are obviously among the least productive of the planet's ecosystems. But they nevertheless contain an exceptional proportion of 'oddball' species and communities. An example is the jojoba shrub, Simmondsia chinensis, of southwestern USA and northern Mexico, which is so unusual that it is assigned to a family of its own, the Simmondsiaceae: it is the only liquid wax-producing plant in the entire plant kingdom, hence offers numerous industrial applications. Other monotypic plants of drylands seem able to supply multiple utilitarian benefits for modern industry and medicine. Why this should be so is not clear, but certain observers believe it could be because the harsh environments accentuate 'biological warfare' among species and communities as they develop through the evolutionary process, and thereby throw up monotypic forms and other curiosities.

At the same time, semi-arid and arid zones are among the most fragile ecosystems on earth (Council on Environmental Quality 1980; Ehrlich et al 1977; Harris 1980; Myers 1979; Rapp et al 1976). They can very quickly undergo irreversible degradation at the hand of man: their threshold of critical injury is reached after only a moderate or even marginal modification through human activities. Desertification is now thought to be overtaking 60 000 km^2 per year, an area roughly the size of west Virginia or England south of the River Thames (United Nations 1977, 1978). About a century ago, deserts occupied 14 percent of the world's potentially usable land area (not counting tundra, polar and high mountain regions, and other areas permanently inaccessible to agriculture). By 1950, the proportion had expanded to 35 percent, and by now it is still more again. At present rates of desertification, the world's deserts, now covering some 8,4 million km^2, will expand by one fifth before the end of the century. In point of fact, the process is likely to accelerate, due to increasing numbers of people who direct greater pressures on drylands for stock-raising, crop agriculture and fuelwood. Latest estimates suggest that around 21 million km^2 (roughly equivalent to the area of the United States and Canada put together), can be considered to face desertification risk that is 'high' or 'very high', ie an area more than twice as large as present deserts. The territories at risk include many major wildlife tracts of savanna Africa, notably in southern Sudan, Ethiopia, Kenya, Tanzania, Botswana, Namibia, Zimbabwe, Zambia, Angola and Mozambique; plus similarly extensive semi-arid and arid zones in Asia and Latin America, especially in the tropical realm but also in sub-tropical areas such as northern Mexico and south western United States.

Mediterranean-type environments

Certain ecological zones not only support exceptional numbers of species. They feature many species that are found nowhere else. These twin characteristics of certain ecological zones are key factors for conservation strategies, on the grounds that these areas deserve priority protection. One such ecological zone is collectively known as Mediterranean-type environments. The zone comprises not only the Mediterranean basin itself, but parts of California, central Chile, south western and southern Australia, and the south western Cape sector of South Africa. Of the zone's 25 000 species of flowering plants, around half are endemic, and many are extremely localized in range (Myers, 1979). For example, a hillside overlooking the Pacific Ocean near San Francisco features the Presidio Manzanita (*Arctostaphylos refugioensis*), a plant known to science only since 1972, with possibly only one individual left - a condition that probably several other California plant species could match.

As has been documented elsewhere in this volume, and as is worth briefly repeating here, a notable example is the Fynbos Area, or the Cape Floristic Kingdom, in the southernmost part of South Africa (Hall, 1978). So diverse is this area, that it ranks as one of earth's six distinct floristic kingdoms - and whereas the Boreal Floristic Kingdom covers 42 percent of the earth's land surface, the Fynbos accounts for only 0,04 percent, stretching in a narrow band about 45 km wide and 1000 km long. At least, it used to account for only 0,04 percent: during the past three centuries, its extent has diminished by close to 60 percent, due in the main to the advance of 'civilization', until it has now been reduced to some 18 000 km^2. In terms of species density, this is by far the richest floristic kingdom, over three times better endowed than the next kingdom. More than 8000 species are found in the kingdom, with well over half endemic to its relict patches, featuring dominant elements of over 600 species of the genus *Erica*, 500 species of the family *Proteaceae* and 450 species of the family *Restionaceae*. So far as can be determined, over thirty species are already known to be extinct, and a further 1200 are either extremely rare or exceptionally endangered. The principal form of threat has been loss of habitat due to various human activities. For example, an exceptionally attractive plant, *Moraea loubseri*, discovered by botanists only in 1973, now appears to be confined to a single granite outcrop, a last habitat that is now being quarried for building stone.

Islands

A further catch-all category can be considered under the heading Islands, on the grounds that islands feature large numbers of endemics and are generally characterized by severe threats (Myers, 1979).

Why so many endemics on islands? The apparent reason is that small isolated communities have presented first-rate circumstances for adaptive radiation and rapid evolutionary change. An island effectively seals off a segment of a gene pool that, in the context of a continent, could spread across a much larger territory. Since isolation fosters local specialization, evolutionary processes find outstanding opportunities for speciation on islands. Of Cuba's 6000 plant species in the island's 116 000 km^2, over half are probably endemic.

A classic instance of island endemism is the Hawaii Islands. In the islands' small expanse, one or perhaps two ancestral species of drosophilid flies probably provided the origins from which Hawaii's 500 known species have evolved, an array that represents roughly one-third of all drosophilids listed in the world - though it is a measure of how little we know about insects, even in Hawaii which is part of a scientifically developed nation, that there may be another 200 drosophilids on the islands awaiting discovery.

Hawaii also represents a prime instance of extinction patterns for endemic species on islands. The islands' plants did not develop botanical defences such as prickles, stinging hairs, acrid or poisonous chemicals, or tough root systems that plants often have in areas where large herbivores abound. They did not need such protection. Because of the localized conditions that fostered speciation, 97 percent of Hawaii's 2400-plus species and varieties of flowering plants are endemic. Then came Captain Cook in 1778 who introduced pigs and goats, followed in 1793 by Captain Vancouver who brought sheep and cattle to the islands. These two catastrophic events wreaked more havoc than the volcanic upheavals that have marked the Hawaiian Islands' millions of years of geological history. By the present day, many of Hawaii's highlands have been converted to pasture for domestic livestock, and the lush lowlands have been mainly given over to crops, industry, military bases, housing and other forms of economic development. On top of this, more than 3000 species of exotic plants have been introduced. The upshot is that 273 native plants have gone extinct, and 800 of the remainder are endangered, together with another 99 that are rare and 34 that are highly localized. Of the islands' roughly 250 tree species, 225 are endemic - and about one-half of these are restricted to only one of the eight islands, many of them having a range of only a few square kilometres, some being known from no more than a single locality such as a mountain or a valley. Hawaii now has more endemic trees on the USA Endangered Species List than all the other forty-nine states combined. Moreover, probably at least one-third of Hawaii's insects have become extinct since modern man's arrival, including nearly all of the lowland entomofauna.

Many other sorts of ecological islands exist, not all in such obvious form as lakes. In tropical lowland forests, certain localities show marked biological difference from surrounding areas. During the Pleistocene with its Glacial Periods, the amount of rainfall in the tropics varied sharply. This caused forests to expand during wet periods and to contract during dry phases. By consequence, many distinctive localized ecosystems have arisen within tropical lowland forests - in effect, islands. Amazonia's forests, for example, are far from being one large unvarying tract. Rather it is a remarkably diversified zone, with much local differentiation in habitat conditions. This, together with other factors of tropical evolution, has led to a good deal of speciation in certain localities, leaving some species restricted to only a few hundred, or even a few dozen square kilometres. In turn, this means that broadscale development projects, extending across thousands of square kilometres (Prance 1981), can eliminate whole concentrations of species. Conversely, of course, if conservation can 'lock away' an area of high variety and endemism, the move can achieve far more per dollar than through protecting a similar-sized area elsewhere.

CHALLENGES

After this review of prospects for habitats in selected biomes, let us go on to consider some ways in which we can confront the challenges implicit in the situation.

First of all, the issue of disappearing habitats is receiving exposure from both scientists and politicians. This is timely, since the issue should be a primary concern not only of ecologists and conservationists, but of political leaders, economists and other officials who are responsible for the well-being of our one-earth home.

A couple of statements by leading scientists serve to place the issue in perspective. A leading biologist of Harvard University in the United States, and a man well known for his opinions on the social implications of biology, Professor Edward O Wilson, declares that the foreseeable consequence to society from mega-extinctions of species would be 'worse than economic collapse, limited nuclear war, or conquest by totalitarian government' (Wilson 1980). In the words of Dr Thomas E Lovejoy, of the World Wildlife Fund-US, "There have appeared, during the unfolding of life's story on earth, the Palaeozoic, the Mesozoic and the Cenozoic Eras, that is to say the Eras of Ancient Life, Middle Life and Recent Life. In theory we are still in the Era of Recent Life. But perhaps we should declare that Era terminated, and designate a new one, the Era of Life's Impoverishment".

To cite a statement from a leading economist, Nobel Prize winner Professor Jan Tinbergen, "We urgently need quantitative information in order to design an optimal policy for conservation in the world at large. To this end, a number of policy instruments can, and must, be used to warrant a safer future of humankind, thus supplying an important new dimension to the 'North-South' dialogue" (Tinbergen 1976). Kindred forthright assertions with regard to environmental safeguards, this time within the framework of the New International Economic Order, have been proposed by a range of authorities, notably the Brandt Commission (1980), Cockburn and Ridgeway (1979), Laszlo (1977), Orr and Soroos (1979), Pearson and Pryor (1978), Pirages (1978) and Steinberg and Yager (1978).

It is this latter angle - that of habitat conservation within the context of developed-world/developing-world relations - that merits our attention here. Developing-world leaders, located as they mostly are in the tropics, are becoming aware that they possess the great bulk of the earth's biotic riches, especially in the way of genetic resources. At the same time, it is the developed nations, technologically advanced while biotically impoverished (by comparison with the tropics) that can best exploit the germplasm reservoirs of the Third World (Duke and Hurst, 1975; Duke 1978). A number of plants with anti-cancer properties are being discovered in tropical rain forests; and the countries in question are realizing that the benefits will accrue, for the foreseeable future at least, to so-called advanced societies of the temperate zones, on the grounds that tropical-zone citizens do not generally live long enough to contract cancer. To the extent that developing nations of the tropics are trying to preserve their species, their efforts amount to a 'resource handout' to developed nations, a situation that Third World leaders increasingly protest about, and wish to see raised within the context of North-South negotiations. As Senor Luis Echeverria, former President of Mexico, has put it, "How can a developed-world conservationist speak of the International Union for Conservation of Nature without speaking at the same time of the New International Economic Order?" (Myers 1981b). This approach contrasts with the conventional view of traditional conservationists of the rich nations, who believe that extinction of species represents an impoverishment for the entire global community insofar as species constitute part of everybody's natural heritage. Developing-nation leaders, however, are inclined to perceive the problem, with ever-growing urgency, as part of the 'resource confrontation' between the North and the South.

To resolve these two different approaches, two initiatives could help. The first would be an explicit acknowledgement by the community of nations that, whereas habitats of species-concentrations represent an indivisible part of humankind's patrimony, a disproportionate share of the conservation burden now falls on those nations least able to bear it. A second initiative could lie with a proposal that some observers consider realistic (and others idealistic): it suggests that rich nations might consider a cost-sharing arrangement to assist developing nations with the expense of habitat-conservation programmes in the developing tropics.

Without initiatives along these lines, key habitats and their species may increasingly be regarded as a further set of high-value resources through which the 'South' expresses its grievances against the 'North'. Thus, at any rate, have been certain in-the-corridor rumblings at recent meetings of United Nations agencies.

True, there are already some tentative steps along these lines, such as UNESCO's World Heritage Trust and its Biosphere Reserves project. Both these initiatives are, however, absurdly under-funded. As a minimum requirement, each of earth's biogeographical provinces, almost 200 of them, should feature at least one Biosphere Reserve; to date, less than one-quarter of these provinces possess such a Reserve. To establish a typical Reserve costs around \$100 000, and to maintain it another \$50 000 per year; so a programme to set up another 150 Reserves, and to run them until the end of the century, would cost \$165 million - the equivalent of a value-added tax of 0,1 percent on internationally traded oil (as has been proposed by Saudi Arabia) extended over a mere 20 months. Kindred sources of revenues could lie with a value-added tax on international trade of all kinds, this measure impinging most directly on those sectors of the global community that benefit most from exploitation of the earth's natural resources, viz the developed nations. A trifling 0,1 percent tax would yield \$1 billion a year.

Global taxes of this sort would accord with the spirit of the New International Economic Order. Professor Jan Tinbergen, the economist mentioned above, not only considers the possibility of taxes along these lines to be valid and feasible; he goes further, by advocating a number of international institutions to articulate and formalize the established phenomenon of interdependency relationships among the global community. For example, he advocates a World Authority to regulate the use of 'international resources' together with a World Treasury to fund collective activities on the part of the global village (Tinbergen, 1976). Similar steps have been recently proposed within the broad-ranging framework of the Brandt Commission's Report on North-South relations.

Pragmatic measures of this kind would help to put operational muscle behind the World Conservation Strategy, released in early March 1980 by the International Union for Conservation of Nature and Natural Resources (IUCN, 1980). A major part of the strategy focuses on threatened habitats; and whereas the conceptual analysis of the Strategy is first-rate, the document does not spell out clearly enough how we get from here to there. The main problem lies with funding, and with the cost-benefit arithmetic of conservation activities that involve all nations of the world and that will benefit all generations into the future. However warm-hearted one may feel about threatened creatures and their life-support systems, one must be hard-nosed in devising the institutional mechanisms, the political initiatives and the economic rationale, to enable a conservation strategy to survive in our workaday world.

Tentative steps towards collective responsibility

Although funding at present is grotesquely inadequate for habitat conservation, we can be encouraged by noting that a number of institutional initiatives have been undertaken to express the interests of society at large in this direction. Indeed the situation is already marked - albeit in extremely limited fashion by emergent concepts of collective responsibility for environmental resources, such as exceptional-value habitats, of international significance.

For example, there are now more than 40 multilateral conventions dealing with natural resources of various kinds, almost all of them offering support for habitats. Many of these conventions are regional arrangements, tackling, for example, joint management of Baltic and Red Seas, and various inland waters. In addition, we now have a number of agreements at global level. They include not only the World Heritage Trust and the Biosphere Reserves network (mentioned above), but also the Convention on Wetlands of International Importance and the Convention on Conservation of Islands for Science. These legal devices serve as a measure of efforts on the part of the international community to take a few cautious steps towards communal responsibility for unique habitats of exceptional value to humankind.

Conclusion

To end on a brighter note, a whole-hearted decision on the part of the community of nations to accept collective responsibility for earth's threatened habitats could lead to an important spin-off benefit. The effort could help to articulate the common interest of society at large. After all, conservation of habitats and their species can be presented as a less likely source of political friction than many other international challenges. A strategy to conserve habitats and their species might even encourage governments to adopt a more collective approach to other collective issues that confront the global community.

In the sum, efforts to conserve outstanding habitats could, by promoting a consciousness of humankind's unity, prove a solid step toward a new world order.

SUMMARY

We are witnessing a fundamental modification, if not a gross degradation, of many of earth's habitats. The changes could well prove to be as extensive as those caused by great geologic upheavals of prehistory; and they are occurring on a compressed time-scale that far surpass, in intensity, any disruptive phenomena of the earth's past. So significant are these changes that our grandchildren may well look out upon a planetary ecosystem that has lost virtually all its wildland habitats as conventionally understood; and together with the loss of these habitats will occur a mega-extinction of species. This will all represent the greatest biological debacle since the first emergence of life some 3,6 billion years ago, and it could well lead to a permanent diversion and a persistent impoverishment in the course of evolution. This situation postulates a major effort on the part of the constituent elements of humankind - nations, governments, citizen groups, private agencies, international bodies, etc - to recognize the scale of the challenge, and to get to grips with the problems with all due urgency. Through sufficient cooperative endeavour, humankind can still safeguard the habitats of the 5-10 million fellow species that share the one-earth home - and thereby humankind will safeguard its own life support systems.

CHAPTER 2 THREATENED HABITATS: THE CHALLENGES FOR HUMANITY

Robert Prescott-Allen

INTRODUCTION

The natural habitats of plants and animals are today widely threatened, and their conservation is a vitally urgent problem. It is a major challenge to find practical solutions to this so as to secure both adequate qualities of life and reasonable chances of long-term survival for both humanity and the other species sharing the Earth.

It is important to define the main terms of habitat conservation. In the World Conservation Strategy (IUCN 1980a), conservation is defined as the 'management of human use of the biosphere so that it may yield the greatest sustainable benefit to present generations, while maintaining its potential to meet the needs and aspirations of future generations'.

Two features of this definition should be stressed. It allows conservation to include preservation and protection but is by no means restricted to them: it also includes restoration, enhancement and sustainable use. The use of the word conservation to mean preservation and protection (although etymologically and lexically correct) should be avoided since these two words are adequate for their purpose. Further, such use might imply that conservation is intended for maintaining the ecological status quo which would foster some simplistic and unwelcome misapprehensions about it, retarding an acceptance of its larger role in human affairs.

The second feature of the definition is more important. It is that conservation is a thoroughly anthropocentric pursuit, for and about people. If there were no people, there would be no need for conservation; and people are conservation's beneficiaries. These may be truisms but they are easily forgotten. Recalling them helps one steer a course between the Scylla and Charybdis of ecological philosophy (Lovelock 1979). Scylla stands for the loftily Gaian view that nothing really matters save Life itself: as long as the biosphere wins through in the end it matters little whether or not the human species manages to survive with it (Lovelock 1979); Charybdis being a latter-day 'Noah-like' view that all life matters, that any genotype that happens to have survived until today should be saved from extinction.

There are elements of both views in conservation writings, though the second is the more frequent. Either tends to give conservation an air of both unreality and remoteness from human concerns. This is one of the reasons why the habitats of so many species continue to be threatened. One should therefore stress that the aim of conservation is not simply to maintain a biosphere rich in species and their habitats: it must also provide a fit habitat for humanity. More prosaically, if development for humanity involves producing the goods and services necessary for civilization, then conservation is concerned with maintaining the biosphere's capacity for that production.

It is conservation's job to ensure that certain critical elements of the biosphere are not consumed, and that the rate of use of the rest is kept within limits. The biosphere can then, in theory, renew itself for continuing consumption by humanity and by other species. This requires meeting three objectives:

1. The maintenance of the essential ecological processes and the systems that support life;

2. The preservation of genetic diversity; and,

3. The utilization, by humanity, of species and ecosystems in such a way that adequate yields can be sustained for indefinite periods.

Conservation and particularly protection of habitats are necessary for meeting all three objectives. A habitat is defined as the place where an organism, a population, an ecotype, a species or a community lives. In the case of a community, 'place' may mean the non-living environment alone, while for an organism, population or ecotype it includes the context of the associated species (Odum 1971).

The first task in this chapter is to show which groups of habitats are of primary concern for conservation. A discussion follows on their global status and threats to their survival. The chief obstacles to habitat conservation are discussed, and ways for overcoming them are reviewed. The prospect and challenges for habitat conservation in the future are discussed in a concluding section.

THE HABITATS OF CONCERN FOR CONSERVATION

The main habitats with which conservation is concerned are those required for meeting the three objectives listed above. Keeping these objectives in mind helps in setting priorities and avoiding some of the less necessary controversies of conservation.

One such controversy revolves around the notions of wilderness and naturalness. The preservation of so-called wilderness, the landscapes untouched by human hand, foot or bulldozer (though not necessarily unbathed by acid rain, organochlorines and low-level radioactive fallout) may not be essential for achieving conservation's aims. Such preservation may be important for the peace of mind and spiritual enrichment of groups of individuals in some societies, but so may be preserving those artefacts of the marriage of culture and nature which are especially pleasing, such as alpine meadows in Europe or rice-terraces in South-East Asia. Whether or not an ecosystem has been influenced by humanity does not matter to conservation, as long as it continues to function and meet established objectives.

By the same token, the distinction between natural and artificial threats to a species or habitat may not be helpful. In an extreme example, it would be inconsistent for conservationists to reject the still remarkable ecosystems of New Zealand as unnaturally impoverished by the extinctions of thirty-four bird species at the hands of the Polynesians, but to accept the New Guinea land-bridge islands as natural because, although they lost even more birds, they did so as a result of non-human forces (Diamond 1980). In practice, of course, conservationists would not be as purist as this. The usefulness of reserve may be judged better by its effectiveness in meeting stated objectives rather than its aboriginal diversity alone.

This brings us to examine the three main objectives of conservation and the types of habitat that are likely to be important for achieving them.

The objective of maintaining essential ecological processes and life-support systems

Essential ecological processes can be defined as those that are governed, supported or strongly moderated by ecosystems and are essential for food production, health and other aspects of human survival and sustainable development (IUCN 1980a). They include the cycling of oxygen, carbon and other essential elements; soil formation and protection; the cleansing of air and waters; waste disposal and the recycling of nutrients; pollination and seed-dispersal.

Some essential processes involve direct ecological linkages between species, as in the pollination of plants by insects, the dispersal of seeds by birds or the natural controls of pests by predators and parasites. In such cases it is possible to identify the habitats that are crucial for maintaining each process. The pollination of alfalfa by the alkali bee *Nomia melanderi* depends on the availability of alkaline flats or low mounds with sparse vegetation, or some artificial equivalent, for the bee's nesting habitat (Free 1970). Other processes can be seen to be community-specific. For example ocean nutrients are scavenged and accumulated by coral communities, allowing them to be used and distributed later by dependent fish populations. Another example is the role of mangroves in coastal protection and as nurseries and sources of nutrients for several crustaceans and fish species.

Other processes are not known well enough for an understanding of their relationships with habitats. It may not be possible to identify the habitats essential for some indispensable processes, such as the global cycling of oxygen, carbon, sulphur, nitrogen, phosphorus and other vital elements, since they may not be precisely definable. The ecosystems that affect these processes may have enough back-up systems or internal redundancy to make them resilient to losses of species or even entire communities, up to some threshold value.

This topic provides fertile ground for debate, ground broken by the intriguing speculations of Lovelock (1979). In developing his argument that the biosphere is a single, self-regulating system, capable of adjusting to external perturbations and maintaining optimum conditions for life, Lovelock suggests that a critical role may be played in several major processes by wetlands, shallows and the muds of continental shelves. For example, the anaerobic zones of lakes, wetlands and the seabed may help to regulate the oxygen balance of the planet. They may do this by acting either as a sink for carbon and adding oxygen to the atmosphere; or by producing methane which by oxidation may significantly reduce oxygen-levels. It is suggested that if the oxygen content of the atmosphere were to rise above an optimum for life, methane production would increase. Oxidation of this methane would then tend to restore the former oxygen-balance. If the oxygen content were to fall, there would be less fermentation in the anaerobic zones, leading to greater sedimentation of carbonaceous material and more release of oxygen.

The objective of preservation of genetic diversity

Genetic diversity is the range of heritable variation present in the world's organisms. A sound strategy for its preservation needs both ex situ protection in germ-plasm banks, zoos, botanic gardens and the like, and in situ protection in the natural habitats of the organisms concerned (Frankel 1970; IUCN 1980a). For the purpose of a preservation strategy, the organisms can be classified into six groups:

1. Cultivated or domesticated organisms;
2. Wild relatives of cultivated or domesticated organisms;
3. Other species of economic, ecological, scientific or cultural value, and their relatives;
4. Threatened species;
5. Unusual species; and, finally,
6. All other organisms.

For the first two of these groups, it is desirable to preserve as much variation within each species as possible. This is to keep secure the stocks needed for breeding new strains and cultivars. Cultivated or domesticated organisms are normally not candidates for in situ conservation as this would be complicated by the need to preserve critical aspects of the artificial habitat. Although the management methods for this would be similar to those that maintain successional stages of a human-altered habitat (for example a European chalk meadow), their costs would probably outweigh their benefits except in special cases. A simple special case is where there is gene-exchange between a cultivated crop and wild relatives occurring as weeds and it is considered useful for introgression to continue.

In such cases, and also in the cases of the wild relatives of crops, the aim is to conserve a wide range of genetic variation. This involves large numbers of different ecotypes and hence a great many habitats whose differences from each other may be quite subtle. Often the degree of differentiation that will be of interest will be at the level of the micro-habitat.

This is progressively less likely to be the case as one moves down the list given above. With group 3 (other species of value and their relatives), the aim is to maintain the fitness of stocks exploited in the wild and to retain as much variation as possible for use in selection and breeding, should the species be domesticated. But since, by definition, breeding work is not being done, the cost of identifying and evaluating different genotypes would not be justified.

With groups 4 and 5 (threatened and unusual species) the aim is to ensure adequate chances of survival. Genetic variation is needed within the species mainly to promote long-term viability.

Within the sixth group (all other organisms), even the comparatively coarse-meshed approach of species-preservation imposes an impracticable burden of detail. To preserve as much genetic diversity as possible, one must be content with protecting 'unique' ecosystems and 'representative samples' of ecosystem-types, thus dealing at best with aggregations of habitats.

The objective of sustainable utilization of species and ecosystems

In order to utilize the products of species and ecosystems in a sustainable way, one should first find out their productive capacities. Measures should then be adopted that ensure that uses do not exceed these capacities. The measures should include both quotas and restrictions on access to the resource, as well as protection of the habitats essential for the survival of the exploited species. Critical habitats are in the case of animals the places needed for feeding, resting, breeding and care of the young; for plants they may simply be the prime growing area and any other territories needed for associates such as pollinators and seed-dispersers. The groups of species of concern for sustainable utilization are (in order of presumed importance): those on which people depend for subsistence, those which are commercially exploited and those which are used for sport or recreation.

The concept of sustainable utilization is applicable more to species than ecosystems. When applied to ecosystems there is the analogous and equally necessary exercise to identify and make secure any essential support-systems.

Habitats requiring priority for conservation

The habitat groups of importance for each conservation objective can be considered as belonging to three types. These are habitats which respectively, provide process-support, genetic resources and production support. A single habitat such as a coral reef may serve all three roles.

The first priority for conservation among the process-support habitats (if indeed they exist) are those which keep the entire biosphere going. These are the 'black boxes' or clusters of interlinked feedback loops that enable the biosphere to regulate both itself and the chemistry of the planet so that the Earth remains fit for life. As noted above, such a role has been postulated for the oozes of relatively shallow aquatic ecosystems (Lovelock 1979). Other habitats may also be involved and it is urgent to discover them and their roles. If the health of the biosphere does depend heavily on certain habitats, nothing would endanger humanity more than their disablement.

Second-priority process-support habitats are those which govern large-scale systems essential for food production and the supply of other human necessities. The main ones are certain forests (principally those of tropical cloud-belts and other watershed types), freshwater wetlands and floodplains that help to regulate regional hydrological systems; coastal wetlands, seagrass and algal meadows, and coral and other living reefs. These reefs are, among other aspects, the negentropy centres of the coastal zone and sea, concentrating and 'upgrading' dispersed nutrients and then releasing them, thus making life a little less arduous for a host of dependant species, including us.

The third priority in this group are those habitats which support more local, but nonetheless essential, processes. These include the habitats of mobile link-species and keystone mutualists (Gilbert 1980); those of crop pollinators and of the enemies of agricultural pests; and those that make significant contributions to local nutrient-supply, erosion-control and so on. Locally, as in a nature reserve or in a mixed farming or horticultural community, these habitats would be given a higher priority for conservation, but from a global perspective they are clearly much less important than the first two.

Among genetic-resource habitats, the second priority (it is convenient to leave the first until last) is for those that have the wild relatives of cultivated or domesticated organisms, particularly the plants or animals which are likely to be threatened by pressures leading to extinction. This is because the germ-plasm they contain is generally of direct utility for crop improvement and may often be indispensable not only for strengthening strains but also for preventing catastrophic losses of production.

By the same criterion of actual or likely importance for people, third priority is accorded to other species of economic, ecological, scientific or cultural value, again particularly those which are likely to be threatened. This category, being somewhat a catch-all, calls for an internal ordering of priorities:

1. Species known to play a crucial role in essential ecological processes;
2. Species which are economically important, especially if few, or no substitutes are available;
3. Species which are important for scientific research and for other intellectual, social, or cultural purposes, especially if few or no substitutes are available; and
4. Unusual species, especially narrow endemics and those which are highly distinct, such as the member of a monotypic family.

It may be noted that threatened taxa are not given a separate category. Instead it is proposed that the degree of threat be used as a means of determining priorities within each set of genetic-resource habitats. Thus an endangered ecotype of wheat or a threatened species of whale would be given priority over wild crop relatives or other important taxa that were not in hazard. This procedure would also apply to the first-priority group of genetic-resource habitats and concentrations or clusters of others. Maximum attention should be given to protecting close aggregations of such priority habitats, in the light of the greater importance per unit area justifying a bigger conservation effort, the return on which would be correspondingly higher.

Finally, in the case of production-support habitats, it is suggested that first priority be given to those that are critical for species that are essential for human subsistence. Second priority can be given to commercially important species, and third to the critical habitats of the animals and plants of importance for sport or recreation. Again the principles apply of giving priority, within these categories, to threatened or closely aggregated habitats.

GLOBAL STATUS OF CONSERVATION-PRIORITY HABITATS

Surprisingly little is known about the global status of habitats of primary concern for conservation. Yet it is clear that obliteration of habitats and damage to them are occurring on a vast scale. Of the 787 full species of vertebrates that are listed in the IUCN's Red Data Book as endangered, vulnerable or critically rare, 531 or 67% are threatened by destruction or degradation of their habitats (IUCN 1977, 1978a, 1979a, 1979b). This threat far exceeds in impact the two others of great concern for vertebrates: over-exploitation (278 or 35%) and effects of introduced species (132 or 17%). (Note that some species are affected by more than one threat).

In Appendix 1 a preliminary analysis is given of the distributions of vertebrate species threatened by habitat destruction. The analysis, a preliminary revision of an earlier study (Allen and Prescott-Allen 1978), gives the distributions by biome for the land species and by major ecosystem-group for aquatics and troglodytes. The analysis suggests that the biomes and ecosystem groups under greatest pressure are those given in Table 1.

Table 1. Major ecosystem groups with highest numbers of vertebrate species threatened by habitat alteration

	No of species threatened	% of total no threatened by habitat alteration
Lotic fresh waters (rivers, streams)	94	18
Tropical humid forests	92	17
Islands	76	14
Freshwater wetlands	34	6
Tropical dry/deciduous forests	31	6
Mountain systems	28	5
Intertidal and neritic ecosystems	25	5
	380	72

The numbers and percentages for freshwater ecosystems and tropical forests are in fact higher than those shown. This is because two of the largest categories, multiple/varied land biomes (58 species, 11%), and multiple/varied freshwater ecosystem groups (40 species, 8%), which cover species whose habitats are in more than one biome or ecosystem-group, are not listed here. However, many of the species in the former category are from tropical forests, and all of the latter are of course from freshwater ones.

Less is known about the distribution of higher plants threatened by habitat alteration. Lucas and Synge (1978) indicate that they are concentrated in five biomes or ecosystem-groups: 1. Tropical rain forests 2. Islands 3. Freshwater wetlands 4. Warm deserts and semi-deserts 5. Evergreen sclerophyllous (Mediterranean-type) biomes.

The nine major ecosystem-groups where either vertebrates or plants seem to be most threatened by destruction and degradation of their habitats probably are the same as those that would be short-listed intuitively as most in need of conservation. Indeed, intuition is virtually all one can go by since in most regions there are few data on what habitats are mainly in hazard within each priority group, and still less on the extent of the threats. (See Table 2).

Of the habitats and habitat-groups identified for priority in conservation, only the tropical forests have had their status assessed globally. Four estimates have been made: by Sommer (1976) and Myers (1980), of 'tropical moist forests'; and by Lanly and Clement (1979) and the Council on Environmental Quality (1980) of 'tropical forests'. These differ greatly in their estimates of the rate of removal or alteration in the remaining areas of some 11 million km^2 of tropical forest. Sommer, extrapolating from a sample of thirteen countries, suggests that the average annual rate of loss is 110 000 km^2, which would lead to a 30% reduction in area by the end of the century. The other three estimates are based on reports and statistics from most of the countries concerned. Much of this information is out-of-date, unreliable, incomplete or misleading, and has had to be interpreted by the analysts on the basis of interviews, experience, hunches and assumptions. The outcome is a comparatively low estimate by Lanly and Clement of an annual rate of loss of about 56 000 km^2 (leading to a 12% reduction by the century's end), contrasting with an estimate of 200 000 km^2 lost per annum (40% reduction by the year 2000) from the Council on Environmental Quality.

Myers has recently estimated the rate of loss of tropical moist forests to be higher still, about 260 000 km^2 per annum. Like the other analysts, he points out that not only is the data-base weak, but the rates of destruction vary greatly among the countries. Whatever the global rate of loss, it is abundantly clear that certain forest areas of great importance for the conservation of genetic resources are rapidly disappearing. Some, such as the coastal tropical rain forest of Brazil, have almost gone altogether. Indeed, it may well be that attempts to define the global status of priorities for conservation among habitat-groups are a waste of effort. It is quite sufficient to know what are the most important habitats and which of those are the most threatened. On that basis alone it would be possible to determine priorities for action, which is surely the point of the exercise. It is unfortunate that even at this level of information, data are only available for tropical forests on any usefully global scale.

Table 2. Status of identification of priority habitats

Process support habitats

1st priority: 'biosphere regulators'
None known; needs research

2nd priority: governors of large-scale essential processes
Tropical cloud forests
Other tropical forests
Other watershed forests
Large freshwater wetlands
Active floodplains
Coastal wetlands (mangrove swamps, salt marshes, lagoons, estuaries)
Seagrass and algal meadows
Coral and other living reefs

3rd priority: governors of local essential processes
Not appropriate for global review

Genetic resource habitats

1st priority: clusters of priority habitats
Not yet identified, awaits outcome of work on 2nd and 3rd priorities

2nd priority: habitats of wild relatives of domesticated species
Not yet identified. Habitats of wild relatives of crops are being identified through research for IUCN and the International Board for Plant Genetic Resources (IBPGR) by Christine Prescott-Allen and Robert Allen

3rd priority: habitats of other valuable species
Not yet identified

Production support habitats

1st priority: habitats of species essential for subsistence
Not yet identified; possibly not appropriate for global review

2nd priority: habitats of commercially important species
Not yet identified. Identification of habitats of wild species that contribute (directly or indirectly) to production of food, pharmaceuticals and industrial products produced or imported by Canada, USA and the UK, is one of the aims of research for IUCN and World Wildlife Fund-US by Prescott-Allen and Allen. Important habitat groups are sure to include:
Tropical forests
Coastal wetlands
Seagrass and algal meadows

3rd priority: habitats of important sport/recreation species
Not yet identified; possibly only those of importance for international tourism are appropriate for global review, in which case they include:
Tropical forests
Tropical grasslands
Coastal lagoons and embayments (for example, for whale watching)
Coral reefs

How habitats are destroyed

A brief catalogue of the ways in which people degrade or destroy habitats suggests that there is scarcely any human activity that is not at least potentially damaging:

1. Replacement of the entire habitat by settlements, harbours and other human constructions; by mines and quarries; and by cropland, pasture and plantations;

2. The effects of dams (drowning of plants' and animals' critical habitats, blocking of migrations, and alteration of chemical and thermal conditions);

3. Drainage, canalization and flood-control;

4. Pollution of air and water by chemicals, nutrients and solid wastes (from domestic, agricultural and industrial sources, and from mines, oil wells and transport);

5. Over-extraction of water from aquifers, rivers and other natural sources (for domestic, agricultural and industrial purposes);

6. Removal of materials (such as vegetation, gravel and stones) for timber, fuel, construction and so on);

7. Dredging and dumping;

8. Over-grazing and over-browsing;

9. Introduction of exotic plants or animals of which some ultimately prove to be pests; and

10. Trampling and other intensive land-uses on sensitive terrain, that lead to erosion and siltation.

Many of the activities that cause harmful changes are necessary to feed, clothe and shelter people, to combat their diseases, to employ and entertain them, and to keep their increasingly shaky economies and societies from falling apart. Human pressures are increasing, along with the problems of rising human numbers, wide-scale poverty, and bewildering combinations of recession and inflation. However, most activities which are symptoms of maladjusted development (nearly all of those listed above) can be regulated by integration with conservation, by improving environmental planning, and by strengthening national capacities for corrective action, so that their harmful effects on the biosphere can be minimized. Activities which are symptoms of poverty and gross under-development (spontaneous settlement, unsustainable shifting cultivation and fuel gathering, subsistence over-hunting, over-fishing, over-grazing and over-browsing) can only be controlled and reduced by enabling people to meet their needs in other less harmful ways.

OVERCOMING OBSTACLES TO HABITAT CONSERVATION

It is useful to have three categories for the obstacles to habitat conservation and the respective kinds of action to overcome them, as follows:

1. Proximate obstacles, needing tactical action;

2. Penultimate obstacles, needing strategic action; and

3. Ultimate obstacles, needing basic action.

Proximate obstacles are the activities listed in the previous section. The tactical action needed to deal with them is essentially technical, such as measures to check soil erosion, the establishment of protected areas to safeguard genetic resources, or the introduction and enforcement of regulations to control the use of species and ecosystems. Such action is indispensable and must continue to be taken, but it addresses symptoms, not causes, and unless supported by strategic action it is unlikely to succeed for long. This is a well-recognized problem and the usual response is to call for what might be termed basic action to tackle the ultimate obstacles, such major problems as human population growth, poverty, excessive consumption by the affluent, and international trade and monetary systems that favour the developed countries at the expense of others. Such action is indeed also indispensable, as shown below, but it demands an unusual degree of political will and international co-operation, which even the optimistic agree will take time to achieve, too long to justify postponing other, strategic, action.

Strategic action is at the heart of the programmes proposed in the 'World Conservation Strategy' (See Appendix II to this chapter: IUCN 1980a). The programmes are chiefly concerned with overcoming the penultimate obstacles to conservation, which are given as follows:

1. The mistaken belief that living-resource conservation is a specialized activity rather than a process that cuts across (and should be considered by) all sectors of activity;

2. The consequent failure to integrate conservation with all kinds of development;

3. Development processes that are generally inflexible and needlessly destructive, because of inadequate environmental planning and a lack of rational allocation of land and water uses;

4. The lack of the capacity to conserve, due to inadequate legislation and enforcement; poor organization; shortages of trained personnel; and limited basic information on priorities, on the productive and regenerative abilities of living resources, and on the trade-offs between one management option and another;

5. Lack of support for conservation; and

6. Lack of development for humanity, notably in the rural areas of developing countries.

These obstacles and the strategic actions needed to deal with them are described in the 'World Conservation Strategy' (IUCN 1980a), in the sections on priorities for national targets. Such actions can be expected to be of great benefit in both short and long-term time-scales. It will equip countries not just to save a few species or to protect a few areas, but to conserve the greater part of their living resources and to develop in balance with their environment.

This account will be confined in detail only to those obstacles and actions that are most pertinent to the conservation of threatened natural habitats, and which seem to have been generally overlooked.

Lack of integration of conservation with development

It is evident from their destructiveness of habitats that development decisions seldom take adequate account of the requirements of habitat conservation. Progress has been made in some countries with the assessment of the effects on environments of proposed actions and their alternatives. While the methods may be satisfactory, the measures that call for them do not go far enough. This is because they are restricted largely to a limited number of 'major' actions, often those under some degree of government control; and they tend to come too late in the development process to make much difference. Too often they are used to identify ways of mitigating harm rather than showing decision-makers the environmentally most acceptable ways to achieve development.

There are good reasons for this. A development proposal is an intermediate product of a network of previous decisions. Beginning with an overall policy statement, the proposal is elaborated in a sectoral policy, and costed and scheduled in a programme or plan. If the government is exceptionally well organized, it may test for conflicts and compatibilities with other schemes. Having steered the proposal safely through this minefield, government or industry may be disinclined to have to abandon the proposal or change it in a major way for the sake of some sensitive species, habitat or living resource.

Several steps need to be taken to overcome this obstacle. Firstly, conservation must be elevated to the policy-making level. The maintenance of biological productivity should become as much a part of routine planning as promoting economic output and preventing unemployment. A first step to achieving this can be the inclusion of a conservation chapter in the national economic development plan. Secondly, each government should have an explicit conservation policy concerned with all living resources, not only with wildlife or protected areas. Thirdly, environmental planning should be much improved and the uses of land and water areas strictly allocated according to its principles.

This last point is important for habitat conservation, for which some areas may need to be allocated to preservation alone and others to precisely defined combinations of uses, fixed by special zonings. In the intense and increasing competition for land and water, nature reserves for protecting species and their habitats are often the losers. They may be either restricted to areas that are marginal for farming (where they may not be optimal for conservation either); or, if they do happen to occupy potentially valuable farmland or forest-land, or a fine site for a dam or some other construction project, in the end these other uses may prevail. To avoid either fate, and to ensure that habitats in need of protection are indeed protected, the 'World Conservation Strategy' recommends that countries should allocate land and water uses on the basis of ecosystem evaluations, supplemented by environmental assessments (IUCN 1980a).

Ecosystem evaluations are much the same as land evaluations and capability assessments. But they apply also to water bodies, and they are intended to take account of the dynamic quality of ecosystems and the linkages between them. The procedure for allocating land and water uses proposed in the 'World Conservation Strategy' is set to meet short and long-term demands for goods and services, all within the capacity of ecosystems to supply them (IUCN 1980a). Uses that depend on unique irreplaceable ecosystem characteristics are given priority over others for attention by conservationists.

Ideally, this procedure should enable governments to apply simultaneously ecological, social and economic criteria to the assessment of a project, and so to make holistically informed choices before financial and other resources become committed. It can direct attention to development options that are productive and sustainable; and it can provide a means of comparing the advantages and disadvantages of protecting a natural area with those of using it in some other way.

It would allow anticipation of problems and opportunities in a way that environmental assessments alone cannot. It is thus an instrument for policy formulation rather than simply a means of adjusting policies at the project level.

Good planning can help make habitat protection more secure in other ways. For example, it may anticipate the spontaneous settlement that generally occurs once a forest area in a developing country is opened up by large-scale logging. Invariably such settlement is destructive, but it need not be if governments plan in advance to help the settlers develop the land sustainably by providing firewood plantations or alternative fuels and by conserving watersheds, soils and important genetic resources.

Poor organization

One of the most serious problems confronting conservation is that it is ill-organized and fragmented, often split up amongst sectors such as agriculture, fisheries, forestry and wildlife. This may result in duplication of effort, gaps in coverage, competition for money and influence, and conflict. It is for this reason that the 'World Conservation Strategy' strongly recommends that every country review the mandates of all government agencies responsible for living resources, and prepare a cross-sectoral policy to integrate their work (IUCN 1980a). Mandates that emphasize production at the expense of maintenance mean that government agencies in charge of agriculture, forestry or fisheries do not pay enough attention to such aspects as maintaining natural processes, the protection of habitats and the conservation of genetic resources. These cannot be translated directly into bushels of grain, cubic metres of wood or tonnes of fish, but are the main factors upon which such production depends.

Lopsided mandates are also in part responsible for the lamentable lack of co-ordination among the various governing agencies responsible for living resources, as well as between them and non-governmental interests. The effect of this can be illustrated in the field of genetic resource-conservation. Lack of co-ordination exists between the bodies responsible for protected areas on the one hand, and the plant-breeders and crop geneticists on the other. This has probably been the main reason why the protection of a singularly important category of genetic resources, the wild relatives of cultivated plants, has been neglected. Although several international meetings (notably the 1972 UN Conference on the Human Environment) have urged the in situ conservation of the wild relatives of crops, very little appears to have been done. This may be due to plant breeders being more concerned with collection of propagules for ex situ protection in gene-banks and the like, while those involved in protecting areas aim to conserve ecosystems and species-diversity rather than genetic variants within species. This results not only in a lack of safeguards for the wild genetic resources of the plant-breeder, but also inadequate documentation and poor provision for the plants' evaluation and utilization.

Conservation of the wild relatives of the coffee plant reflects the difference between ecosystem conservationists (the main advocates of in situ protection) and plant breeders, who should be among those most able to make use of the protected germ-plasm. Coffea arabica, the most valuable of the coffees, grows wild and semi-wild as an understorey shrub or small tree in the montane forests of south-western Ethiopia. Because of the species' value and difficulties in its ex situ conservation, there are from time to time calls for making reserves for it (Mengesha 1975; IBPGR 1980). The tropical montane forests of East Africa are poorly represented in reserves: Lamprey (1975) describes them as seriously threatened and in need of immediate protection. Even natural areas within forest reserves are subject to exploitation for timber, and extensive encroachment by plantations of softwoods and cultivation. This last threat is the main one facing the forests of south-western Ethiopia (IBPGR 1980), no part of which is in any kind of protected area at all.

It is extremely important that a reserve be established as soon as possible for the protection of a viable portion of these forests. However, if the reserve were designed solely with the goals of conserving species and ecosystems, it might fail to conserve the important variability of Coffea arabica which is needed by the plant breeder for such aims as finding strains resistant to forms of leaf rust and berry disease. Conversely, there is no assurance that a design with the goal of conserving the plant as a genetic resource would at the same time meet the need for the security of ecosystems and other species. Management of the reserve should not be so strict as to prohibit the collection of seeds. In fact it would be desirable to cater for seed collection to some safe limit that would not damage the populations' regeneration, and to provide for evaluation and documentation of the results as a direct aid to the plant breeder. This could be done with co-operation with a body such as Ethiopia's Institute of Agricultural Research.

It seems perfectly possible for a protected area to fulfil several functions, provided there is sufficient forethought and co-ordination among the bodies concerned. The advantages are obvious: the costs of protection can be spread across a range of objectives such as protecting watersheds and critical habitats, research, recreation and tourism, and the conservation of genetic resources. Indeed, the different reasons for protecting an area can be mutually reinforcing, increasing the security of an area by adding to the incentives for protecting it and at the same time reducing the costs per benefit. These are vital considerations in the light of rising pressures on natural habitats and the frequent need to press for better budgets for their care.

Priorities and political positioning of conservation

There are two other aspects of organization that deserve attention. They are the capacity of conservationists to agree on priorities and then to stick them; and the 'positioning' of conservation with respect to other issues that preoccupy politicians and their public who put them in office. Both matters tend to be overlooked in spite of their importance to conservation managers, scientists and activists, whether they be in government, academia or non-governmental organizations.

The 'World Conservation Strategy' represents a first, largely successful attempt at agreement on international conservation priorities with respect to both problem areas and to actions required. How far the priorities will be followed remains to be seen, but there are hopeful signs as noted in the conclusion to this chapter. Perhaps this is not surprising, since the priorities are broad, particularly among the widely acknowledged problem-areas of losses of 'tropical forests, desertification, threatened species, areas needing protection, the open ocean and its resources, the atmosphere and climate, Antarctica and the Southern Ocean, international river basins, and international seas'. The list is unexceptionable. It is also far too much for conservationists, in their present strength, to handle unless they go on to choose priorities within each problem-area. The 'World Conservation Strategy' recommends this and also gives some guidance on how to determine priorities (IUCN 1980a). For example, it is suggested that conservation priority be given to areas where several threatened species occur together, to increase the benefit from unit effort and to lessen the chance of multiple species-loss if the area were neglected. Tables 3 and 4

Table 3. Countries with 20 or more vertebrate species known to be threatened (Source: IUCN 1977, 1978a, 1979a, 1979b)

USA[1]	152	Burma	31
Brazil	77	South Africa	30
Mexico	49	Vietnam	30
China[2]	47	Cameroon	28
India	47	Ecuador	28
Indonesia	47	USSR	27
Colombia	46	Kampuchea	26
Madagascar	44	Bolivia	25
Australia	41	Lao	25
Thailand	38	Paraguay	22
Malaysia	36	Venezuela	21
Argentina	35	New Zealand	20
Peru	33		

[1] 'USA' does not include Puerto Rico. [2] 'China' includes Taiwan.

Table 4. Countries with 10 or more endemic[1] vertebrate species known to be threatened. (Source: IUCN 1977, 1978a, 1979a, 1979b)

USA[2]	125
Brazil	44
Madagascar	40
Australia	37
Mexico	22
New Zealand	19
Indonesia	17
South Africa	17
Colombia	16
Mauritius	15
Cameroon	13
China[3]	12
Seychelles	12

1. 'Endemic' is here defined as 'occurring in only one country'
2. 'USA' does not include Puerto Rico
3. 'China' includes Taiwan

show those countries with most vertebrate species and endemics listed in the Red Data Book (IUCN 1977, 1978a, 1979a, 1979b). It would clearly make sense for a sub-strategy for threatened vertebrates to focus on these countries. Fully 73% of the 530 endemic vertebrate species known to be threatened occur in the thirteen countries listed in Table 4.

Giving attention to conservation's political 'positioning' in relation to other issues is a vital key to attracting and retaining the attention of the prime movers in society, notably opinion-leaders in the governmental and private sectors. It is abundantly evident that the message of conservation is too often ignored. It is surely high time that conservationists should ask themselves why this should be so in the light of the import of the message and the obviousness of the remedial action required. The message is that the productive and regenerative capacities of the Earth have already been reduced virtually permanently and will continue to be lowered unless remedial action is taken now.

One reason why the message is not getting through is no doubt the greed or obtuseness (or both) of many developers and politicians. Developers seldom like to hear about constraints on development, especially if it refers to their own projects; and politicians are irritated by scientific advice and tend to ignore it, especially when it shows that the biosphere is more complex, fragile and mysterious than they would have it be. However, conservationists and bureaucrats are also at fault by being too absolutist. They have fixed their eyes on True Ecological North with no deviation from the conservation dogma of the day. In nature, however, there are few absolutes. There is extinction, of course; and there are ecological thresholds. Yet some extinctions convulse the universe less than others; and whether crossing an ecological threshold matters a lot, a little, or not at all depends partly on the consequences of doing so and partly on the political, economic and social outcome of avoiding such transgression.

Conservationists have been inclined to overlook the trade-offs involved in decisions. In fact, conservation has much to offer by being brought in at this modest level, as an ingredient of cost and benefit studies. A policy incorporating conservation can help ensure a regular, adequate supply of goods and services of reasonable quality for whatever numbers of humanity and other species the biosphere can sustain. This version of conservation's message is a good deal less melodramatic than threats of a second flood, mass starvation or some other dreadful calamity, but it is more realistic, more telling and really more important.

Conservationists must not overlook the needs of people. As human numbers, needs, aspirations and interdependance increase, and as a growing amount of unpleasant ecological, social and economic thresholds are encountered, so competition among different uses of land and water will become more acute, the options fewer and the decisions more agonizing. Many decisions will be taken out of the hands of the 'decision-makers' altogether, as they have already in areas of acute rural poverty or in the proliferating shanty-towns of the tropics. In such circumstances, conservationists should avoid pressing for actions that might be dismissed as extreme and insensitive to human needs. When they take a stand on an issue, they would do well to remember that conservation is intended for benefitting people. The whole point of saving habitats or ecosystems rich in species is because, in the end, directly or indirectly, they will benefit people. If the costs clearly outweigh the benefits (both broadly interpreted) of preserving an area, then how conservationist is it to insist on preservation?

This brings us to a most important feature of the 'World Conservation Strategy': the ethical part of its definition of conservation (IUCN 1980a). The purpose of conservation is given as 'to yield the greatest sustainable benefit to present generations while maintaining the potential to meet the needs and aspirations of future generations'. The aim is not to maximize benefits only for today's people or species, still less for any particular community, group or nation. Instead, the strategy is largely a response to the belief that 'we have not inherited the Earth from our parents, we have borrowed it from our children'. The aim is to return the planet to our children in at least as fruitful a state as when it came into our hands.

This ethical factor raises problems. How does one balance the known needs of today against the unknown of tomorrow? To what extent should a community make sacrifices for their children's future offspring or humanity at large? In other words, the phrase 'conservation is for people' begs the questions: who, when and how? These questions are pertinent for habitat conservation, since it often involves loss or deferral of benefits for a particular group in the supposed interests of the public at large. In practice, benefits and even recipients may differ from those intended.

To illustrate this, one of the more telling arguments for conserving tropical rain forests is that they are storehouses of organic compounds of great potential value to humanity. So they are; but which parts of humanity will benefit from the altruism and restraint that will have to be shown in developing countries by country peasants, in not turning those storehouses into palm oil, chocolate or hamburgers? The omens invite cynicism. A sweet protein, thaumatin, has been isolated from berries of a wild plant, Thaumatococcus danielli, a native of the West African tropical rain forest. When purified, thaumatin is 11 000 times sweeter than sucrose (Adansi and Holloway 1979). The sugar company Tate and Lyle has already started to cultivate the plant; but it is also seeking to transfer the genes for thaumatin synthesis from the plant to a bacterium, which could then be grown industrially so that production could be freed from the uncertainties of supply by a developing country (Anon 1980).

One way of dealing with this would be for countries to charge royalties on the sales of products derived from the germ-plasm they have conserved. Among other ways of doing this, countries could refuse to grant rights of exploration and collection without an agreement to pay. Conservationists should concern themselves very much with such issues: not to do so invites suspicion that their claims that habitat protection is good for the nation, particularly if it is a developing one, are at best disingenious and at worst devious propaganda. The position of conservation should be not to oppose development, nor to equivocate about it, but actively to espouse it. Ways should be actively sought to combine conservation and development so that both can be made sustainable into the distant future.

Lack of support for conservation

For all the lip service that is paid to conservation, there is still far too little understanding of it, or support for it. This applies with special force to the conservation of habitats, especially those that are important for their genetic diversity. It is easy to grasp a need to conserve watersheds, control pollution and stop erosion; also there is popular support, certainly in developed countries, for conserving certain species that are appealing for their beauty, charm, power or oddity. But on the whole, the contribution of natural habitats to human welfare is scarcely grasped, and hence the significance of their conservation is not appreciated.

Circumstantial evidence for this lack of awareness is widely seen. A trivial example is a recent questionnaire, prepared for the USA magazine Natural History, which was intended to reveal current attitudes to the environment. To the question 'which of the following do you consider to be our most critical environmental problem?', six possible answers were provided (Gerlach et al 1980).

1. Water pollution
2. Air pollution
3. Nuclear and other hazardous waste build-up and storage
4. Increased societal costs of pollution control
5. Inadequate or unenforced regulatory legislation, and
6. Loss of land to highways, development, urbanization, etc.

There was no mention of destruction of habitats, extinction of species, or loss of genetic diversity.

More reliable evidence comes from a 1978 survey of public attitudes to wildlife in the United States of America. This reveals that Americans would overwhelmingly support protecting such animals as the bald eagle, eastern mountain lion, American crocodile, or silverspot butterfly, if they were endangered by an energy development project. But they would oppose protecting a spider, a fish such as the snail darter or a plant such as Furbish's lousewort, if it would increase the cost of an energy project, or block a water scheme for such essential purposes as hydroelectric power generation, irrigation or domestic water supplies (Kellert 1979). The survey showed an encouraging willingness by a majority of Americans to pay more for timber, energy or water, and to some extent to forego certain economic benefits for the sake of those species that rank high in terms of the following eight criteria (Kellert 1979):

1. Aesthetics;
2. Similarity or apparent relatedness to humans;
3. Reason for endangerment (the American public is much more likely to leap to a creature's defence if it is being over-exploited rather than if its habitat is being destroyed);
4. Direct economic value of the species;
5. Number and types of people affected by efforts to conserve the species;
6. Knowledge of the species and familiarity with it;
7. Cultural and historical relationships; and
8 Perceived humaneness of the activity threatening the species.

This is surely encouraging, however, to those conservationists whose interests are limited to the small minority of species to which these criteria apply.

Great progress has been made in making the public aware of conservation. This has been supported by many eloquent statements of the economic, scientific, cultural, and aesthetic worth of ecological and genetic diversity. Further buttressing has come from the publicity given to efforts to 'save' spectacular species such as tigers, elephants, rhinos, apes, whales and seals. But it seems this last progress has been won at a price. It has probably contributed to an identification in the public mind of conservation with preservation keeping things as they are, or as they were a little while ago; and it has done little to dispel, and may have confirmed, the widespread impression that conservation is a marginal pursuit. Very few people, one suspects, would include lack of conservation in an off-the-cuff list of big issues, along with poverty, injustice, inflation, disease, crime or the threat of war. Most would regard the slogan 'conservation is for people' as just one of those things conservationists say to push their case.

Conservation scientists and managers have the responsibility of promoting the wider concerns of their work. They must demonstrate that conservation is in the mainstream of human concern and a vital component of efforts to satisfy human needs, to reduce poverty, sustain economies and secure food supplies. Success in persuading people of the major importance of conservation will only come from a thorough approach tailored to the interests and experience of each audience. General statements supported by global illustrations may give the broad picture, but the citizens of Chattanooga, USA would have difficulty relating their interests to examples drawn from Chittagong, Bangladesh, and vice versa.

One goal is the building up of adequate capacities for conservation at global, national and local levels. Another is the integration of development with conservation. The degree to which both are achieved will depend heavily upon success in convincing all peoples of the Earth that conservation is indispensable for their well-being and, indeed, survival.

Lack of development

Lack of development may seem a surprising obstacle to conservation: it has for so long been seen as conservation's biggest bugbear. However, in many countries (mostly developing) plants, animals and their habitats are being destroyed, not due to bad planning, greed or evèn ignorance, but because the people involved have no choice. Compelled by abject poverty, lack of will or means to control population growth, and inequitable land distribution, they find themselves undermining their means of survival ever further by over-cultivating, over-grazing, over-hunting, and over-cutting for fuel.

The only cure for this disastrous vortex is development. Often the measures needed are quite modest, such as providing the products of technology directly designed to meet the user's greatest needs (for example, fuel-efficient stoves); giving incentives and training to convert from shifting agriculture to settled farming; offering a direct stake in revenues from tourism, and so on. Unless such measures are taken, traditional conservation actions (such as the establishment of protected areas and prevention of poaching) would almost inevitably fail or at worst, backfire.

If protected areas restrict the traditional access of impoverished people to their fuel, food, forage, building materials or the cash bonanza of ivory, skins or other products of dead wildlife, then the chances are that the areas will be encroached upon. To avoid this, and also as a matter of simple equity, the making of protected areas should be linked to simultaneous programmes of development: pasture improvement, fuel-wood plantations, and the provision of credit or alternative food, fuel or fibre, should be undertaken. If the programme takes time to give results, it should be supplemented by measures bringing immediate benefits. For example, if a reserve is threatened by wood-cutting for fuel, it would be necessary not only to start a fuel-wood plantation, but also to provide an alternative, temporary source of energy that can be used at once. It would also be prudent to provide the community with the means of conserving fuel supplies, such as more efficient cookers.

Protected areas can be made to bring real benefits to local communities. Through their undisturbed functions they can assure regular supplies of water from non-eroded marshes, streams and water-tables. They may also provide habitats for wild animals that could be hunted in a sustainable way when surplus stock is allowed to leave the reserve: examples are the Royal Chitwan National Park in Nepal and the Amboseli National Park in Kenya.

Local communities should gain a share of the economic benefits from a protected area in their traditional territory, such as from the incomes from recreation and tourism. Indirect benefits may come to them if receipts by the national treasury are spent on such services as roads, water supplies and health clinics. However, co-operation with a protected-area project will flourish best if direct, local benefits come to the community in such matters as employment and commerce.

Ultimate obstacles to habitat conservation

Fundamental problems underlie the above penultimate obstacles to the conservation of habitats. These are the ultimate obstacles, and include the basic maladjustments between people and nature, and between peoples and peoples, and must be overcome if humanity is to avoid future existence as little more than relict communities of paupers.

Of these ultimate obstacles to conservation, the one most often quoted is the continuing increase in numbers of people. If adequate qualities of life are the aim, then it is clear that people must achieve a balance between their numbers and the carrying capacity of the biosphere. What the carrying capacity is and how to achieve that balance is still a matter for speculation and debate. Three major considerations for resolving this are as follows:

1. What variables indicate an acceptable optimum (or maximum) population-size?

2. What incentives exist for achieving optimal human numbers?

3. What reforms are needed for achieving balance between communities with different kinds and intensities of land-use?

Firstly, an 'optimum' population for the human species is not simply the function of two variables, the number of people and the carrying capacity of the biosphere. An optimum population-size also depends on the local _per capita_ ecological demand. This is based on what resources each individual consumes, how they are consumed and where; the quantity of waste, and the means and place of its disposal; the extent of human adaptability, and the quality of life that people find adequate; and the amount of pressure on living resources that the biosphere can tolerate. Indeed, one may ask whether the biosphere will cope with the wrenching roller-coaster of extinctions and other abuses that humanity is to impose on it in the next few decades, and of course whether humans will tolerate the biosphere's responses.

Secondly, people must be given the incentive and the means to have small families. It is obvious that people must have ready access to contraceptives and (if necessary) abortion. However, much less obvious are the incentives for parents to have fewer children than are traditional in expanding populations. The over-simplified theory of the demographic transition holds that industrial development is most likely to provide the conditions in which people will limit their numbers (Teitelbaum 1975). There may be much truth in this: more generally, the satisfaction of basic needs and a degree of economic security are probably the most basic pre-conditions for adequate family planning. If this is so, then development made sustainable by inclusion of conservation principles is a pre-requisite for security and for fewer children. Conservation then contributes to removing excessive population-growth as an ultimate obstacle to its progress.

Thirdly, population-growth is not the only basic problem facing conservation. Quite as important are poverty, injustice, and inequalities among and within nations. Most of the acute problems of competition between humanity and other species stem from those existing between people. For example, peasant communities may be forced to cultivate steep, unstable slopes because their rising numbers have exceeded the capacities of the fertile, easily managed valley-bottoms, which in any case have been largely taken over by wealthy land-owners. In such cases land-reform will be just as necessary as halting population growth.

Many developing countries have so few natural resources and operate under such unfavourable conditions of international trade that they may have little choice but to favour options with short-term viability. They are driven to convert conserved areas to pasture and plantations and exploit forests, fisheries and other living resources in ways that cannot be sustained in the long-term. Remedies for this would include the liberalization of trade (especially the removal of trade-barriers to goods from developing countries); improved access to low-interest and interest-free international credit; and increased support for the establishment and expansion of local processing and manufacturing industries. These are some of the preconditions for sustainable conservation.

Reform is also needed in response to the oft-repeated but seldom heeded complaint that the affluent (especially all but the poorest people in developed countries) have a much greater impact on consumption from natural habitats. Boycotting hamburgers derived from former tropical forests is probably not a practical or very effective response. Instead what is needed is progress towards a more equitable economic order for the world, together with a much larger flow of investment to developing countries.

Developing countries should be assisted financially in meeting the demands of conservation placed upon them by international opinion and by fortunes of geographical location of plants and animals. Virtually all the countries particularly rich in genetic resources are developing ones that can ill-afford to bear alone the burdens of in situ conservation. The 'World Conservation Strategy' calls for an international system for compensating the countries that have to cope with especially demanding conservation problems (IUCN 1980a). A partial model for this is the World Heritage Fund. Run by the World Heritage Convention, the Fund helps ensure that areas of significance are not lost because of a local lack of money and skills, at the same time not diminishing the responsibility of each state to protect its unique natural areas.

A start in the right direction has been made for genetic resources of crop-plants. Assistance is provided for ex situ conservation by the International Board for Plant Genetic Resources. In situ conservation of all types of genetic resources is still under-supported and should draw aid from all bodies likely to benefit directly from it in the long-term, including governments and commercial enterprises. It has been urged that industries which depend on a particular species should sponsor the creation and maintenance of protected areas for them (IUCN 1980a). Any sponsorship from commerce should not confer special rights on the sponsor, but be seen as a rightful duty. Of course, it would be reasonable for sponsoring corporations to have rights to use the areas for research and to draw upon them for germ-plasm needed for breeding programmes.

Conservation is for people. It is also of and about people, inseparable from the social, economic and political contexts in which it is pursued. It is an article of faith among many conservationists that however powerful, ingenious, rich or just a society might be, it would fail in the end without conservation. The converse is also true. No society, however conservationist, could survive if it did not meet the economic, social and political needs of its peoples. One cannot be sanguine about the prospects of conservation in countries where there is a serious abridgement of human rights, a marked divergence of goals among the main social groupings, or where many people have little confidence that their ordinary needs and aspirations can be met through the currently imposed order.

This apprehension applies strongly to the conservation of habitats, which relies for its social and political support on the prospect of meeting long-term rather than immediate needs. Support for conservation must depend on a measure of unselfishness and a willingness for long-standing co-operation among communities and nations. Where these qualities are absent, through ignorance or desperation, or because the community feels deprived of resources by others, the future of habitat conservation is surely bleak.

This issue is crucial and faces almost every country: Canada and USA with the Indians and Inuit; the USSR with its many native peoples and other minorities; and the developing countries of Latin America, Black Africa, the Arab World, and South and East Asia. Many of the countries in these regions seem to be insensitive to the needs of their minorities, particularly if they do not appear to fit in with new orders and national images, such as nomads, hunter-gatherers and hunter-gardeners.

South Africa, in particular, provides an illustration of this most potent obstacle to habitat conservation. The concept of the Black Homelands, as it seems presently to be applied, is most unlikely to provide a solution. At the very least it should be based on an equitable distribution of land. Already the crowding of a large and rapidly growing portion of the population into a relatively meagre proportion of the land area is causing severe conservation problems. The Wildlife Society of Southern Africa (1980) states that the main cause of an 'insidious erosion of the country's natural resources' is the 'lack of an appreciation of conservation principles by most of the country's 77 000 white farmers who control 71% of the nation's land, while over-grazing in Black National States, where some 33% of the country's 25 million people occupy 12% of the land area, has drastically reduced the productivity of many areas'.

CONCLUSION: PROSPECT AND CHALLENGE

The human species is going through a crisis, the duration of which is uncertain, the outcome unpredictable, but the symptoms clear: the elimination of species and rape of natural habitats; insane rates of military expenditure and arms production; spreading violence and totalitarianism. People are out of sorts with nature, but still more are they out of sorts with each other. Even an optimist will wonder what ingenious perversity could continue to wring starvation and penury from so bountiful a planet, and what spiritual and cultural anaerobiosis induces so many people to oppress and terrorize their fellows. A pessimist will have no difficulty in predicting a fate for humanity worse than death, far more punitive than the cosmic dismissal of extinction: an existence for the bulk of the species of the sort that Thomas Hobbes falsely attributed to the Pre-Columbian Amerindian, 'solitary, poor, nasty, brutish and short'. This is not an improbable prospect. There is ample evidence that humans will survive and reproduce in abject misery. We are survivors but we have not yet learned to live well.

Under the circumstances, with so many daunting obstacles to overcome, what expectations can we have for habitat conservation? The actions and commitments to act that have flowed from the 'World Conservation Strategy' (IUCN 1980a) provide some encouragement. Shortly after publication, governments of the following eight countries began work on their own conservation strategies (a key recommendation) or expressed the intention to do so: Egypt, India, Malaysia, New Zealand, Oman, Spain, USSR and Zambia. In five other countries (Australia, Italy, Kenya, Senegal and Tanzania), governments are considering the preparation of national or sub-national strategies. In South Africa, a national conservation policy and strategy has been prepared by a non-governmental organization, the Wildlife Society of Southern Africa (1980). Non-governmental organizations have called for national conservation strategies in Brazil, Canada, and Japan. For the first time, conservation chapters have been included in the latest economic development policies or plans of India, Senegal and Thailand. India has also decided to establish a Forest Survey of India, and is considering setting up an Environment Ministry so that the work of the several bodies with statutory responsibilities for living resources can be both more conservation-oriented and better co-ordinated.

These are small but significant indications of progress. The IUCN with the help of its sponsors and collaborators on the 'World Conservation Strategy', UNEP, WWF, FAO and UNESCO, is making great efforts to promote the document's full adoption and implementation (IUCN 1980a). It is also considering ways of evaluating the results so that in due course the usefulness of the document can be assessed with respect to the number and type of actions taken in response to it by governments and non-governmental organizations, and whether those actions led to any significant and sustainable improvement for species and ecosystems. Progress is bound to be laborious, but there is a reasonable chance that many countries will take the strategic actions required to overcome at least some of the penultimate obstacles to conservation, and that they will do so during the 1980's.

Do we have that much time? If the conservation pundits cited by Soulé (1980) are to be believed, apparently not. For there is so much inertia in all the major political and administrative systems, that time-lags between the strategic actions and results make it most unlikely that we will have created a 'highly buffered conservation system' on the planet within twenty to thirty years. These deadlines may in fact be rather artificial, owing much to the imminence of the year 2000 (pundits who said 30 years in the early 1970's say 20 years now). Yet we can be sure that substantial units of the biosphere will have been obliterated and many species made extinct well before the end of the 20th century, and also that, barring some unforeseen catastrophe, we will enter the 21st with nature still functioning and able, if unwilling, to support us. For many species and ecosystems it is already too late for practical rescue attempts to be made. For others, immediate action is necessary. For still others there is little time to spare. The question stands: on which species and ecosystems within the latter two groups should we concentrate our efforts?

In their introduction to what has quickly and deservedly become the bible of species and ecosystem conservation, the book entitled Conservation biology, Soulé and Wilcox (1980) urge biologists to involve themselves in conservation, both in their research and by exerting their influence as scientists and citizens. The need for conservation biologists is very great; but in particular there is an acute urgency for such people to turn their attention to the problems of our own species and to be joined in this research by conservation-minded economists, sociologists and political scientists. What are the most vital food-webs which have co-evolved with humanity and how can we ensure that their processes continue? What are the mobile links, keystone mutualists and species-mosaics that we humans simply cannot do without? What new adaptations should we educate ourselves to attempt? What models do we have already among the enormous diversity of human cultures? The future of the human species and a great many others lies in the answers to such questions and how we respond to them. For with those answers we should be able to devise a new accommodation with the biosphere.

The conservation of extensive wilderness is no longer an option except where there is both space and affluence. To continue to strive for it elsewhere is to invite such incomprehension and hostility as to deny any possibility of maintaining a lesser but still precious diversity. Instead, we still have a chance of forging new and different alliances between people and the rest of nature. That is the prospect. To realize it we must reconcile production and maintenance, subsistence and co-existence, living on and living with our fellow creatures on this singular planet. That is the challenge.

SUMMARY

Conservation and habitat are defined. The main types of habitat of concern for conservation are noted in relation to three objectives: the maintenance of essential ecological processes and life support systems, the preservation of genetic diversity, and the sustainable utilization of species and ecosystems. Priorities for conservation are proposed among the habitat-groups which correspond to these objectives.

Habitat destruction is the main threat to many plant and animal species, particularly in fresh waters, tropical forests, islands, mountains and the coastal zone. The global status of tropical forests is well enough known, but there is a serious lack of information on the relative importance and endangerment of the other priority habitat-groups. The many and diverse human activities which destroy habitats must be modified to minimize their harmfulness, but the needs they are intended to satisfy must continue to be met.

Distinctions are drawn between proximate, penultimate and ultimate obstacles to habitat conservation and, respectively the tactical, strategic and basic actions needed to overcome them. The penultimate obstacles are: lack of integration between conservation and human development, poor organization, lack of support for the requests of conservationists and tardy development-rates for humanity. Strategic actions to deal with each penultimate obstacle are proposed. The ultimate obstacles are human population growth and inequities, both among and within nations. Basic actions on these are recommended.

In conclusion, it is noted that the human species is going through a crisis, of which habitat-destruction is one of a number of symptoms. There are grounds for hope in the steps being taken to implement the World Conservation Strategy. An urgent need now is for a clearer understanding of the conservation biology of the human species, so as to guide people in devising a better accommodation with the rest of nature.

Appendix I. Distribution by biome or major ecosystem group of vertebrate species threatened by habitat destruction or degradation

Biomes and major ecosystem groups	FISH	AMPHI-BIANS	REP-TILES	BIRDS	MAM-MALS	TOTAL
Land						
1 Tropical humid forests		1(1)[1]	1	40	50(1)	92
2 Subtropical and temperate rain forests		1		11	2	14
3 Temperate needleleaf forests						-
4 Tropical dry or deciduous forests		2	4	12	13(3)	31
5 Temperate broadleaf forests		1		1		2
6 Evergreen sclerophyllous forests		3	4	4(1)	5	16
7 Warm deserts and semideserts			2	7	7	16
8 Cold-winter deserts and semideserts					2	2
9 Tundra and barren arctic desert						-
10 Tropical grasslands						-
11 Temperate grasslands		1			4	5
12 Mountain systems		1	2	13	12	28
13 Islands		3	14	47(1)	12	76
14 Multi/varied (more than one of 1-14)			2	20(5)	36(2)	58
Fresh waters						
15 Lentic	17(1)	3	1	2		23
16 Lotic	81(4)	6(1)	1	4(1)	2	94
17 Wetlands	8	2	2	16(6)	6(5)	34
18 Multi/varied (more than one of 15-17)	20(2)	3(2)	5(2)	8(5)	4(3)	40
Land						
19 Caves	4(4)	2(2)			2	8
Sea						
20 Intertidal and neritic	4(3)		5(2)	9(7)	7(2)	25
21 Pelagic and deep benthic						-
22 Multiple/varied (both 20 and 21)						-
Total	134	29	43	194	164	564
Less half the number of species in two groups	(14)7	(6)3	(4)2	(26)13	(16)8	33
TOTALS OF SPECIES THREATENED	127	26	41	181	156	531

[1]Figures in parentheses give the number of species also assigned to another group.

Source: Analysis of IUCN's Red Data Book by Allen and Prescott-Allen (1978) updated for this paper.

Note: Biomes are defined by Udvardy (1975), adjusted for Indomalayan and Oceanian realms (see source for details). With only a few exceptions, species with habitats within an azonal ecosystem (fresh waters or caves) have been assigned to one of the azonal ecosystem groups and <u>not</u> to one of the land biomes.

Appendix II. The Executive Summary of the World Conservation Strategy (IUCN 1980a).

The World Conservation Strategy is intended to stimulate a more focused approach to the management of living resources and to provide policy guidance on how this can be carried out by three main groups:

- Government policy makers and their advisers;
- Conservationists and others directly concerned with living resources; and
- Development practitioners, including development agencies, industry and commerce, and trade unions.

1. The aim of the World Conservation Strategy is to achieve the three main objectives of living resource conservation:

   a) To maintain essential ecological processes and life support systems (such as soil regeneration and protection, the recycling of nutrients, and the cleansing of waters), on which human survival and development depend;

   b) To preserve genetic diversity (the range of genetic material found in the world's organisms), on which depend the functioning of many of the above processes and life-support systems, the breeding programmes necessary for the protection and improvement of cultivated plants, domesticated animals and microorganisms, as well as much scientific and medical advance, technical innovation and the security of the many industries that use living resources; and

   c) To ensure the sustainable utilization of species and ecosystems (notably fish and other wildlife, of forests and grazing lands), which support millions of rural communities as well as major industries.

2. These objectives must be achieved as a matter of urgency because:

   a) The planet's capacity to support people is being irreversibly reduced in both developing and developed countries:

      - Thousands of millions of tonnes of soil are lost every year as a result of deforestation and poor land management;
      - At least 3000 km^2 of prime farmland disappear every year under buildings and roads in developed countries alone;

   b) Hundreds of millions of rural people in developing countries, including 500 million malnourished and 800 million destitute, are compelled to destroy the resources necessary to free them from starvation and poverty:

      - In widening swaths around their villages the rural poor strip the land of trees and shrubs for fuel so that now many communities do not have enough wood to cook food or keep warm;

- The rural poor are also obliged to burn every year 400 million tonnes of dung and crop residues badly needed to regenerate soils;

c) The energy, financial and other costs of providing goods and services are growing:

- Throughout the world, but especially in developing countries, siltation cuts the lifetimes of reservoirs supplying water and hydroelectricity, often by as much as half;

- Floods devastate settlements and crops (in India the annual cost of floods ranges from $140 million to $750 million); and

d) The resource base of major industries is shrinking:

- Tropical forests are contracting so rapidly that by the end of this century the remaining area of unlogged productive forest will have been halved:

- The coastal support systems of many fisheries are being destroyed or polluted (in the USA the annual cost of the resulting losses is estimated at $86 million).

3. The main obstacles to achieving conservation are:

a) The belief that living resource conservation is a limited sector, rather than a process that cuts across and must be considered by all sectors;

b) The consequent failure to integrate conservation with development;

c) A development process that is often inflexible and needlessly destructive, due to inadequacies in environmental planning, a lack of rational use allocation and undue emphasis on narrow short term interests rather than broader longer term ones;

d) The lack of a capacity to conserve, due to inadequate legislation and lack of enforcement: poor organization (notably government agencies with insufficient mandates and a lack of coordination); lack of trained personnel; and a lack of basic information on priorities, on the productive and regenerative capacities of living resources, and on the trade-offs between one management option and another;

e) The lack of support for conservation, due to a lack of awareness (other than at the most superficial level) of the benefits of conservation and of the responsibility to conserve among those who use or have an impact on living resources, including in many cases governments; and

f) The failure to deliver conservation-based development where it is most needed, notably the rural areas of developing countries.

4. The World Conservation Strategy therefore:

a) Defines living resource conservation and explains its objectives, its contribution to human survival and development and the main impediments to its achievement;

b) Determines the priority requirements for achieving each of the objectives;

c) Proposes national and subnational strategies to meet the priority requirements, describing a framework and principles for those strategies;

d) Recommends anticipatory environmental policies, a cross-sectoral conservation policy and a broader system of national accounting in order to integrate conservation with development at the policy making level;

e) Proposes an integrated method of evaluating land and water resources, supplemented by environmental assessments, as a means of improving environmental planning; and outlines a procedure for the rational allocation of land and water uses;

f) Recommends reviews of legislation concerning living resources; suggests general principles for organization within government; and in particular proposes ways of improving the organizational capacities for soil conservation and for the conservation of marine living resources;

g) Suggests ways of increasing the number of trained personnel; and proposes more management-oriented research and research-oriented management, so that the most urgently needed basic information is generated more quickly;

h) Recommends greater public participation in planning and decision making concerning living resource use; and proposes environmental education programmes and campaigns to build support for conservation; and

i) Suggests ways of helping rural communities to conserve their living resources, as the essential basis of the development they need.

5. In addition, the Strategy recommends international action to promote, support and (where necessary) coordinate national action, emphasizing in particular the need for:

a) Stronger more comprehensive international conservation law, and increased development assistance for living resource conservation;

b) International programmes to promote the action necessary to conserve tropical forests and drylands, to protect areas essential for the preservation of genetic resources, and to conserve the global commons - the open ocean, the atmosphere, and Antarctica; and

c) Regional strategies to advance the conservation of shared living resources particularly with respect to international river basins and seas.

6. The World Conservation Strategy ends by summarizing the main requirements for sustainable development, indicating conservation priorities for the Third Development Decade.

CHAPTER 3 CONSERVATION IN THE REAL WORLD: REAL-CONSERVE OR CONSERVATION-AS-USUAL?

Michael E Soulé

INTRODUCTION

Most conservation pundits agree that we have something like 20 to 30 years to create a highly buffered conservation system on this planet. Habitats and biota uncaptured and unsecured by the end of the century are doomed, particularly in the tropics. This is precious little time. The situation calls for a ruthless approach to the evaluation of tactics and programmes which includes, in their planning and execution, a realistic cultural analysis. In short, conservation projects must be assessed in light of what we know of human nature and recent social-political trends. We need a 'human-nature litmus' for conservation. The objective of this paper is to examine certain aspects of long-term habitat and species management using such a litmus for reality testing. No attempt is made to review all or even most points of contact between conservation programmes and their social and scientific milieu. Rather, I have chosen some examples, that, in one way or another, influence the long-term survival and evolutionary potential of populations residing in nature reserves.

THE STAGE: REAL-CONSERVE VERSUS CONSERVATION-AS-USUAL

By self-appointment, if not by election, conservationists are the sergeants-at-arm in a packed assembly, an overpopulated world looking more and more like a mob about to riot in a frenzied scramble for the last available spaces. But whether we see our role as that of a policeman, prophet or an usher for this assembly, it is clear that conservation practices of the last few decades are, at best, insufficient, and, at worst, grossly ineffectual in dealing with the world as it is. This is especially so in our recent attempts to export the national park concept from high latitude, industrialized nations to tropical lesser developed countries (LDC's). For these reasons, I have coined the term 'Real-conserve' to suggest and dramatize the need for a radically different approach to conservation planning on an international scale.

Real-conserve is a philosophy of conservation based on an integration of conservative goals and social reality. It shares with Realpolitik a healthy respect for pragmatism and an admiration for decisive action.

Unlike Realpolitik, however, which is basically amoral and concerned with ends, not means, Real-conserve rests on the same scientific, economic and moral foundations as does 'normal' conservation or conservation-as-usual. Actually, the difference is one of degree only - the degree to which planning and implementation of programmes takes into account the impact of probable social, political and economic events.

This should not be understood as a denigration of the role of population biologists and managers. Their expertise is an absolute necessity for ultimate success. (Soulé and Wilcox 1980, chapter 1). Rather, the point is that the task of preservation is too important to be the sole preserve of scientists. Not only are most scientists ill-equipped to anticipate and deal with many of the social and economic problems that inevitably accompany any large conservation project, but the pace of science itself is too slow to catalogue, let alone solve the technical problems. For example, long before taxonomists have described and named most of the plants and invertebrates in tropical forests, these forests will have been pulled down and the species bulldozed to oblivion. Biologists alone cannot prevent this. The solution, if one exists, will have to be found by economists and moral philosophers, explained and communicated by educators, and financed by governments. Time is short and problems are manifold. It is with this feeling of urgency that the following remarks and recommendations are made.

Three scenarios

What, from the Real-conserve perspective, is going to be the fate of those vestiges of the Pleistocene floras and faunas now in the process of being fragmented and incarcerated in nature reserves? I suggest that the choice of futures can be summarized by three, obviously oversimplified, scenarios which I'll call Dystopia, Utopia and Maritopia. The objective in describing these is to spotlight the challenges that must be met.

Dystopia had arrived by 2020. While nuclear war had somehow been avoided, society had gradually become meaner and anarchic. The trends were already established and could have been extrapolated from the then existing patterns of international, economic and civil behaviour. These trends included:

1. Continuation of the costly arms race among the superpowers;

2. Increasing inflationary pressures and economic instability;

3. Decline in real income and living standards in industrialized countries due to increasing pollution and the cost of energy and raw materials;

4. No real increase in international aid;

5. No change in the frequency of civil and international warfare in the tropical countries. (In sub-sahara Africa, between 1945 and 1980, at least one-third of the nations had been totally involved in at least one war with a significant loss of wildlife in nature reserves. Among these were Angola, Mozambique, Rhodesia, the Central African Republic, Uganda, Somalia, Ethiopia, Burundi and Nigeria. On the average, each African nation had a war with significant impact on wildlife every 75 to 100 years);

6. Failure of the United Nations to effectively enforce peace and stability in the world;

7. Population growth close to the 'middle' UN projections resulting in a quadrupling of populations in the LDC's by 2015 and concomitant increase in deforestation, poaching, cultivation of marginal lands, soil erosion and migration to cities, the latter exacerbating the already stressed and under-capitalized development programmes and contributing to political instability;

8. The rapid disappearance of wildlife in the tropics, except for small 'weedy' species and some mountain and desert forms; and

9. The total destruction of nature reserves in most tropical nations as a consequence of wars, population pressures, and deepening economic problems.

A sample of the biotic changes that had occurred in the tropics between 1980 and 2020 includes:

1. Desertification of most low rainfall, grassland habitats in Asia, East and southern Africa;

2. The disappearance of tropical humid forest in West Africa, India, Southeast Asia, Central America and most of South America;

3. A rise in average temperature of 1,69 degrees Celsius and a concomitant rise in sea level of 3,3 metres, causing the drowning and abandonment of many coastal cities and most ports; and

4. The siltation of most dams and rivers causing extensive flooding, loss of agricultural land and the death of most continental shelf coral reefs.

It is estimated that two-thirds of the planet's five million species are now extinct in nature including all large tropical carnivores, ungulates and primates (except for those few remaining in the garrison preserves of Venezuela and South Africa), most tropical forest species of plants, birds, reptiles, amphibians and invertebrates, most coral reef and estuarine animals, and most savanna species.

The World Famine of 2014-17 has left 2,5 billion dead, four billion starving and has caused the total collapse of most public services in Asia, Africa and Central America. All national parks and reserves were plundered, and have virtually ceased to exist, except in Europe, China and North America.

Utopia was achieved by 2020. One of its outstanding accomplishments was the high priority given to the coordination and intensive scientific management of all nature reserves. This was considered necessary because of the recognition of the high rates of extinction in unmanaged nature reserves (Brown 1971; Diamond 1972; Terborgh 1974; Soulé et al 1979). The project required the education of cadres of highly trained botanists, zoologists, ecologists and geneticists. In addition, Biosphere Reserves and similar parks were provided with funds for security forces and for educational and political liaison teams whose task it was to maintain friendly relations with and facilitate 'eco-development' for the local peoples. Members of these teams were trained by anthropologists and sociologists familiar with the local cultures and languages. Working closely with community, agricultural and forestry development personnel, these teams also assisted the local villagers along the road to economic self-sufficiency.

The funds to support this project come largely from the northern industrialized countries which contributed ten percent of their GNP to conservation, as well as to economic and agricultural development in the lesser developed countries. This revolutionary change in foreign policy (or outburst of altruism) was facilitated by an end to the arms race and the implementation of the New International Economic Order (a fairer distribution of the world's resources), an element of the prescription enunciated by the World Conservation Strategy published in 1980: "Humanity's relationship with the biosphere ... will continue to deteriorate until a new international economic order is achieved, a new environmental ethic adopted, human populations stabilized, and sustainable modes of development become the rule rather than the exception".

This achievement was preceded by the permanent democratization of the African, Asian and Latin American nations and the ensuing political stability. This had been absent in the Twentieth Century when tribal, civil and international wars exacerbated the process of ecological destruction. The conditions for democratization were a rapid decline in the birth rate, universal literacy, the restoration of a healthy agrarian and public health infrastructure based on international aid and agreements that assured cheap energy and reasonable trade balances. Border conflicts and other international disputes have been resolved by the World Court.

Nature reserves succeeded in protecting over 80% of the world's species diversity. In large part, this was made possible by financial support from the World Conservation Fund. In the Twentieth Century the LDC's had lacked the funds to pay and equip management and security personnel.

For example, in 1980, the average annual budget for a thousand square kilometre nature reserve was about USA $20 000 in the LDC's - only one-tenth that of the industrialized nations (Soulé and Wilcox 1980, chapter 1). By 2020 the money available for such a reserve was more than eight times this (in 1980 USA dollars).

Parenthetically, there will probably be elements of Utopia and Dystopia occurring simultaneously for the next few decades. Two models of Utopia are now in vogue. On the one hand there are the heralds of a new higher consciousness proclaiming the Aquarian Age (eg Ferguson 1980) and the 'evolution' of widespread paranormal powers and God-like communion among newly enlightened people. On the other hand here are the technologists who foretell of a new industrial revolution based on highly miniaturized and inexpensive microprocessors (Dertouzos and Moscs 1979; Smith 1981). The computer/information society clearly exists in Japan and California. No doubt a minority of people, mostly in the northern temperate states, will realize Aquarian and siliconian nirvana.

In stark contrast others, such as Norman Myers (1979) and the Ehrlichs (1981) are warning of impending ecological disasters such as already described. It is our job as conservationists to awaken the more optimistic futurists of the temperate zones to the fact that this is one world and the ecological and social disasters of the tropics will, inevitably, send shock waves towards the poles.

Maritopia assumes the validity of the assumptions listed above for Dystopia, but is a slight variation on that scenario.

In 1989 a semi-secret group of wealthy industrialists met as the 'Club of Cadiz' to discuss a proposal to salvage the remnants of the world's tropical macroflora and fauna. They approved a scheme to acquire three groups of islands in the Molucca and Carribean Seas and in the Indian Ocean. Under the guidance of an expert cadre of biologists, anthropologists, geologists and horticulturists, much of the native flora of the islands was gradually replaced with plant associations from Malaysia, the Amazon Basin and Central and East Africa, respectively. The indigenous people were educated, acculturated and over two generations, assimilated into the 'pioneer' stock of scientists. The Maritopians produced and orbited their own satellites for communications and security.

As the forests and other habitats matured, captively bred and wild-caught animals were introduced. In one hundred years, the Maritopians had successfully established quasi-natural, but intensively managed ecosystems that closely resembled those that had once existed on the nearest continents, but which had been virtually destroyed between 1980 and 2050.

Plans to invade or infiltrate the Maritopian Federation were successfully neutralized by the technologically sophisticated Maritopians. Following the famines and pandemics of 2014-25 and 2039-43, the World Government succeeded in bringing economic and social order out of chaos. The human population began its controlled roll-back from its pre-famine peak of twelve billion to two billion and the third generation Maritopians began the task of restocking and restoring the biota of the continental tropics.

A major role for ex situ conservation?

Which of these scenarios is most probable? I frankly believe it is Dystopia. The optimal future, Utopia, requires fundamental changes in human nature which will be too slow in coming.

On the other hand, the fanciful Maritopian Federation, or something like it, requires selfless generosity on the part of many wealthy persons and long range planning and organization on a scale unknown in human history.

Why indulge in such fantasies in the first place? My reason is that much, if not most, of conservation planning today is based on equally unrealistic fantasies, on sanguine assumptions about what the future holds, and that we thereby do a disservice to our descendants. We owe future generations of all species a conservation strategy that makes sense in terms of economics and politics.

It is probable that only a small fraction of nature reserves in the tropics will survive intact the next 100 years. Conservationists should start preparing now for this contingency. The deterioration of these reserves will follow different paths. At one extreme, for example, many forest reserves in many LDCs will be totally devastated. Not only will all of the macrofauna and macroflora (trees) be eliminated, but ecosystem services will be forfeited. For regions formally covered by tropical humid forests, the predicted results are erosion, laterization, siltation of rivers, lowering of water tables, dry-season droughts, higher temperatures and pest out-breaks. (Gomez-Pompa et al 1972; Siolo 1975; Myers 1979). In less humid regions we will see the elimination of large animals and the gradual destruction of the habitat from wood-cutting, slash-and-burn agriculture and overgrazing.

In less extreme cases, reserves will survive as recognized geographic entities, but periodic collapse of civil authority and security will precipitate cataclysmic and episodic faunal extinctions brought about by uncontrolled slaughter of animals and other forms of incursion. We have several examples of this already in Africa, Asia, and the Middle East. Recent history provides no evidence for a trend toward increased political stability, nor is there an apparent trend towards the reliance on non-military means of conflict resolution.

This might not be so bad if species were like art treasures. Great works of art can survive without museums. They can be hidden away and protected even in the worst of times, to be dusted off and hung again when the conflagration has passed. Not so with species - as the habitat goes, so go most of its genetic treasures. For species the analogy to a secret attic or basement is captive propagation, but only a relative handful of species can be propagated because of the cost (Conway 1980; Frankel and Soulé 1981).

It is not too soon, therefore, to begin considering alternatives to *in situ* preservation of ecosystems. *In situ* preservation is certainly the *optimal* choice, biologically and *economically*. Nevertheless, the time may be fast approaching when *ex situ* preservation is the only realistic conservation strategy. Previous suggestions along this line (Wilson and Willis 1975) have not been taken seriously by most biologists. Now, I would hazard that the idea of establishing semi-natural ecosystems in highly secure sites will not be received as so far-fetched. In 20 or 30 years it may already be too late to begin planning such final redoubts for some mediterranean and tropical habitats.

In the meantime, *in situ* nature reserves must be made as secure as possible, both as staging grounds for *ex situ* preserves and because a few of them may survive the coming 150 years of exploding human populations. In the light of the preceding discussion, the following remarks and proposal seem singularly tame. Hopefully, braver and less myopic commentators can go further in suggesting approaches consistent with the true nature and dimension of the challenges.

The following section may provide a useful rubric for such action. It should be noted, however, that an implicit and very speculative assumption of this section is the continuing survival of the majority of tropical nature reserves.

A DECISION FLOW-CHART FOR THE GENETIC MANAGEMENT OF ANIMAL POPULATIONS IN NATURE RESERVES

The presentation of the accompanying flow-chart (see Figure 1) is not meant to imply that I believe that it can serve as a basis for decision making in all or perhaps even in most situations confronting the managers of a particular animal species. Rather, I view it as a kind of road map. If you have a good road map and you know approximately where you are, then you can anticipate decisions that will have to be made on your journey and the sequence of those decisions. But, just as a road map cannot predict every contingency on a journey, such as when and where there is likely to be flood necessitating a detour, so the flow-chart can only be a kind of cognitive blueprint on which to base a more detailed strategy. Thus, the purpose of this flow-chart is to help managers visualize where they stand with regard to possible choices and management options, and what may lie ahead. The assumptions that underlie this approach will become apparent in the following discussion.

A two-level process

This scheme is divided into two sections. The first requires decision making at the local level. The second requires decision making at the international level. Local decision making is meant to be synonomous with decision making within a single nature reserve; that is, the nature reserve is perceived as the unit of management. One might ask why a single conservation organization or state or national conservation agency is not the unit of management, and why it is that decision making must leap-frog from the nature reserve to an international body rather than first passing through an intermediate stage of semi-local or national jurisdiction?

There are three reasons. One is political, one is scientific, and one is moral. Politically, conflicts and disagreements between agencies, reserve managers, and conservationists can be as divisive and rancorous within a nation as they are between nations. In fact, regional within-nation jealousies and chauvinism are often especially charged because competition for funds and prestige are more important considerations within a bureaucracy than they are between nations. Even when disagreements are basically scientific in nature, the tools that are available for the resolution of such conflicts may not function optimally within a single political unit. The political advantages of an international body include the prestige associated with multi-national committees, the freedom from certain parochial political constraints and a certain emotional distance from the situation.

The scientific basis for going directly to the world community with regard to management of threatened species in nature reserves has to do with the arbitrary position of national boundaries. For example, a decision as to whether to transfer animals from one nature reserve to another will depend on many factors: the distance between the reserves, the similarity in environment and habitat distributions within the reserves, the genetic and phenotypic differences between the populations in the reserves and the ability of the staff in the country to successfully implement the operation. In many situations, the best animals for movement (if transfers are being considered) might come from a reserve in an adjacent country rather than a reserve in the same country. Similarly, the most skilled personnel

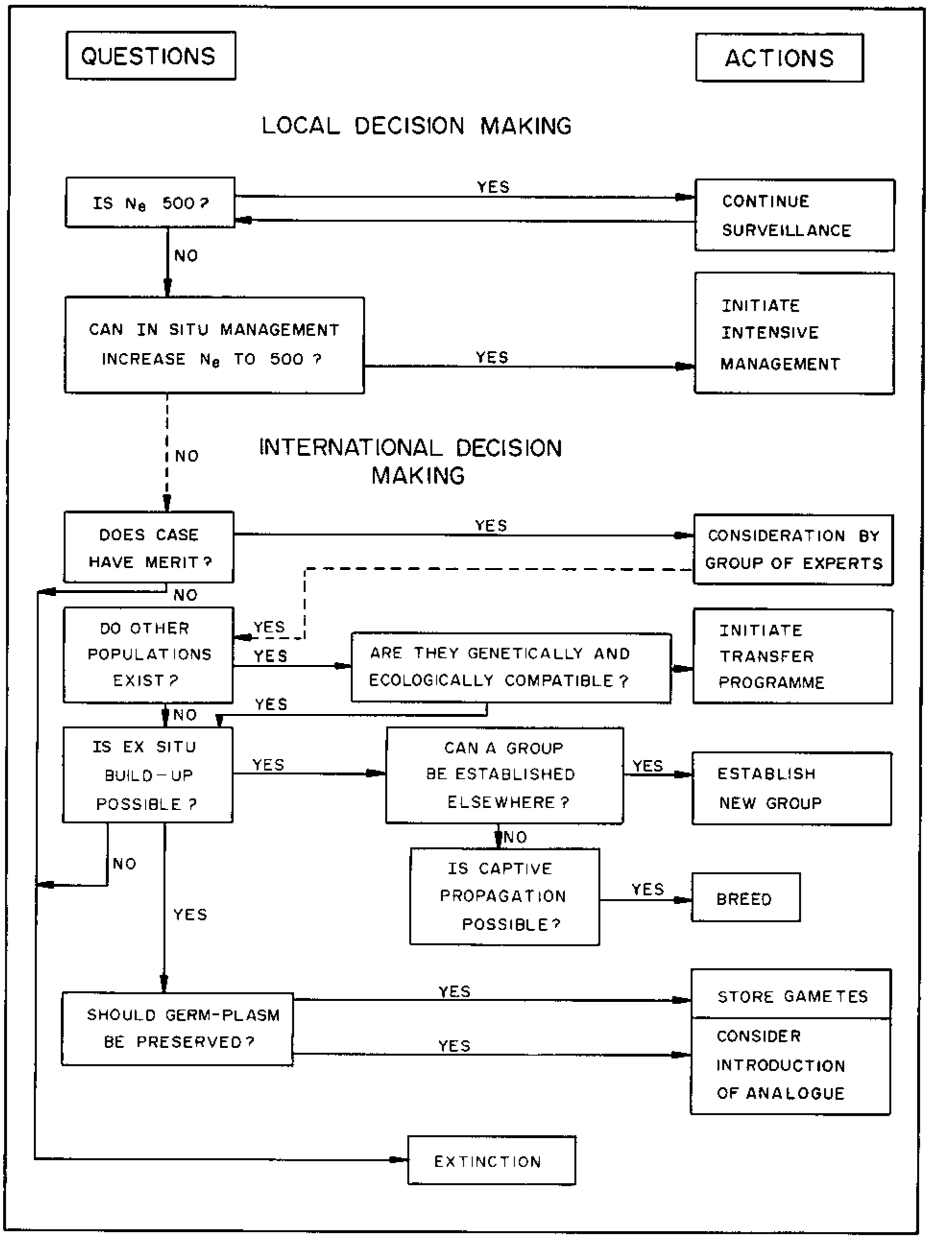


Figure 1. A decision flow-chart for management of numerically endangered populations in nature reserves. N_e is the effective number of breeding individuals in a population of a species.

or technicians may be found across an international border. Even before such a transfer is made, a whole battery of scientific questions may have to be answered, including the possibility that karyotypic differences exist between the stocks. The country in which this operation is to be carried out may or may not have the facilities and personnel to carry out such research.

There is another, moral argument: it is that no country has absolute jurisdiction over an endangered species. In other words, no nation or other governmental jurisdiction 'owns' an endangered species; the world's flora and fauna can no longer be thought of as 'property'. The cooperation of the United States, Jordan and Israel in the captive propagation and reintroduction of the Arabian Oryx exemplifies this tacit assumption.

Criteria for minimum population sizes

Beginning at the top of the chart, the first decision has to do with whether the population in question is numerically endangered. Much lip-service has been paid to the problem of minimum population sizes, but until recently, few concrete recommendations had been proferred. Elsewhere, (Soulé 1980; Frankel and Soulé 1981), I have discussed this subject in some detail, so I will only briefly summarize the subject here.

The establishment of minimum viable population sizes is one of the principal goals of preservation genetics. In arriving at such minimum sizes it is necessary to consider all aspects of the biology of the species involved, not just genetics. Other important criteria include the demography and life history of the species, and certain ecological variables, for example, the probability and severity of catastrophe.

Very little in general can be said about the latter subject because the nature and consequences of catastrophes are highly dependent on the life history of the species and particularly on the kind of environment in which it lives.

Given sufficient demographic information, it is sometimes possible to produce estimates of minimum viable population sizes for a species. But even when the demographic information is at hand, the genetic approach to the problem is relevant and could be the dominating consideration, assuming that the minimum sizes based on genetic criteria are larger than those based on demographic or ecological criteria.

The 'time scale of survival' is a useful device for structuring a discussion of preserving genetic variation. Somewhat arbitrarily, there are three problems or issues (Soulé, 1980):

1. A short-term issue of immediate fitness - the maintenance of vigour and fecundity during an interim holding operation, usually in an artificial environment, such as when breeding domesticated or semi-domesticated fish stocks. (If, however, breeding is expected to continue for more than N_e generations, where N_e is the effective number of breeding individuals in the group, the programme, in effect, becomes a long-term operation);

2. The long-term issue is adaptation - the persistence of vigour and evolutionary adaptability of a population in the face of a changing environment; and

3. The third issue is evolution in the broadest sense, ie speciation, or the creation of evolutionary novelty. For our purposes, the first and second issues are the most relevant and the third is the least relevant.

Long-term preservation requires rather large population sizes, large enough so that an equilibrium will be maintained between the loss of genetic variability due to drift and selection on the one hand and its generation from mutation on the other. When $2N_e$ is a large number, say greater than 500 or 1000, the effect of drift will be negligible compared to that of natural selection. When $2N_e$ is small, say less than 100, the randomization of gene frequencies between generations will not only fix many loci, it will also counteract all but the strongest deterministic forces, particularly directional selection, thus essentially precluding adaptation by natural selection.

Admittedly the consequences of small population sizes are irrelevant when considering the genetics of the majority of plants and animals. This is because the populations of most species are large. There will, however, always be some populations in a natural ecosystem, particularly large predators, which have quite small numbers. The loss of keystone predators from a natural community can have serious effects on the diversity of prey species, as has been documented by many workers, particularly with marine invertebrate systems.

Franklin (1980) argues that a minimum effective size of 500 is needed to preserve useful genetic variation, because:

1. The relevant phenotypic traits in conservation are quantitative (polygenic). For such traits the average effect of a gene is small, and most of the genetic variation is additive.

2. Weak directional or stabilizing selection does not erode additive genetic variation at a significant rate.

3. The significant evolutionary forces, therefore, are mutation and genetic drift. That is, if a population is below some threshold size, it loses variation by drift at a faster rate than it gains variation by mutation.

Franklin derives his number from the work of Lande (1976) on bristle number variation in Drosophila. The evidence is meagre but Franklin believes his number (500) is about the right order of magnitude. Simple theory also yields this number (Frankel and Soulé 1981, chapter 4).

It is necessary to caution again that the employment of any number is subject to many qualifications, namely that effective size translates into a much larger number of breeding adults when dealing with real, not ideal, populations. For example, when populations decline or 'crash', the survivors constitute a genetic 'bottleneck' in the history and evolution of the population. Any deviation in the genetic makeup of these survivors from the gene pool of the original population will be reflected in future generations. More particularly, if the progenitor's gene pool is less diverse than that which existed in the original population, future generations will have a corresponding deficit in genetic diversity.

If the minimum population size is very small, due either to normal fluctuations or to an environmental change or catastrophe, it is tantamount to squeezing the genetic variability of the source population through a very narrow channel and eliminating a significant amount of this variability. Bottlenecks inevitably accompany the establishment of a captive stock for breeding purposes.

Prevention of further genetic erosion, or recovery to the original level of genetic variation, depends greatly on how fast the population grows to a size of several hundred or more. If a preserved population is subject to fluctuations in numbers (as it most probably will be), the influence of the minimum absolute size on effective population size is more relevant to preservation of genetic diversity than is the average absolute size.

The loss of genetic variability concomitant with the bottleneck event has both qualitative and quantitative aspects. Qualitatively, specific alleles may be lost. Once this happens it is very unlikely that they will be replaced by mutation as long as the population remains small. Quantitatively, the variability for specific traits will be reduced; the mathematics of the loss of the variance of quantitative traits have been described by Falconer (1960) and others.

The qualitative effect is usually greater than the quantitative one; that is, the loss of alleles, especially low-frequency alleles, is much greater than is the loss of genetic variance per se. Incidentally, several workers have pointed out that the number of founders in a colony, so long as it is greater than about five individuals, is not nearly as important as the long-term maintenance size of the colony (Nei et al 1975; Denniston 1978). That is, a single bottleneck event followed by rapid growth to a large size, say $2N_e$ greater than 500, does relatively little damage, compared to a chronically small N_e.

Botanists and plant breeders were the first to worry about such matters, and they have been mainly concerned with the loss of qualitative variation, namely rare alleles that could adapt the species to extreme edaphic or climatic conditions and to disease organisms. Very large samples (on the order of thousands) are required if the target alleles are very rare (ca. one percent or less; see Marshall and Brown, 1975).

Instead of emphasizing rare alleles, zoologists have tended to worry about conserving quantitative variation (Franklin 1980). For this reason, the minimum population sizes recommended for animals have been lower (Franklin 1980; Soulé 1980) than those suggested for plant germ plasm collections. Zoologists should probably be more conservative in this regard. For example, from experience with resistance to pesticides in insects, we know that some resistance alleles occur at very low frequencies in natural populations. Such genes are likely to be lost during a bottleneck. Therefore, it would be expected that populations passing through bottlenecks might not be noticeably affected until a disease epidemic swept through the population, and by then it would be too late. (Frankel and Soulé 1981, chapter 3).

Several other factors determine N_e. Among these are the sex ratio; N_e is lowered by deviations from an equal sex ratio. Another of the characteristics of a genetically ideal population is that the number of progeny are randomly distributed among families. When this condition does not hold, for example, when the reproductive output of a few families is especially great, N_e will be lowered. It is incumbent on persons dealing with captive populations, for purposes of either preservation or culturing, to be aware of these effects and to maintain the N_e at a level that will maintain the fitness of their stocks. In some cases, it will be desirable to consult with a population geneticist, especially if the breeder is in doubt about the estimation of N_e.

Management at the local level

Using rather dramatic symbology we might say that if a population has less than 500 individuals it is in 'condition yellow', meaning that it is likely that the population is gradually losing its stored genetic variation. Such a population, over a long period of time, will lose its capacity to react appropriately to changing environmental conditions. To ignore such a population is to put it in jeopardy, and a population with so small an effective size should be considered a strong candidate for immediate genetic management. Whether or not management is implemented will depend on a large number of factors, including:

1. Historical evidence about the population, particularly whether it has always been small or whether it has been shrinking in historical times due to habitat encroachment, hunting, or for other reasons;

2. Whether it is one of many such relatively small populations and is worthy of costly conservation efforts;

3. Whether it is a marginal population; that is, whether it is likely to fail in the present environment even if heroic measures are taken for its rescue.

A second stage alert, perhaps we can call it 'condition red', exists when a population is at or below an effective size of approximately 50. At this population size, not only is the population continuously leaking genetic variability and being drained of its capacity for long-term survival and evolutionary adjustment to changing conditions, but according to some biologists, (Franklin 1980; Soulé 1980), it is continuously losing absolute fitness as well. That is, in every generation there will be a finite and significant loss of viability, fertility, fecundity, among other components of fitness. Recovery programmes should be initiated long before a population has sunk to this level of debilitation.

Regardless of whether a population is in the 'yellow' or 'red' stages, however, a decision must be made as to the potential feasibility of increasing the effective size so that the population is out of danger, both in terms of short-term and long-term survival and fitness. If it is concluded by the local managers that the reserve in question cannot possibly support at least 500 individuals, or that the reserve does not have the technical or economic capacity to successfully manage the species, even if the habitat space is available, then the matter should be immediately referred to an international body such as the IUCN, or more specifically, the Species

Survival Commission (SSC). Other international bodies should also be informed, such as the United Nations Environment Programme, and the World Wildlife Fund.

Management at the international level

The first question that should probably be addressed by the international body is whether the issue has sufficient merit to justify attention by the international conservation community. If it does, then a task group should be named to recommend detailed mitigating actions. The group should have representation from the nations directly involved, and should also include a population geneticist, and scientists familiar with the behaviour and ecology of the organism.

One of the first questions that must be studied by the task group is whether other stocks or populations exist and whether it would be desirable to interbreed them as a means of increasing N_e. Assuming that it is impossible to increase the effective size to a safe number by in situ management, (management in the original reserve), then transfer of individuals or germ plasm becomes an issue.

The transfer controversy

Should gene flow between the remnant populations of this species be initiated in order to increase the effective population size? This is perhaps the most technically complex issue confronting the group of experts. It involves such questions as: are the two or more populations in question genetically compatible; that is will descendents suffer from any chromosomal or other genetic disturbances as a result of the mixing of the gene pools? In part, this question can be answered a priori by karyotypic studies (eg Benirschke et al 1980). At another horizon, the question must be asked in ecological terms, that is, will hybrids between the two or more groups be well adapted to the environment in which they find themselves? This will depend on whether the environments in which the two groups naturally occur are significantly different, and whether the populations themselves have evolved local, ecotypic, evolutionary adaptations to these environments.

The issue of transfers tends to polarize biologists, eliciting dogmatic statements such as: mixing of sub-species or races should be avoided and only practised as the absolute final resort in any rescue operation; inbreeding is to be avoided at all costs. Those who espouse the former view can refer to a fairly large body of anecdotal information which suggests that hybrid populations, especially those derived from geographically remote gene pools, often suffer from genetic and ecological handicaps. Greig (1979), has documented this. Those who espouse the latter view, can refer to another large body of experimental data and results and anecdotal observations from zoos and breeders suggesting that inbreeding virtually always leads to a highly significant reduction in fitness and that any such reduction in fitness in inimical to the survival of a population. (Ralls et al 1979, 1980; Frankel and Soulé 1981, chapter 3).

While extreme positions in arguments such as these generate catchy slogans and usually facilitate the recruitment of small armies of patriotic followers, the biological stakes are too high for this form of emotional adversary science. It is necessary in each case and for each species to objectively examine the particular conditions and problems. Quantitative aspects of artificial gene flow between nature reserves are discussed elsewhere (see Frankel and Soulé 1981, chapter 5).

Each case of possible transfer will have its own unique characteristics, and this is one of the reasons why there needs to be a special group of experts to oversee the management of each taxon. (Obviously, there is a limit to the number of such expert groups that can be formed. Most such groups will have to oversee many taxa, calling upon consultants to advise on specific cases). It is abundantly clear that generalizations coming from an analysis of one species, one genus, or one family, will not apply or should not be applied without close scrutiny to any other species, genera or families.

This is also why each group of experts should contain representatives of all the relevant disciplines including someone conversant with the genetic issues, (outbreeding depression and inbreeding depression, chromosomal analysis and interpretation, multigeneration inheritance of Mendelian traits and quantitative genetics) as well as behaviourists and ecologists.

Ex situ build-up

We now reach the place in the diagram where the conservation options are few: successful in situ preservation in the original reserve has been ruled out because of insufficient habitat or other factors that mitigate against the achievement of threshold population size; transfers between reserves or between reserves and captive groups are ruled out for genetic and ecological reasons. At this junction, the only real option left is ex situ preservation.

The possibilities for ex situ preservation extend from more or less natural habitats where little or no management is necessary to totally artificial environments where the population is closely managed. A recent example of the former is the introduction of the snail darter (*Percina tanasi*) into the Holston River following the elimination of some of its native habitat due to the construction of the Tellico River Dam. The white rhinoceros and the whooping crane have been introduced into parts of their original ranges where they have been extirpated.

The state of the art and potential utility of captive propagation (CP) has been summarized recently (Soulé and Wilcox 1980; International Zoo Yearbook 1980). While the flow-chart does not indicate temporal overlap in conservation actions, it should be noted that the utility of captive groups is enhanced if they are initiated before there is only one vestigial population of a species left (Conway 1980).

Mercy extinction

Finally, the chart addresses a very uncomfortable problem. What do we do if the situation is hopeless. That is, what if the population cannot be increased to a safe number by in situ management, by gene flow or by ex situ build up? In other words, how do we confront the situation where all of our available tools are useless? Do we allow the group in question to senesce and go extinct gradually and naturally, or do we decide to take drastic action and remove the last remnants of this population and introduce an ecological analogue in its place? Like many of the former decisions, this one is difficult and requires not only an objective and scientific approach, but an intimate ecological knowledge of the particular reserve. For example, if the species in question happens to be an ecological dominant, an important mobile link or keystone plant (Gilbert 1980), the disappearance of which could cause significant ecological change in the habitat, then it might be desirable to eliminate it quickly and to introduce a similar form as soon as possible. Such action might minimize the resulting impact.

Whether or not such programmes are implemented, it is obviously desirable, when a population is so threatened, to store reproductive products so that it will be possible, at some future time, to generate organisms that are biologically similar to the extinct forms.

THE GENETIC EVOLUTIONARY CONSEQUENCES OF DESIGN AND MANAGEMENT TACTICS

In the preceeding Section, I discussed two of the major issues in genetic management, including (1) minimum population-size criteria, and (2) the pros and cons of artificial gene flow. In this section I take up one further issue (corridors) in detail and briefly mention three others - culling, habitat manipulation and general structural criteria for nature reserves.

Corridors

The phase of nature reserve establishment is rapidly coming to an end and will probably terminate almost completely by the turn of the century. Nevertheless, in some cases it is still possible to talk about design criteria for nature reserves and there is already a relatively large amount of literature on this subject.

One issue which deserves more attention is the issue of corridors between reserves. Diamond (1975) and others have pointed out that, where possible, the effects of isolation in nature reserves can be ameliorated by the physical provision of corridors between reserves. Such corridors allow for recolonization following local extinction and also permit gene flow which could maintain the fitness of endangered populations. (Brown and Kodric-Brown 1977).

Corridors in tropical nature reserves would not be as beneficial as they might be in temperate zone reserves (Frankel and Soulé 1981). The main reason for this is that corridors would normally follow natural topographic features, particularly rivers. Rivers are bordered by relatively unique and often successional habitats. The problem is that the species for which the corridors are intended are the least likely, in many cases, to use them. That is, the species of a primary or climax forest will simply not tolerate the unfamiliar ecological conditions of corridors. Their habitat preferences and intrinsic psychological barriers, (Ehrlich and Raven 1969; Diamond 1975; Terborgh 1975), will prevent them from moving into the secondary or successional habitats along the corridor.

My main point, however, is not that corridors will be only marginally beneficial or neutral in their effects, but rather that corridors could prove to be disastrous, particularly in the short run for populations of large generalists such as large carnivores and herbivores, and indirectly, on the reserve as a whole, should these populations become extinct. In most cases corridors will end up being 'fish traps', - one way passages to annihilation for the individuals who use them. The reason is that corridors, by definition, have a very high ratio of edge length to area. This being the case, animals passing through the corridors will be exposed to an unusually high risk of mortality from disease, and particularly, mortality from human hunters.

In most parts of the tropics the areas surrounding reserves and corridors will be settled and the corridors will pass through developed regions. Ultimately, these regions cannot be policed effectively. Furthermore, there will be a tendency for many species, including large mammals, to move into the corridors during their dispersal stages, and it is likely that in a reserve of a modest size, (less than 2000 km^2), many, if not most of the individuals of a particular species, will, by chance, at one time or another, enter a corridor and have to face an obstacle course of guns, snares, traps and other weapons along its route, not to mention diseases from direct and indirect contact with domestic animals.

Another danger is inherent in the use of corridors. The establishment of corridors between nature reserves will permit those who are opposed to large reserves to point out that the corridors themselves mitigate many of the negative effects of small size. The argument is that a system of several small reserves linked together by corridors is as good as one large reserve. It is sounder, biologically, in my opinion, to argue from the beginning that corridors should only be considered as temporary expedients during the early stages of the life of a reserve system, and that in all probability, the corridors will have to be closed at some point, because of human activity and settlement. Thus, corridors cannot be used to justify the establishment of smaller nature reserves.

When, if ever, should corridors be considerd to be an essential design component of nature reserve systems? There are several criteria that must be met. First and foremost, the per capita income in which the reserve system is located must have a high mean and a low variance. This minimizes the danger of poaching along the corridors, although a certain level of poaching and hunting is impossible to avoid, especially in countries where men and boys occur. Second, corridors are more likely to be effective in temperate regions. This is because the temperate zone climax species are less likely to be habitat specialists and are more likely to disperse through the corridors. For example, in the chaparral and oak woodland habitats of California, corridors between small urban reserves, such as protected canyons and steep hillsides will protect and allow the dispersal of such large mammals as mule deer, bobcat, coyote, fox, and striped skunk. If these corridors are riparian habitats, the sycamore and oak trees that occur in them will serve as havens and passageways for owls, hawks, sapsuckers, woodpeckers, quail and a variety of other birds.

Notwithstanding such exceptions, I think it is the long range interests of the conservation community to de-emphasize the significance of corridors or, at least, to examine each situation carefully before recommending them. This is particularly true in the tropical countries.

Rational culling

Elsewhere, (Frankel and Soulé 1981, chapter 5), I have discussed the genetic issue raised by culling. Culling is an important management tool, both for the demographic health of some populations (eg Goodman 1980) and for the ecological health of habitat in danger of damage from overpopulation, usually of herbivores.

The problem, from a genetical and evolutionary point of view, is that considerable genetic damage is possible if culling is too severe or too selective. That is, if too few individuals remain or if they are too closely related, then erosion of genetic variability and inbreeding could result.

In general, social groups such as herds of elephants or troops of baboons are composed of one or more family groups (Packer 1978). As such, the elimination of entire social groups, while perhaps not decreasing genetic variance for quantitative traits to a significant degree, is likely to eliminate rare alleles and, possibly, adaptive (coadapted) combinations of alleles. For genetic reasons, it is better, therefore, to cull individuals from several social (kinship) groups than to remove the same number of individuals from one or a few special groups.

In summary, a rational, scientific approach to culling and other forms of close, 'hands-on', management should consider behavioural, demographic, and genetic factors. Management conflicts will, of course, arise, but with goodwill these can be resolved.

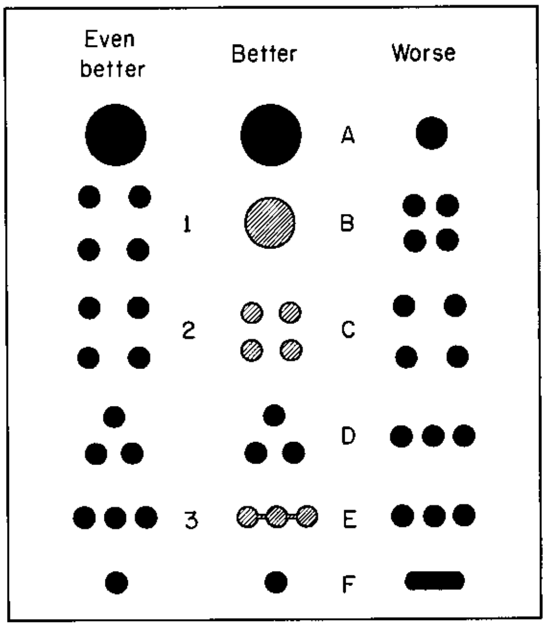
Rational habitat manipulation

The problem with purposeful, artificial habitat disruption is parallel to that of culling. It will often be necessary to disturb habitats in order to set back succession to an earlier stage, especially in small reserves (Pickett and Thompson 1978). The ecological reason is that even the temporary loss of successional species probably can trigger a cascade of extinctions because many early successional plants are essential resources for keystone species, particularly in tropical forests, (Foster 1980; Gilbert 1980). One danger, especially in small reserves, is that too many individuals of certain species will be eliminated during a disturbance operation. Managers should have census and distribution data, particularly for large, rare plants, and must avoid destroying individuals in species with low numbers.

Structural criteria for nature reserves

Diamond (1975) presented a pictorial summary of geometrical design criteria for nature reserves based on the state of knowledge of biogeography at that time. Recently, these principles were reprinted in the World Conservation Strategy (1980). Diamond's recommendations are shown in Figure 2 along with three suggested changes. Starting at the top of the figure, there is no change in the first (A) case: larger reserves are superior to smaller reserves, given that only a single reserve is possible.

Figure 2. Suggested physical design criteria for nature reserves. The right-hand and middle columns constitute Diamond's (1975) proposal based on biogeography. The cases in which the consideration of habitat diversity and epidemic potential have led to the modifications are shown in the left-hand column. See text.



In the second case (B) a change back to manifold reserves is recommended. The reason is that with only one large reserve in a region, the stage is set for the outbreak of epidemics. In a single, large reserve the probability of extinction from disease would be a constant menace, and replication of species in reserves is the best guarantee against extinction. In addition, there is a problem of genetic drift and inbreeding among the few survivors of a disease or catastrophe. Epidemics are not uncommon among wildlife (Frankel and Soulé 1981, chapters 2 and 5), and they are likely to increase in frequency and severity as nature reserves become evermore snugly encircled by human habitat. Domestic plants and animals are a major reservoir of pathogenic organisms infecting wildlife (Simberloff and Abel 1976).

Another factor is that extinction of large animals is high, even in the largest reserves (Soulé et al 1979). Even in a large reserve it will be necessary, therefore, to employ intensive management procedures to minimize extinctions. Granted that fewer species would have to be managed in a large reserve, this advantage is outweighed by the preceding epidemic argument.

In the third case (C), I would argue that proximity of reserves for the benefit of migratory, volant species is only advantageous to a small minority of birds and perhaps some bats. Clustering will not benefit the vast majority of taxa because it is unlikely that reserve clusters would be compact enough to provide for gene flow in most species. Furthermore, compact clustering could decrease the 'quarantine value' of reserves, and finally fewer habitats are likely to be preserved in a compact system versus a more dispersed one. Of course, this issue is almost impossible to discuss away from a concrete situation involving real topography, real habitats and real cultural institutions.

The only other recommended change is for case (E) - the issue of corridors which has been discussed on page 60. I would argue that reserve design in the tropics should start from the presumption that any corridors that exist at the outset will eventually be closed for security or encroachment reasons.

SUMMARY

A. The objectives of conservation would be best served if conservationists were conscious of the cultural, political and economic forces and trends affecting the vigour and longevity of their programmes. Such an inclusive approach to conservation is called Realconserve.

B. A Realconserve statement about tropical nature reserves could be that most of them will disappear in the next century. Some of these will be quickly and utterly destroyed during predictable intervals of social upheaval; others will die more gradually, being nibbled away by expanding human populations and by the exploitation of their plant, animal, water and mineral resources. Sufficient funds for the proper, scientific management of nature reserves, especially in the lesser developed countries, are not available, nor are funding priorities likely to change significantly in the next few decades.

C. For these reasons, ex situ conservation may be the only viable, long-range solution for large regions of the tropics, and implicitly the nature reserve approach may, in the future, be seen as applicable only to the rich, developed, high latitude nations.

D. In applying Realconserve to the management of endangered species in nature reserves, the following conclusions are reached:

1. The nature reserve per se is the natural unit of management for a numerically endangered species. If, however, such a reserve is incapable of establishing a viable population, the matter should come under the jurisdiction of an appropriate inter-agency or international body. The reasons for the immediate involvement of international organizations in these matters are political, scientific and moral.

2. The decision to implement a rescue operation for an endangered species must be based on historical, economic and ecological grounds, but as more and more populations and species dwindle in numbers, the criteria for rescue will perforce become more restrictive.

3. The issue of artificial gene flow to increase effective population size is controversial. In airing it, it is apparent that conservationists as a group entertain two mutually exclusive dogmas; these are, 'maintain the purity of subspecies (races) at all costs', and 'avoid inbreeding at all costs'. Both positions can be sustained by evidence and reason, but such generalizations will be of little use in any given, real situation. Conservation biologists must approach each case with an open mind.

4. In the difficult task of managing the remnants of this planet's wildlife, the planned extinction of some populations, and even some species, will be an uncomfortable but necessary tactic.

E. Particularly in the tropics, corridors between nature reserves should be dismissed as a permanent design component for the great majority of species. Corridors are passageways for pathogens as well as death traps for large carnivores and herbivores.

F. Genetics should be considered in both culling and habitat disturbance or manipulation.

G. In considering reserve design, a multiplicity of (smaller) reserves has several advantages over a single large reserve, even though more species will have to be intensively managed in the former.

CHAPTER 4 THE GARDEN OF THE UNICORN – THE ECOSYSTEM CONTEXT FOR THE MANAGEMENT OF ENDANGERED SPECIES

Daniel B Botkin

INTRODUCTION

One of the most famous medieval tapestries, now hanging in the Cloisters in New York City, depicts a unicorn caged in a garden. Viewing that tapestry, I am impressed that it is the garden and its plants, not the unicorn that is drawn with great precision and reality. The management of endangered species seems like that tapestry: it is the ecosystem - the garden - that is the reality. If we fail to focus on the ecosystem, the endangered species will become extinct, and join the mythology of the unicorn. For there is no such thing as conserving a species; there is only the conservation of ecosystems and their constituent populations. Individuals are alive, but life is sustained over long periods of time by ecosystem processes: the flow of energy and the cycling of chemical elements necessary for life. Although these are truisms of ecology, they have been ignored to a large extent in the management of endangered species, and for that matter in the development of a theory of population dynamics which has underlain such management.

Often the focus of management of endangered species is on some long-lived terrestrial organism: a large mammal, bird or woody vegetation. For these an ecosystem context is crucial, because individuals of such species live long enough to be affected by changes in ecosystem mineral cycling: because the abundance and distribution of these species are controlled by the availability of essential chemical elements: and because these species are capable of strongly affecting the local availability of the chemical elements necessary for life.

In the last several years there has been a growing recognition of the need to take an ecosystem view of the management of an endangered species, and there is now also a wealth of information from ecosystem research that can provide a basis for a new management approach. It is time to seek a synthesis of these studies and to set down the basic generalizations that can form this new management approach. Such a synthesis is the purpose of this paper. It is particularly appropriate to seek these generalizations at this meeting, for it is in recent attempts to understand and manage the preserves of eastern and southern Africa that an ecosystem context has been given the strongest consideration (Sinclair 1975; Walker et al unpublished; Owen-Smith in press).

HOW DOES ONE MANAGE A SPECIES?

How does one manage a species? How does one explain changes in the population of a species, like elephants or acacia trees? How does one explain a species' reproductive rates, mortality rates, and changes in distribution in time and space? The answer given throughout much of the twentieth century has been: solely by examining the population dynamics of that species. Much of the literature on the population theory employed to provide a basis for the management of large mammals is restricted to an analysis of the population dynamics of a single species, and to an attempt to determine the basic rates of reproduction, mortality and population growth. The population dynamics are then explained by a resulting growth equation like the logistic or the Leslie Matrix equations. Carrying capacities and optimum or maximum sustainable yields and abundances are calculated from such equations.

Thus the management of the great whales, as in the discussion in the proceedings of the International Whaling Commission over the last two decades (International Whaling Commission, 1959-1979) and elsewhere (May et al 1979) has focused almost exclusively on an attempt to define these rates as if they were constant in time and independent of any other factor except the population's own size. Considerable effort has been expended to estimate the pre-exploitation abundances to provide a single estimate of carrying capacity, and to determine density-dependent reproductive and mortality responses, as the population size changes. Similarly much of the attempt to apply population theory to the management of the African elephant has been restricted in this way (Caughley 1976; Fowler and Smith 1973; Hanks and McIntosh 1973).

That such a single species approach is insufficient is illustrated by a comparison of two well-known endangered species: the North American whooping crane (*Grus americana*) and the Californian condor (*Gymnogyps californianus*).

In terms of such classical population theory, both species appear similar: they are long-lived birds which have low reproductive rates and low mortality rates. Estimates of longevity are similar. Both are protected from hunting and by large preserves set aside especially to protect them. Yet their fates seem quite different. The whooping crane population was reduced to 14 individuals in 1938, but the population has recovered remarkably, numbering more than 60 in 1970 and close to 100 in 1980. In contrast, the Californian condor presently numbers 25 and is declining. Almost all experts agree that the Californian condor is in trouble and likely to become extinct, while ornithologists are optimistic about the whooping crane. What accounts for the difference? Certainly not the population characteristics abstracted from the environment, the habitat, or the ecosystem.

The whooping crane feeds on small crustacea, which are abundant in both summer and wintering grounds; the vegetation in the habitat is characterized by a growth form that provides adequate protection yet is open enough to allow these birds to fly and land. The condor on the other hand feeds on the carrion of large mammals, and the natural population of wild mammals has been eliminated or reduced to a small fraction of its original abundance in the condor habitat. The condor preserves have been protected from fire and the vegetation has changed.

The original habitat was grassland and shrubland; the habitat now is heavily chaparral. Carrion, where present, is less visible. Some experts also claim that one of the condor's major problems is finding landing and take-off strips large enough for it. Others claim that the bird, being extremely shy, is adversely affected even by rather occasional human visitation. The latter is reinforced by the recent death of a condor chick that was being handled and measured by a wildlife scientist. The strategy of attempting to preserve the condor as a population is failing because the ecosystem is not in the right state to allow for the persistence of that species. Food is lacking, the vegetation cover is inappropriate, and the proximity of human beings provides a behavioural stress for the birds.

The difference in the status of the condor and the crane does not lie simply in differences in fundamental population characteristics of birth, growth, and death rates, but in a complex interrelationship among behavioural, physiological, morphological, population and ecosystem attributes. The managerial lesson from these two cases is clear: one would rather have an ecosystem in 'good' condition and a small population of a desired species than a large abundance of that species and an ecosystem in the 'poor' condition. Unless the condor's ecosystem is restored, the condor's fate is sealed.

These are however comparatively simple cases, which demonstrate the necessity of an ecosystem context for the understanding and management of an endangered species.

THE NEED FOR AN ECOSYSTEM CONTEXT

During the past two decades, there has been a growing recognition of the scientific importance of ecosystem phenomenon, but the study of population theory and the study of ecosystems have proceeded in large measure independent of one another. Those who have studied ecosystems have tended to focus on geological and climatological processes as they impinge on the surface of the earth and its biota. An ecosystem study has generally involved the measure of the inputs and the outputs of chemical elements, as affected by the status of the soil and in some cases by the status of the gross features of the vegetation (Likens et al 1977). Vegetation, however, is generally the only part of the biota examined closely. A few studies have examined the relationship between the successional stage of the vegetation of an ecosystem and its effects on geochemistry, but little attempt has been made to integrate the effects of life forms except vegetation on these large scale phenomena (Gorham et al 1979; Vitousek and Reiners 1975). Meanwhile those pursuing population theory have continued to explore this theory essentially abstracted from such geochemical considerations (May 1976; Pielou 1977).

There is, however, among wildlife managers a growing recognition that an individual species cannot be managed nor its changes over time explained in the absence of an ecosystem context. Another example is useful to illustrate this point.

THE ABUNDANCE OF LONG-LIVED ORGANISMS IS PARTLY CONTROLLED BY ECOSYSTEM NUTRIENT CYCLING

The abundance and distribution of long-lived organisms are controlled to an important extent by ecosystem cycling of chemical elements. This point is obvious in regard to vegetation. However, the idea is much less obvious for large mammals and has been largely ignored until quite recently in the management of endangered species. In the early 1970's the need for such an ecosystem context became clear to several of us when we conducted a study of the factors controlling the population of moose (Alces alces) and the population of wolves (Canis lupus) at Isle Royale National Park, Michigan, USA (Botkin et al 1973). There we determined the age structure of the moose population, the reproductive rate, the mortality rate and annual changes in biomass. We examined the mortality rate of the moose due to predation by wolves, and we examined six of the crucial elements required for mammalian physiology: nitrogen, phosphorus, sodium, potassium, calcium, and magnesium. We examined the Isle Royale ecosystem for its content and flux of these six chemical elements. We measured the amounts in the soil available for vegetation growth, the amount available in the vegetation, the amount in vegetation eaten by the moose, and the amount required by the moose population. At that time the moose herd numbered approximately 1000 adults with an annual recruitment of approximately 400 calves. These animals were fairly evenly distributed over the entire 550 square kilometres of the island. That island ecosystem has a complex and diversified topography and an equally complex and diversified set of habitats. The island is a series of parallel ridges and valleys made up of sedimentary and igneous rocks with differential mineral composition and soil fertility. The more readily erodible rocks, sandstones, which occupied the valleys were often overlain by marshes, swamps, lakes, ponds, or streams, or flood plains.

We found that the amount of nitrogen, calcium, potassium, and magnesium available in the leaves and twigs of terrestrial vegetation eaten by the moose greatly exceeded the amount required for the moose population. Available phosphorus in the vegetation slightly exceeded the moose population requirements. In contrast the amount of sodium was considerably less than required. The sodium required for all new growth of the moose population plus that needed to balance losses was 243 kilograms per year; the amount available in all the terrestrial vegetation within reach and capable of being eaten by the moose was 170 kilograms per year. This represents 70% of the population's needs, but it is not all available because all of this vegetation greatly exceeds the consumptive capacity of the moose population. While the moose had a marked impact on the forest vegetation, they removed only 10 to 20% of the annual production within their reach. This could provide only 7 to 14% of their annual requirements.

From a geochemical point of view, this lack of sodium is not surprising. Green plants do not require sodium, and do not concentrate it; in fact some evidence suggests that trees discriminate against sodium and exude it from their roots into the soil (Smith 1970). Moreover, in a mid-continental ecosystem far from the influence of ocean particulate fall-out, there is little atmospheric input of sodium. The average concentration in the leaves and twigs of terrestrial vegetation is on the order of 10 parts per million (ppm): only 1% of the level recommended for the diet of domestic ruminant livestock (NRC 1970).

Moose are well known as feeders on aquatic vegetation in the summer. We calculated that the energy required for the moose to find and eat this vegetation exceeded the energy they could have obtained from it. We were surprised to discover that the aquatic vegetation was extraordinarily high in sodium content and the concentration of sodium increased as the habitat of an aquatic plant changed from the shore to the deeper parts of a fresh water pond. Shore plants, like irises, had hundreds of parts per million of sodium, while floating and submerged plants like water lilies or potomagetom, had from thousands to tens of thousands parts per million sodium. Since there are 45 large lakes and innumerable small ponds and open water areas and large bogs at Isle Royale, it was clear that the aquatic vegetation provided sufficient sodium for the moose.

From this study we concluded that the moose population was limited by sodium, and the diversity of habitat provided the moose with both its caloric and mineral requirements. Isolate the moose from the aquatic habitats and the moose population would be endangered by sodium deficiency. Isolate the moose from their terrestrial habitats and they would lack winter food and bulk caloric intake and also be in danger.

Although sodium limits the abundance of moose, one never saw a moose at Isle Royale illustrating classical physiological symptoms of sodium deficiency. Nor would such an observation be expected; any moose that was even slightly lacking in vigour due to such deficiency was immediately killed by wolves. In this case the wolves provided a proximal cause of death, while the mineral cycling limitations provided an ultimate cause.

These observations are analogous to those made by Anthony Sinclair about the African buffalo in the Serengeti (Sinclair 1978). He described 'simple starvation' which does not occur in the natural habitats of the African buffalo in the Serengeti but does in contrast occur for Indian water buffalo introduced on to the Australian continent without their normal complement of parasites and predators. These introduced populations were observed to undergo simple starvation when they destroyed their food supply in their habitat and, lacking essential nutrition, not only calories but also chemical elements, died a slow physiological death. In contrast, the wild African buffalo are quickly killed by parasitism and predation when they are weakened even to a small extent by a nutritional problem, Sinclair argued. Both the study of moose in North America and buffalo in east Africa suggest that an ecosystem context is required for the understanding of the changes over time and space of a population of large mammals and that such an understanding is required to develop a proper management policy.

WHAT ACCOUNTS FOR THE LARGE ABUNDANCE OF MAMMALS IN AFRICA?

The need for an ecosystem context and the importance of mineral cycling for management of large mammals is brought home even more clearly when one begins to compare the abundances of large mammals in east and southern Africa with other parts of the world. We are all aware that two of the striking features of eastern and southern African plains, grasslands, and savannas are the great diversity of species of large mammals and their great abundance. If we seek to manage these natural areas, then we will seek to maintain this abundance, and need then to know what controls it.

The great difference in abundance between the grasslands and savannas of east and southern Africa and the prairies and woodlands of North America is particularly striking because superficially these areas appear quite similar. We have reviewed the reported standing crop biomass of large mammals in Africa and North America (Botkin et al in press, Table 5). The lower limit for the abundance of large mammals in Africa is the upper limit for the abundance in North American prairies. Even more striking is the comparison between Isle Royale's moose which are said to represent the highest density for the species known anywhere in the world. The condition of the vegetation suggests that the moose are near the upper limits possible for that island but the biomass of moose, 7 kilograms per hectare (Table 5) is approximately two orders of magnitude less than the abundance of large mammals in some of the parks and preserves in east and southern Africa and one order of magnitude less than any of the east African parks or preserves. There seems to be some basic difference between the northern temperate and boreal forest and grassland habitats and those of subtropical habitats of Africa that allows a much larger carrying capacity in Africa than in North America.

The possible explanation for this great difference in abundance is pertinent to a consideration of the management of endangered species and ecosystems. Clearly any attempt to generalize for the management of all endangered species and ecosystems must be held in question until the common basis for the causes of abundance in North America and Africa are elucidated. Here I will briefly review some possible explanations for this difference and indicate why an ecosystem context is necessary.

First of all the difference in abundance is real and not the consequence of appearances or recent history. Even in the areas in the Great Plains of North America which include the complete complement of large mammals found there prior to European colonization the abundance of large mammals average 30 kilograms per hectare, which is at the lower limit of the abundances in eastern and southern Africa (Dyer personal communication 1980) (Table 5). What might account for this difference? Can characteristics of a single species account for the differences? Let us consider some of the simpler explanations that relate to individual population dynamics and attempt to explain differences in abundance between North America and Africa on such basis.

For like groups of organisms such as herbivorous mammals, relationships exist between body size and basic life history phenomena including longevity, survivorship, conception rates, and ages of maturity. This has been known since Aristotle (Egerton 1975), and is often repeated in contemporary discussion of mammalian physiology and morphology. The relationship between body size and metabolic rate suggests one explanation for the differences in large mammal abundances in Africa and those in North America. Metabolic rate decreases with body size. Total body metabolism decreases at a rate proportional to the body weight raised to the 3/4th power. Metabolic rate per unit of biomass decreases at a rate proportional to the body weight raised to the 1/4th power (Spotila and Gates 1975). Using these relationships, one can derive the ratio of body sizes that would be required for the ten-fold difference in biomass observed between the more abundant park areas in Africa and the American grasslands. From this factor alone, a ratio in body size of 10 000 to 1 is required for a per unit biomass metabolic rate of 1 to 10. If all the large mammals in an

Table 5. Comparative abundance of large mammals. Representative values are given.

	LOCATION	HABITAT	BIOMASS (kg/ha)	RAINFALL (mm/yr)
AFRICA: Tanzania	Serengeti-Mara	Mixed grassland and shrub	125-175	
Uganda	Ruwenzori National Park	Mixed grassland and shrub	214	1000
Uganda	Rwindi-Rutchan	Savanna	236	
Tanzania	Lake Manyara	Mixed grassland	170	900
Tanzania	Tarangire	Acacia Savanna	121	165
Kenya	Tsavo (North)	Mixed grassland and shrub	41	550
Zaire	Albert Park	Savanna Forest edge	236	650
East Africa		Cattle on western style ranches	37-56	
East Africa	Masailand	Domestic ungulates	9-19	
Zimbabwe		Game ranch Dry grassland	33	
Kenya	Amboseli	Savanna	5-31	225-510
Ghana		Rain forest	0,75	
NORTH AMERICA: Western USA		Cattle on ranches	14-37	
Nebraska-Montana-South Dakota		Prairie with Native species	9-36	600
California		Chaparral	19	450
Isle Royale		Woodland	7	120

east African park were adult elephants weighing an average of 2 300 kilograms and all the animals in a North American prairie were deer weighing 70 kilograms, the ratio would only be 33 to 1, quite insufficient to account for the observed differences in abundance. Moreover, the range of body sizes and the average body size of the large mammals in the Serengeti is reported by Sinclair (1978) to be approximately equivalent to those of the North American prairies. Thus the difference in the metabolic rate as a function of body size does not appear to provide any sort of explanation.

It might also be thought that the warmer climates of eastern and southern Africa would require a lower expenditure of energy in the searching of food and in maintaining a proper body temperature. Such an argument would run along the following lines: in North America during the winter one would expect the energy expended in order to keep a mammal's body temperature sufficiently high would be so great as to lead to a great difference in the respiration rate and the utilization of food and therefore a lower standing abundance. We have made calculations for all of these factors. The energy utilized in travelling increases as the body size decreases (see Figure 3). The increase in metabolism M_A in moving one kilogram of body weight, for an animal of size b, over a distance of one kilometre is:

$$M_A = c' b^{-0,4} \qquad (1)$$

where c' is a constant. The total cost of energy in moving d kilometers per unit time is the sum of functions for basic metabolism and for movement. From these it can be shown that a ratio of 1 to 10 in total metabolic rate per unit body mass requires a body mass ratio between 10^4 and $10^{2,5}$ or a ratio of 316 to 1, if we assume that the distances that the animals must travel in North America and Africa are equivalent. If we assume that the distances travelled are different, with the North American mammals travelling a factor x farther than in east Africa, then the required ratios would lie between 10^4:1 and $(10/X)^{2,5}$:1 where x is the additional distance travelled by North American mammals. However, even if we assumed that mammals in North America travel twice as far as in Africa, body size ratios of 56 to 1 would still be required to account for the differences in standing crop.

Finally we might consider the problem of keeping warm in North America. An animal gains heat by absorption from the sun (Q) and from its own metabolism (M). Heat is lost by radiation, which is proportional to the fourth power of its surface temperature (T_r4), by evaporation (E), and by convection. Convection loss is proportional to the difference between the animal's temperature and the air temperature ($T_r - T_a$). Convection loss is also a function of wind speed and the exposed area, which we will denote as f(V,D) where V is wind velocity and D is a characteristic diameter. Thus an animal's energy budget is expressed by the following equation:

$$Q + M = kT_r^4 + E + (T_r - T_a)\, F(V,D) \qquad (2)$$

where k is a constant for a particular surface. Using this equation and parameters as formulated in Gates and Schmerl (1975), it can be shown that

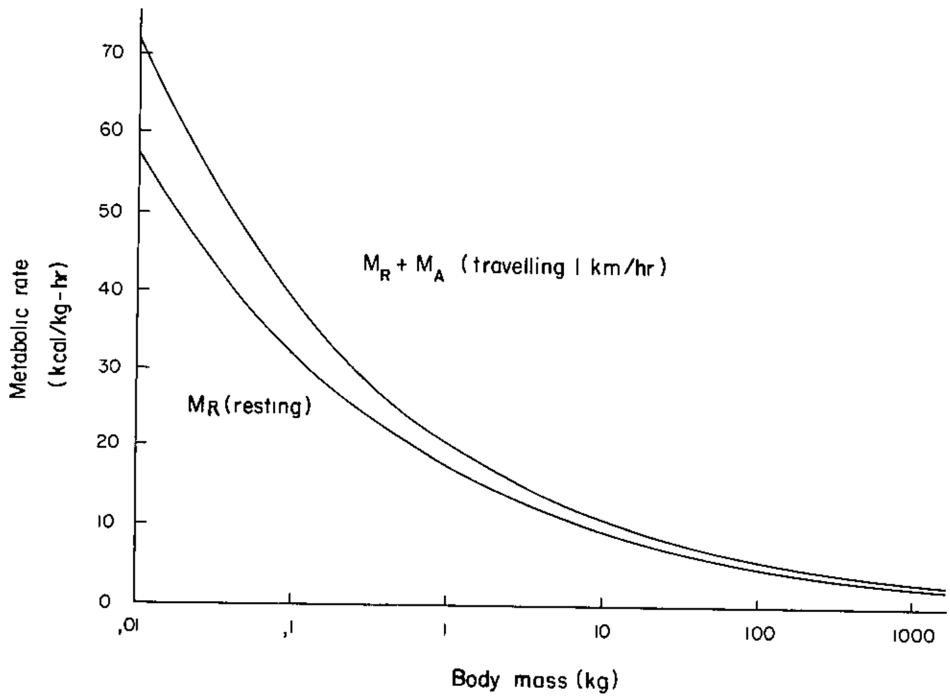


Figure 3. Relationship between body size and metabolic rate for resting (M_R) and traveling (M_A) animals.

in all situations, whether on a clear day or a cloudy day, or on a winter night with a dark sky, a deer in North America even when standing still must get rid of excess heat, merely due to its basal metabolic rate. In Africa the situation is the same, but more severe. For example, consider two extreme situations: a deer standing on a cold night at -10°C in North Dakota and an elephant standing in full sunlight on a day with a 20°C temperature in Africa. Even under these conditions, a resting, 70 kilogram deer must lose 350 kcal an hour just to maintain a constant body temperature while the 2300 kg elephant must lose 6900 kcal per hour. Until excessively low temperatures and high wind speeds are reached the situation is always similar. From this one must conclude that basal and active metabolic requirements for keeping warm and moving do not account for differences in metabolic utilization of energy and therefore do not account for differences in abundances for large mammals. In other words, a consideration strictly of an individual species and its requirements when these species are alike in body size and therefore alike in many life history characteristics, cannot account for the difference in observed abundances between North America and East Africa.

Suppose we move outward from a consideration of a single species to a consideration of a species of a herbivorous mammal and its food requirements or a community of herbivorous mammals and the vegetation they consume. One possible explanation for the differences in the abundances of the large herbivorous mammals in Africa and in North America is that there is merely more forage in Africa because, in the warm subtropical and tropical habitats, there must be a much longer growing season. One could also argue that during the growing season the temperature is warmer in Africa so that the vegetation production is much greater per day and much greater per year than that observed in temperate grasslands and forests. Some evidence however runs counter to this suggesting that growing seasons are little if any longer in eastern Africa than North American woodlands and prairies although the reason vegetation growth ceases is different. For example, based on the cessation of rainfall, the growing season is 4 to 5 months in Zimbabwe. In the North American Great Plains the growing season is about the same length but ceases when temperature falls near to freezing.

In addition, available measurements indicate that the annual net primary production in eastern and southern Africa and in North American grasslands is approximately the same (Whittaker and Likens 1973).

A similar argument that is sometimes put forth begins with the idea that annual net primary production is directly correlated to rainfall in arid and semi-arid regions. From this one then concludes that net primary production can be predicted directly from rainfall. Thus Krebs (1972) states that 'productivity in desert areas can be determined very simply by measuring rainfall' and Whittaker (1970) has written that 'in arid climates there is nearly a linear increase in primary production accompanying an increase in precipitation'. Phillipson (1975) has applied these arguments to estimate the carrying capacity of elephants in Tsavo National Park, Kenya. These statements refer to a large scale spatial correlation but they have been applied to temporal changes over short periods in a single place. Such spatial correlation could not provide an accurate means to estimate temporal variations in net primary production particularly over a short time, since they do not take into account the current state of the vegetation nor do they consider the potential limitations of vegetation growth due to chemical and physical soil characteristics nor the past history of vegetation nor the influence of herbivory or fire or other disturbances. Clearly at Tsavo the net primary production following the famous drought (1970-1971) would be much less than before the drought, even for two years with identical rainfall, because of the great change in the abundance of the vegetation.

This is merely a special case of the assertion that high abundance of vegetation or any kind of organism is not necessarily correlated in a simple way with high productivity. As an illustration the average productivity in temperate and tropical forests is two to three times that of grasslands, but standing crops in those forests is approximately 50 times that of grasslands (Whittaker and Likens 1973). One would not need to set forth this rather obvious point if it were not for the fact that gross relationships between biomass and productivity or simple correlations between rainfall and productivity have been actually used to estimate carrying capacity.

It has also been suggested that the great abundance of large animals in Africa can be explained because the animals are able to eat a great proportion of the vegetation. This is in turn because they are supposed to divide up the vegetation resources with much greater specificity. Such an argument is made in Dasmann's well-known work, 'African game ranching' (1964) where a picture appears of several species of African herbivores utilizing different types of vegetation, with the giraffes feeding on the tops of the tall trees, the elephants feeding at the next highest layer and so on. While this may be a pleasing view of the African savanna, it is contradicted by studies like one of elephants that showed that more than 90% of the mouthfuls taken by these large animals were below 2 metres, placing them in direct competition for food with impala, Thomson's gazelles, Cape buffalo, wildebeests and other smaller herbivores (Guy 1976) - if partitioning of food is not carried out along the basis of simple physical dimensions there are other possibilities. As McNaughton (1980) has reviewed, the mammals may divide the vegetation by species or they may divide the use of the vegetation in time between habitats.

All of these explanations require that a greater fraction of the vegetation is used by the animal. If the net primary production is not greater, then there must be a greater fraction which is useable to the large mammals. This means that the vegetation in Africa must be on the average of a higher nutritional quality if any of these explanations are correct. The question then arises, what would lead to a higher nutritional quality for African grassland and savanna species in contrast to North American grasslands species?

BIOTIC PROCESSES FOR NUTRIENT RETENTION

This discussion forces us to consider what factors might lead to a higher nutritional status for the vegetation in the African grasslands and savannas in comparison to those of North America. To evaluate this we must consider what factors control the nutritional composition of the vegetation and therefore what controls the status of the chemical elements in the soils. For this we must examine soil processes and a little geochemistry. Two processes are potentially important in the nutrient retention in the east African soils. These are illustrated in Figure 4. At the low levels of rainfall purely non-biological, physical processes would prevent the loss of essential elements from the soil. The water falling on the land would be lost through evapotranspiration, and the process of evaporation would leave the dissolved elements near the soil's surface. At higher levels of rainfall, however, water moves out of the soil into streams in subsurface run-off. In an area without life, the soil would become infertile. However in higher levels of rainfall, biological processes serve to retain the essential elements within an ecosystem. Chemical analysis of east African soil supports the argument that mechanisms of nutrient retention are rainfall dependent. As shown on the accompanying graph, at very low rainfall levels, below 500 mm per year, the base saturation of the soil is approximately 100%. With increasing rainfall the base saturation decreased exponentially to minimum of about 15% at 740 mm per year rainfall. A discontinuity occurs at this minimum after which the percent base saturation increases with rainfall up to a maximum of 55% at 1200 mm per year from which it declines as rainfall continues to increase. It is interesting that a graph of large mammalian biomass versus rainfall shows a similar pattern increasing with rainfall to a peak at approximately 100 mm/yr and decreasing to lower values afterwards (Figure 4B). It is interesting to note that the reported linear relationships between herbivore productivity or biomass, net primary production, and rainfall have been calculated mainly for values that lie within a range of increasing biological affects.

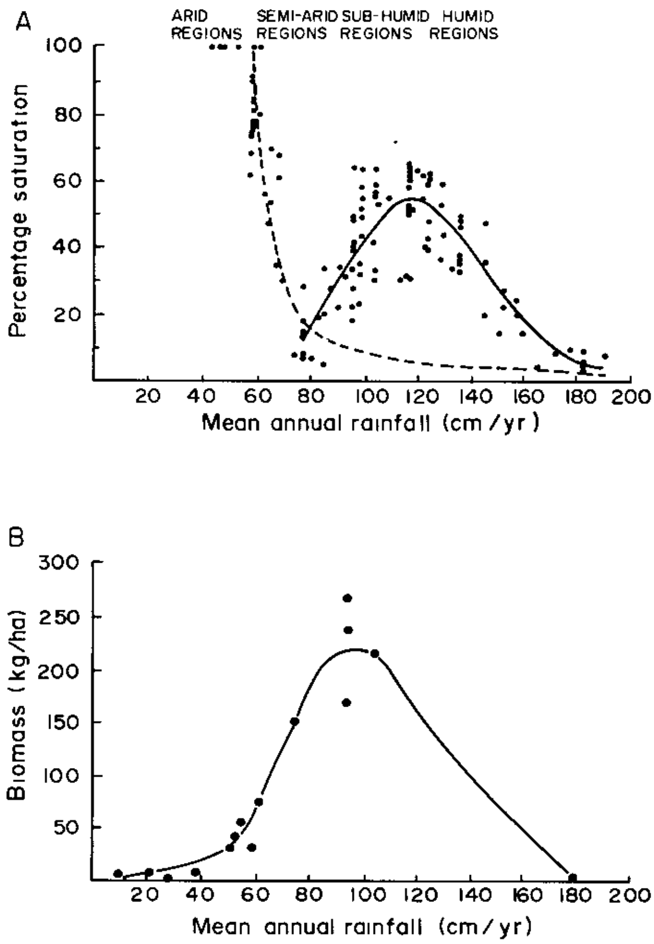


Figure 4.

A. The relationship between percent base saturation of the soil and mean annual rainfall for African soils. In drier regions (rainfall below approximately 80 cm/yr) the percent saturation declines exponentially with rainfall (dashed line). At higher rainfall levels, the percent base saturation increases due to biological effects, reaching a peak at approximately 120 cm/yr and declines afterwards (solid line). The declining exponential curve (dashed line) is continued above 80 cm/yr to indicate the expected difference between the dashed and solid lines representing the effects of the biota on the soil's percent base saturation.

B. The relationship between animal biomass and rainfall in Africa.

The increase in base saturation between 740 and 1200 mm/yr must be in part due to the establishment of tight nutrient cycling between the vegetation and the soil. Elsewhere we have suggested a more general hypothesis: the animals act together with the plants to retain nutrients in the ecosystem (Botkin et al 1981). The biota tend to retain the nutrients against the forces of fluvial erosion which tend to remove these nutrients. Quantitatively, this biotic effect on nutrient retention can be seen as the difference between the upper line in the accompanying figure and the lower dashed line. Qualitatively, the effects of large mammals on the soil and vegetation as well as the reverse effects can be thought of as diagrammed in Figure 5. Landscapes with rainfall greater than the maximum for base saturation would have biotic retention of chemical elements. Areas with rainfall less than the base saturation minimum would have abiotic retention of chemical elements.

Some of the major parks and preserves of Africa have average rainfall levels which place them near the minimum percent base saturation as shown in the preceding figure. For example, Masai Mara in Kenya has average rainfall less than 500 mm/yr as does Tsavo National Park, Kenya indicating that, on the average, nutrient retention in those areas would be under abiotic control. With an annual variation in rainfall it is possible that the same ecosystem could shift back and forth from biotic to abiotic control of nutrient retention. This would allow the persistence of high average animal biomass over a long period in spite of short term environmental fluctuations.

In what way could the animals influence the retention of nutrients? Recent studies of woodlands suggest that the storage of chemical elements increases in an aggrading ecosystem - one with a positive net ecosystem production and particularly in early successional ecosystems (Gorhan et al 1979; Vitousek and Reiners 1975). In contrast both steady state and degrading ecosystems are leaky and decrease in the content of chemical elements. Vegetation responding to a disturbance like fire but growing vigorously takes up more nutrients than vegetation in a long undisturbed habitat. Those factors that tend to increase net primary production and increase the abundance of plants characteristic of early successional stages would also tend to promote the uptake and storage of the biologically essential chemical elements.

Moderate levels of herbivory appear to increase net primary production and shift the dominant species of plant (McNaughton 1976). Too intense disturbance, including too intense grazing and browsing would decrease net primary production, decreasing the uptake and storage of nutrients. Very low levels of herbivory or other disturbances would lead to a vegetation community that was less productive and suffered greater losses of chemical elements. Some intermediate level of disturbance would therefore result in a maximum rate of uptake of chemical elements and this level of disturbance would lead to vegetation that had a high nutritional quality and could support a high abundance of mammals.

If all this were true then the large mammals would have an important effect on nutrient cycling and the large abundance of mammals in Africa could serve to promote and maintain a rapid cycling of the biologically essential chemical elements. In this way the population dynamics of the large mammals might be linked to the ecosystem processes and the abundances of the large mammals in eastern and southern Africa could be explained from an ecosystem context.

At this time such an explanation is conjectural: however a simple experiment would provide a good test. We have begun this experiment at the Serengeti Research Institute. In this experiment one needs to set up two treatments and a control. The treatment would be small plots surrounded by a fence which would serve as enclosures. Within one set of treatments the vegetation would be removed and in the other the vegetation would be

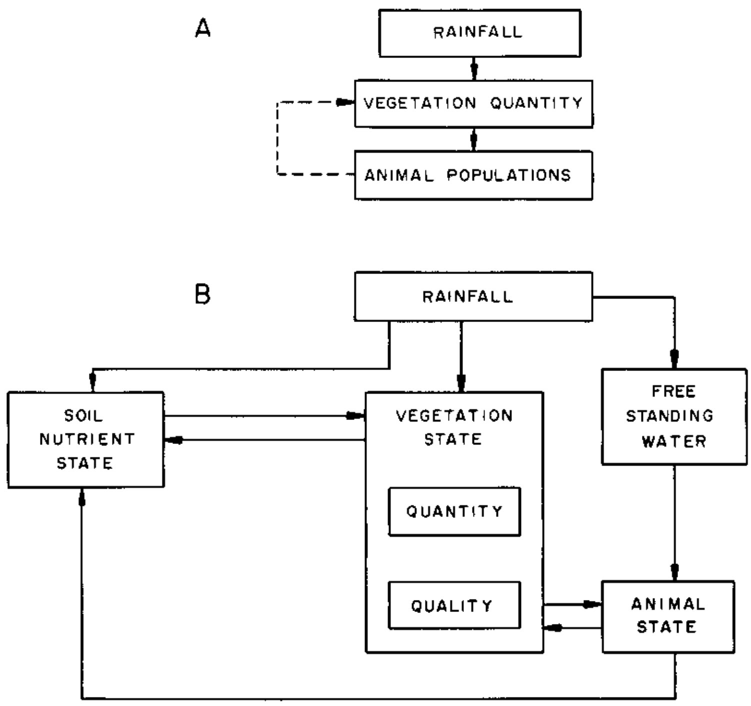


Figure 5. Relationship between rainfall and animal population dynamics.

A. Assuming animals are affected only by the quantity of vegetation.

B. Assuming that animals are affected by vegetation quality and quantity, and that the animals affect the vegetation and soil.

allowed to remain but the animals excluded. In all the plots the flow of chemical elements in fluvial processes would be monitored through the use of lysimeters. If the conjectures that I have just presented are correct then one would expect that the treated plots would undergo a much more rapid loss of chemical elements than the control. Moreover, if this loss were sufficiently rapid so that a significant fraction of the essential elements were lost within one to three years then the chemical elemental cycling would have to be a consideration for even relatively short term management policies.

THE IMPLICATIONS FOR MANAGEMENT

In this paper I have presented a variety of arguments that suggest that even the short term population dynamics of large mammals must be dealt with in terms of an ecosystem context including ecosystem mineral cycling and rates of disturbance. To summarize, the major points of this paper are: the abundance of long-lived and terrestrial organisms are controlled to a considerable extent by the availability of crucial chemical elements. While the status of the chemical elements in an ecosystem depends ultimately on the meteorological and geological processes, that is on rainfall and the fluvial cycle, and on the parent material from which a soil is derived, the proximal, short term, local status of chemical elements in a terrestrial ecosystem is affected by the status of that ecosystem, and on the state of the vegetation and the large long-lived animals.

Aggrading ecosystems, those with a positive net ecosystem production, also have a positive net uptake of chemical elements and increase in the storage of these elements. Such aggrading ecosystems are typified by the early and mid-successional forests as have been studied in eastern North America (Gorham et al 1979). Degrading ecosystems are those in a near or quasi-steady state, with a net ecosystem production equal to or less than zero. These are leaky to chemical elements, and undergo decreases over time in their stocks of chemical elements.

Whether an ecosystem is on the average aggrading or degrading depends on a complex set of interacting phenomena, including the abundance, distribution, and vigour of the vegetation and animals, on the rates of disturbances, and on the ratio of intra-ecosystem cycling of chemical elements to the exchange of chemical elements between that ecosystem and other areas of the surface of the earth.

Large mammals affect the status of the nutrient stocks through a variety of phenomena which influence the growth rate of the vegetation and the status of the soil, including the rates of herbivory, the species selectivity of the herbivores, and the transformation of chemical compounds from relatively stable forms.

The abundance of large mammals depends on the ecosystem state - the availability of nutrient-rich vegetation, which in turn depends on the species composition of the vegetation, on the age structure of that vegetation and its vigour. Young, rapidly growing vegetation in a rich soil leads to high nutrient status in the ecosystem and a high abundance of large mammals.

Certain levels of disturbance maximize the long-term carrying capacity of terrestrial ecosystems for large mammals. Too rapid or too intense, although infrequent, disturbances lead to large losses of chemical elements over time, and to a decrease in the possible vegetation production and thereby a decrease in the abundance of large mammals. Too infrequent disturbance leads to a quasi-steady state ecosystem, which is leaky, and which over a long period will decrease in its capacity to sustain large mammals. Therefore somewhere in between high and low rates of disturbances lies one which will maximize the long-term carrying capacity of large mammals.

Management policies must take these aspects of an ecosystem context into account. A wise manager will know the habitat, in terms of its status of chemical elemental stocks under 'normal' conditions, the normal rates of disturbance, and what factors tend to maintain the status of chemical elements at their normal levels. Such a manager will know whether major changes in the abundance of the species or a group of species will strongly affect the status of chemical elements.

Managerial policies must retain a balanced view in regard to factors that tend to increase the abundance of any one species versus those factors that tend to decrease its abundance. Policies that lead only to an increase in reproduction and growth rates of a population will inevitably lead to catastrophic uncontrolled die-offs. The potential to restrict population growth must be included in a management scheme, and the allowable levels of a population must be determined in relation to the effects of such levels on the ecosystem chemical cycling.

Where disturbance has been a long-term factor, the rates and intensity of disturbances that led to the greatest nutrient retention and to the most desirable biological conditions of the ecosystem must be taken into account. Such rates should be the long-term goal of a manager.

The conservation of endangered species requires the conservation of ecosystems and understanding of the population dynamics of endangered species requires that these populations be viewed within an ecosystem context. Particularly for terrestrial ecosystems it is not possible to view biotic phenomena abstracted from geochemical phenomena.

In a metaphorical sense, we need to return to the perspective of those unknown artists and weavers who created the exquisite medieval tapestries. While we may be charmed by and wish to seek, capture and protect animals almost as rare as a unicorn, we must see their ecosystems with great clarity and realism.

SUMMARY

There can be no such thing as simply conserving a single species; there is only the conservation of ecosystems and their constituent populations. To conserve a species in its natural habitat, we must maintain the flow of energy and cycling of chemical elements necessary for life. This is nowhere more true than in the grasslands and savannas of eastern and southern Africa, where the abundance of large mammals exceeds that recorded anywhere else on the Earth. This great abundance of large mammals appears to be a consequence of these elements within the ecosystem. This recycling and retention appear in turn to be consequences of biotic processes.

We have argued that, in areas of moderate to high rainfall, the temporary elimination of large mammals and higher vegetation could lead to a significant loss in soil nutrients. This loss may be irreversible, or may require extremely long periods, involving geological processes (weathering and aeolian input) for recovery.

Thus the wise management of African wildlife requires careful attention to ecosystem processes. Ignoring these processes, one may grossly underestimate the time and activities required to restore damaged habitats and to prevent the extinction of endangered species. An ecosystem perspective, especially important in the management of large terrestrial mammals, has applications to conservation in many kinds of ecosystems.

CHAPTER 5 MANAGEMENT FOR MAINTENANCE OF SPECIES DIVERSITY

Jared M Diamond

INTRODUCTION

What ultimate biological goals should managers of natural reserves pursue?

To this question, the first response of many biologists would be 'The goal of preserving as many species as possible'. This does not simply mean, 'To have as many species as possible represented within the boundaries of the reserve by self-sustaining populations'. Instead, one might prefer to say 'To have represented, by self-sustaining populations within the boundaries of the reserve, as many species as possible that would be doomed to extinction if the reserve did not exist'. The distinction between this more complicated definition and the first simpler definition may sometimes be significant. For example, given a certain amount of area that political and economic considerations allow for allocation to reserves, one can sometimes obtain a higher number of species within the reserve system by having multiple small reserves rather than a single large reserve of the same total area (Simberloff and Abele 1976; Gilpin and Diamond 1980; Higgs and Usher 1980). However, many of the species most requiring protection are ones that require a large reserve and that would be doomed in a system of multiple small reserves (Diamond 1976a; Terborgh 1976). Finally, biologists may prefer to weigh species rather than merely count them and to consider it more important that reserves protect certain species than others. Examples of motives underlying such judgements include economic value (eg whales and sea otters), scientific value and uniqueness (eg Hawaiian honey-creepers, East African lake cichlid fishes), and aesthetic appeal (eg tigers and birds of paradise).

The chief aim of this chapter is to discuss management for the simple goal of maximizing biological diversity. Also presented are some considerations imposed by particular concern for species that would be doomed outside reserves, or for species considered valuable, unique, or appealing. I shall begin by reviewing the factors that govern species diversity in nature. Without understanding these factors, one cannot hope to manipulate nature so as to maximize species diversity. Second, I shall focus in detail on the multiple relations between area and biological diversity. Finally, I shall illustrate the practical significance of these considerations to reserve managers, by seeking the lessons to be learned from three case studies where tragic declines in species diversity took place. Most of the examples will be taken from animals.

DETERMINANTS OF SPECIES DIVERSITY

Anyone who wants a simple answer to the questions 'What determines species diversity?' is in for a disappointment. Many different factors determine species diversity; the same factor may either increase or decrease species diversity, depending upon the factor's magnitude; and the effect of one factor may depend on other factors. For example, species diversity generally increases with area, but Australia's small area of tropical rainforest is nevertheless richer than its vast expanses of desert.

Let us now provide an overview of what seem to me the eight main determinants of species diversity. The first two of these factors are habitat factors; the next two, geometrical factors; the next three, I term equivocal factors (because they may either increase or decrease species diversity); and the last is the historical factor.

Habitat structure

It is a familiar finding that, all other things being equal, species diversities in different habitats tend to increase with increasing complexity of the habitat's physical structure. For example, tropical rainforests, with their multiple vertical layers and many life forms, generally harbour more species than adjacent savanna woodlands, which in turn harbour more species than low grasslands. A marine analogue to this terrestrial example is that coral reefs are generally richer than sandy bottoms. An intuitive, almost circular way of understanding this relation between species diversity and habitat structure is to appreciate that each species prefers a certain constellation of habitat structural factors, which in part define its niche. Hence habitats with more complex structure 'offer more niches', hence tend to harbour more species. Despite the qualitative obviousness of this correlation, it is not easy to provide quantitative measures of habitat structural complexity that would permit predictions of species diversity. Perhaps the most familiar of such measures is the method devised by MacArthur and colleagues (MacArthur and MacArthur 1961; MacArthur, MacArthur and Preer 1962; MacArthur, Recher and Cody 1966) for quantifying the structural complexity of terrestrial vegetation very crudely by a foliage-diversity index, and using this index with remarkable success to predict differences among habitats in bird species diversity.

Habitat diversity

The preceding paragraph recognized differences in species diversity among patches each homogeneous but differing from other patches in structure. If one instead compares patches that are horizontally heterogeneous in habitat structure, then diversity of species tends to increase with diversity of habitats. One of the most familiar examples involves the turnover of species observed as one goes up a mountain. Hence a whole mountain is likely to be more species-rich than a mid-elevation plateau of equivalent area. For purposes of quantitative prediction it often turns out that elevation itself (eg island elevation) makes significant contributions to variance in species diversity. (In more detail, the altitudinal distribution of area is also significant eg Mayr and Diamond 1976). By the same token, there is also species turnover along depth gradients in aquatic habitats, hence species diversity in lakes or in the ocean increases with the maximum depth sampled (eg fish in African lakes: Barbour and Brown 1974).

An equally familiar gradient is the vegetational gradient on land, from grassland to scrub to woodland to tall forest. Again, species tend to be restricted to particular habitats along this horizontal gradient, and we expect intuitively that more species will be censused as one samples a greater diversity of habitats along this gradient. Quantitative analysis of this embarrassingly obvious trend has been hampered by two difficulties: the difficulty in defining a measure of habitat diversity that is complicated enough to be useful yet simple enough to be measurable and of predictive value; and the difficulty of disentangling the effects of habitat diversity, habitat structure, and area (eg if one compares a reserve of just forest with an equal-sized reserve running the gamut from grassland to forest, the relative diversities will depend on the relative areas of each habitat in the mixed reserve, and on the excess species diversity in forest compared to an equal area of grassland). A hopeful start toward quantification and prediction is Cody's (1975) use of a principal component of vegetation height and 'half-height' (see Cody 1975 for definition) as a measure of position on the habitat gradient, leading to the difference in this principal component measure between opposite ends of the gradient as a simple measure of habitat diversity. This measure of habitat diversity was surprisingly useful in rationalizing bird species diversities in Mediterranean habitats.

Area

Having mentioned these two habitat determinants of species diversity, I now mention geometrical determinants, of which the first is area. Hundreds of studies have shown that, if one compares unequal areas of similar habitat, species diversity increases with area (eg for bird species on Solomon islands of differing areas: Figure 6). The varied reasons for this simple correlation will be discussed in the second section of this paper.

Distance

All other things being equal, the more isolated a habitat is from other patches of similar habitat, the fewer species will the patch harbour. This effect is a function of distance in relation to the dispersal ability of organisms: the poorer is this ability, the lower will be the fraction of the colonist pool that a patch of a given isolation harbours. The clearest examples come from biogeographic studies of oceanic islands, which show that, for islands of equal area, species diversity decreases with increasing distance from the colonization source. Similar conclusions are also expected to apply to island-like habitat patches on land or in the ocean, though documentation is scantier. In the cases of such virtual islands, species diversity depends not only on distance between the patches but also on the nature of the intervening habitat. To mention one example, isolation effects might be severe on species diversity in a forest patch isolated from the nearest similar patch by intervening desert (eg the woodlands of southwestern and southeastern Australia), but the effect of isolation would be less severe if the intervening habitat were a medium-height scrub. In the latter case, some forest species would be able to live in or move through the scrub, so that the isolation would be incompletely effective.

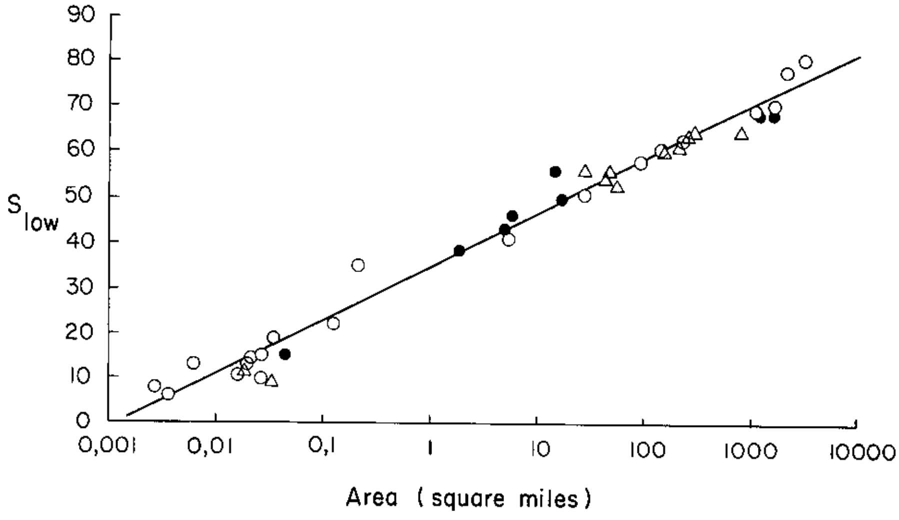


Figure 6. Number of resident lowland bird species (ordinate), on islands of different areas (abscissa, logarithmic scale) in the Solomon Archipelago of the southwest Pacific Ocean. From Diamond and Mayr 1976. One square mile = 2,6 km^2.

Predation

Each of the four previous factors correlates monotonically with species diversity (eg species diversity increasing with area or habitat diversity, decreasing with distance). Three further factors, of which I mention predation first, have equivocal or non-monotonic effects on species diversity. In particular, with an increase in predation pressure, productivity, or disturbance, species diversity may increase but will eventually decrease with further increase in the factor. A classic illustration of the effect of predation on species diversity was provided by Darwin (1859) who noted that plant species diversity was higher on a piece of pasture grazed by sheep than on an ungrazed piece. The explanation is that, on the ungrazed piece, a few plant species became dominant and crowded out other species, whereas the sheep prevented any species from becoming dominant or from growing to a point where competition outweighed predation as an organizing force in the community. A century later, Paine (1966) provided a similar marine example: a rocky intertidal shore harboured a greater diversity of sessile invertebrates in the presence of predatory starfish than when the starfish were removed, because starfish reduced the densities of dominant species and hence permitted competitors of these dominants to survive. It is obvious, however, that predators can also exterminate their prey, and one might expect that with increasing predation intensity the diversity of the prey will pass through a maximum and will eventually decrease. Such a maximum is in fact observed for plant species diversity as a function of grazing pressure (K Harper, quoted by Horn 1975).

Disturbance

Dayton (1971) and Connell (1975) have emphasized that physical disturbances, such as wave exposure, storms and fires, play a role similar to predation in their effect on species diversity. That is, in the absence of any physical disturbance a few species may become dominant, outcompete other species on the same trophic level, and lead to a community of many individuals of low diversity. Physical disturbances create patches where these dominants have been removed and where successional species may colonize. As a result of repeated disturbance, the environment becomes a mosaic of successional patches or alternate climax patches, in which there is high species diversity rather than a few dominant species. If the physical disturbance is very severe, however, then populations are devastated and the whole environment is maintained in an early successional state of low diversity. Such considerations are helpful in understanding the species diversity of tropical rainforest, coral reefs, and communities of marine intertidal invertebrates.

Productivity

That species diversity increases with productivity over a certain range is obvious (MacArthur 1972). A few examples suffice. Iceland's Lake Nyvatn is much richer in abundance and diversity of water birds than is the considerably larger Lake Thingvallavatn, because Lake Nyvatn has much higher productivity. Upwellings of nutrient-rich ocean water are associated with high diversity as well as abundance of marine birds at the top of this ocean food chain, as off the Pacific coast of Peru. Desert rodents (Brown 1975) and lizards (Pianka 1975) provide other illustrations. However, if productivity is very high, a few species may achieve high biomasses and crowd out their rivals, leaving a low-diversity community. Examples abound in fresh-water environments (eg Patrick, Hohn and Wallace 1954).

History

I have now considered seven factors which relate the species diversity of a habitat patch to the present properties of that patch. There remain many cases in which measurements on the habitat patch as it is at present fail to explain species diversity. Why does New Britain, a mountainous and well-watered island of 14 000 square miles only 50 miles off the coast of New Guinea, harbour considerably fewer bird species than Aru, which is nearly five-fold smaller in area, 80 miles distant from New Guinea, entirely lacking in mountains, and much drier? Why are the woodlands of California richer in bird species than one would expect from their structure and present extent? Why are alpine habitats on mountain tops of New Guinea so poor in bird species?

To understand these paradoxes, we must remind ourselves that habitats change with time. Species distributions and species diversities do not adjust instantly to habitat changes. Of particular interest in the last decade have been studies of changes in species diversity following a change in habitat area (eg Diamond 1972; Terborgh 1974; Willis 1974). For example, the end of the Pleistocene brought massive changes to the earth's surface, causing alpine and boreal habitats to shrink, lowland habitats to expand, tropical rainforests to expand at the expense of savanna, and the oceans to rise and flood lands that were less than 100 metres above late-Pleistocene sea levels, thereby cutting offland-bridge islands such as Britain, Trinidad, Fernando Po and Ceylon from their adjacent continents. Today, 10 000 years later, species diversities have still not recovered to values appropriate for modern conditions, and are in some cases intermediate between their inferred late-Pleistocene values and what would be appropriate modern values.

This process, by which species diversity proceeds from an old to a new equilibrium value as conditions change, is termed relaxation. I suspect that a significant fraction of the world's biotas have not yet achieved equilibrium with modern conditions but are still relaxing from the changes at the end of the Pleistocene. To illustrate this by the three paradoxical examples mentioned in the previous paragraph, New Britain is separated from New Guinea by deep water, Aru by shallow water, so that during Pleistocene times at low-sea level Aru was joined to the New Guinea mainland but New Britain was not. Today, Aru still has twice as many bird species as expected for an oceanic island of its size near New Guinea at equilibrium: Aru still retains many New Guinea mainland bird populations that were stranded on Aru when it was cut off and that have gradually been going extinct over the last 10 000 years. Similarly, the Californian woodlands were much greater in extent during the Pleistocene than they are today; their bird species diversity must then have been higher than it is today, and even the modern value has not yet declined from this Pleistocene high value to a value that would be appropriate at equilibrium to the modern limited area of the woodlands. Finally, as regards the New Guinea alpine avifauna, there was a time after the end of the Pleistocene when climate was warmer and timberline higher than it is today. At this time all the New Guinea alpine grasslands shrank drastically in extent, and some of them transiently disappeared completely. The avifauna of these New Guinea alpine grasslands has not yet recovered a new equilibrium value; especially those mountain tops whose grasslands transiently fluctuated out of existence remain poor in alpine bird species today.

THE CORRELATION BETWEEN AREA AND SPECIES DIVERSITY

The most familiar examples of the correlation between area and species diversity come from biogeographic studies of oceanic islands. On such islands species diversity is often found to increase with island area in such a way as to define an approximately linear log-log relation with a slope around 0,3. Alternatively, if one compares species diversity on census plots of different areas within a continuous expanse of habitat, one still finds an increasing species diversity with area, but the log-log slope is less (often 0,10-0,15). Finally, qualitatively similar patterns apply to virtual islands of habitat separated from each other by alien habitats that are inhospitable to their characteristic species. These virtual islands include mountains rising out of the lowlands, forest patches in the middle of savanna, savanna patches in the middle of forest, caves and lakes. Naturally, as with all other correlates of species diversity, the area effect is most apparent in comparison of study sites differing in area but otherwise similar, and may be overridden by differences in habitat or in other factors.

To illustrate the species-area relation, I shall mention some examples drawn from 'inverted islands': ie aquatic habitats separated from each other by land or by alien aquatic habitats. Barbour and Brown (1974) found fish species diversity in 70 lakes throughout the world to increase with lake surface area. Lassen (1975) documented that diversity of fresh water snails in Danish lakes increased with lake area (and also with lake productivity). Diversity of lagoon fishes increased with lagoon area in the Great Lakes region of North America (Mahon and Balon 1977). The number of coastal marine fish species in 13 bays and estuaries along the coast of California increased with bay area, yielding a log-log slope of 0,21 (Horn and Allen 1976). Sepkoski and Rex (1974) studied the distribution of 79 species of fresh-water mussels (family Unionidae) in 49 North American rivers, and found area of drainage basins to be the best predictor of mussel species number.

This correlation between area and species diversity is among the most obvious facts of island biogeography. Unfortunately, its interpretation is not at all obvious, and here again anyone expecting a simple explanation is in for a disappointment. There appear to me to be at least six different reasons for this correlation; two of these reasons represent direct affects of the area itself:

Territory sizes of animals

If an island or habitat patch is smaller than the territory required by a single breeding pair of a species, then the species can obviously not persist on the island or patch. Numerous species, of course, do not have a social system based on exclusive pair territories but live in flocks, and for such species the relevant consideration is the minimum area required by the flock. Thus, for a given overall population density, social species have larger minimum area requirements than solitary species with individual territories.

Extinction rates

An area sufficient for one breeding pair is unlikely to maintain an isolated 'population' of a species for long. Populations fluctuate, are exposed to risk of extinction, and several studies have shown that the probability of extinction is inversely related to population size (eg MacArthur and Wilson 1967; Richter-Dyn and Goel 1972). These include studies of bird populations on the California Channel Islands in the present century (Figure 7), of small mammals isolated on western North American mountain tops since the Pleistocene (Brown 1971), and of birds of Brazilian wood lots during the last 150 years (data of Willis, analyzed by Terborgh and Winter 1980). Apart from these considerations of short-term extinction rates in ecological time, there remains the question what population size is genetically viable over the long run in evolutionary time. It has been suggested, and debated, that an effective breeding population of less than a few hundred individuals of a plant or animal risks eventual extinction due to inbreeding (see chapters in Soulé and Wilcox 1980).

Because (all other things being equal) population size increases with area, extinction rates decrease with area. Hence one expects that at equilibrium an instantaneous survey will find more species in a large area than in a small area. By the same token, the probability that a given species will be found resident on an island or habitat patch at a particular time increases with the area of the island or patch.

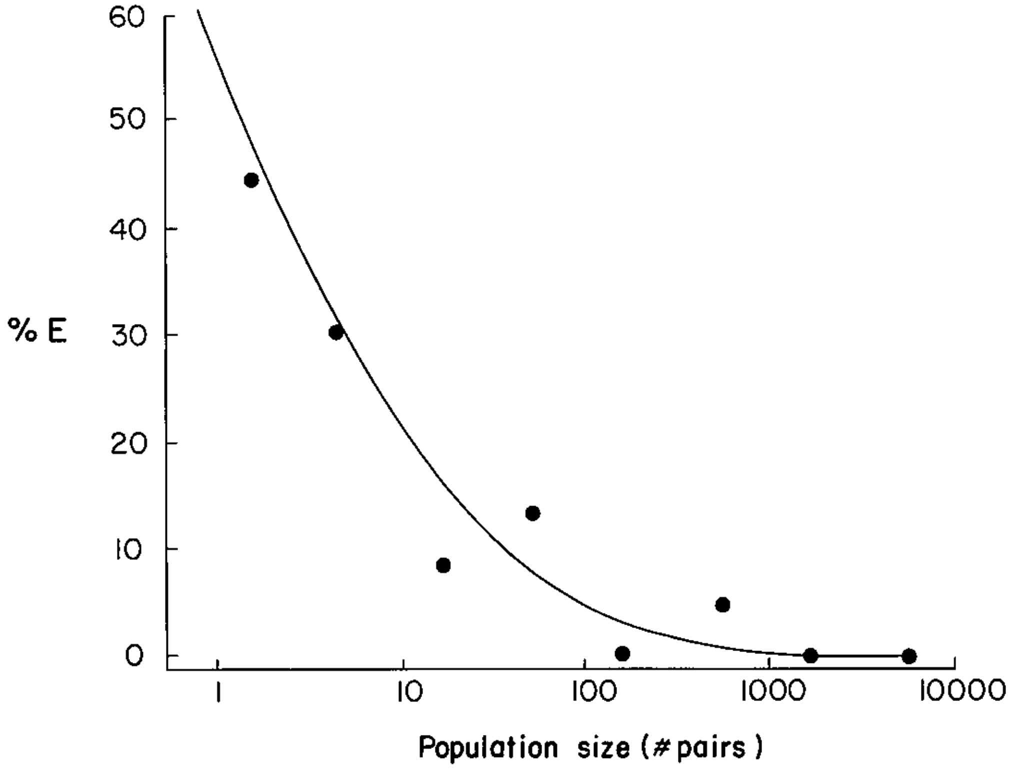


Figure 7. Risk of extinction as a function of population size, among breeding land bird populations of the California Channel Islands. All breeding bird populations of the island were divided into size classes by number of breeding pairs on an island (abscissa). The percentage of populations in each class that became extinct in the course of recent bird surveys is plotted on the ordinate ('%E'). Note that small populations are much more prone to extinction than are large populations. From Jones and Diamond (1976).

Habitat specialists

No area is completely homogeneous. Habitat diversity increases with area. To take an extreme example, we cannot look to find high mountains, deep lakes, and broad rivers on an oceanic island a few hectares in extent. Many species are restricted to mountains, rivers, and lakes, as well as to other specialized habitats such as swamps, grasslands, and savannas. Hence, the larger the area that we sample the larger the range of habitats sampled, the greater will be the variety of species of specialized habitats that we encounter. To mention two of the innumerable possible examples, both drawn from the New Guinea lowland avifauna, the twelve-wired bird of paradise, *Selucides melanoleuca*, is confined to sago swamps; the broad-billed fairy wren, *Chenorhamphus greyi*, is characteristic of tree-falls in primary rainforest. Because the habitat of these two species occupies such a small fraction of the land, their overall population densities are low, and they are virtually absent even from large land-bridge islands that had Pleistocene connections to New Guinea, as their populations even on the largest of these islands were too small to persist for the 10 000 years since the end of the Pleistocene.

Use of multiple habitats

I have just illustrated that the correlation of habitat diversity with area is important in part because habitat diversity means more species of specialized habitat. Habitat diversity is also important for a second reason: some species require several different habitats to complete their life cycle or seasonal cycle. For example, sex and age classes of birds of paradise are differentially distributed with respect to altitude, adult males typically being at higher elevations, adult females at lower elevations, immatures at the lowest and occasionally at the highest elevations. A mountain preserve that provided optimal habitat for breeding adults could doom birds of paradise by not including the altitudinal bands required by immatures. Especially among species dependent on seasonal or patchy food supplies, habitat diversity is important to guarantee food supplies at all times of year. Such considerations are conspicuous with respect to nomadic specialists on nectar and fruit and their associated carnivores. The seasonal movements in Serengeti National Park are a familiar example. Another example is provided by some nectar-feeding parrot species of New Guinea, which breed in the highlands in the wet season and spend the dry season in the lowlands.

Ping-ponging populations

As mentioned under item 2 above, populations are exposed to the risk of extinction. Some species are restricted to large habitat patches and persist there indefinitely, but other species have populations which are simultaneously going extinct and becoming re-established by immigration on many habitat patches. Provided that there are many such patches available, the populations of these species can be in continual state of flux among the patches, like ping-pong balls, and it is unlikely that all populations would disappear simultaneously. However, if there is a small area of habitat and hence few available patches, the risk of simultaneous extinction by chance in all available patches becomes significant. As an example, Figure 8 illustrates the distribution of the warbler *Gerygone flavolateralis* on the islands of the New Hebrides Archipelago in the southwest Pacific Ocean, in the years 1926-27 and 1969-1975. This warbler inhabited eight islands in 1926-27, three islands in 1969-75, but only a single island was inhabited during both periods. Evidently, populations of this species rapidly disappear and are rapidly re-established. This is a safe strategy in a large archipelago with dozens of islands, but an unsafe strategy in a small archipelago of a few islands.

Trophic cascades

I note finally that area effects resulting in disappearance of some species may produce cascading effects on other species. One example comes from

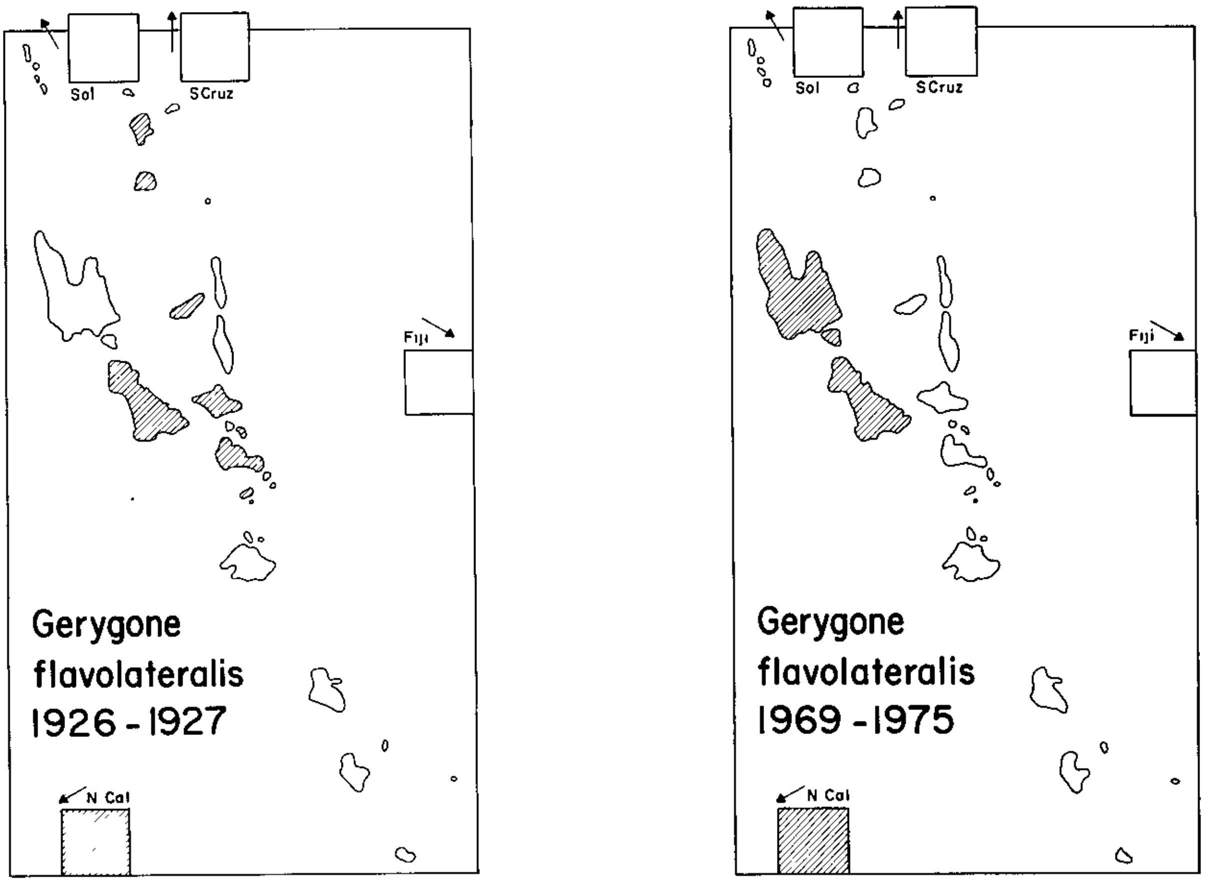


Figure 8. Map of the New Hebrides archipelago in the southwest Pacific Ocean, showing the distribution of the warbler Gerygone flavolateralis in 1926-27 (left) and in 1969-75 (right). In the intervening years this warbler disappeared on seven of the eight islands that it inhabited in 1926-27, persisted on one of these eight islands, and colonized two new islands. From Diamond and Marshall (1977).

Barro Colorado Island, a hilltop in Panama that became an island early in this century when construction of the Panama Canal flooded adjacent valleys. Since its isolation Barro Colorado has lost numerous species of birds that nest on or near the ground (Willis 1974; Terborgh and Winter 1980). The reason appears to be that the area of Barro Colorado in isolation (17 km^2) is too small to sustain large predators such as jaguars, pumas, and harpy eagles. Consequently, medium-sized mammals that were formerly the prey of these large predators, such as sloths, monkeys, agoutis, and peccaries, have increased greatly in abundance and have contributed to the reduction of ground-dwelling birds by eating eggs and nestlings. A further situation in which we should be alert to trophic cascade effects involves decimation of large avian frugivores, which are often prime targets for hunters and among the first bird species to disappear in tropical areas after use of shotguns becomes widespread.

Some tropical tree species require for germination of their fruits that the fruits pass through the digestive tract of a frugivore. Hence we should be concerned that decimation of frugivores may affect the propagation of their associated fruit trees. A speculative example is the suggestion that failure of recruitment in the tree Calvaria major on the island of Mauritius since the eighteenth century is correlated with extermination of the dodo, a large bird presumed frugivorous. This suggestion is supported by successful germination of seeds of this tree following passage through the gut of another bird species not native to Mauritius (Owadally and Temple 1979).

One remaining point about effects of area, and a point of special importance to reserve managers, is that area has differential effects on species. Some species can persist in small patches, while others require large patches (eg Diamond 1972; Willis 1974; Terborgh 1974; Diamond 1976b; Terborgh and Winter 1980).

Population density is one of the main reasons for this relation: the lower the density of a species, the larger an area will it require to maintain a viable population. To cite one of many examples, the land-bridge islands that were connected to New Guinea during the Pleistocene include several whose area exceeds 2600 km^2, an area achieved by few of the world's tropical rainforest national parks. Since these islands were isolated from New Guinea at the end of the Pleistocene, bird populations have been disappearing on them, and some species have fared much worse than others. At the one extreme, the New Guinea harpy eagle (Harpyopsis novaeguineae), the shovel-billed kingfisher (Clytoceyx rex), and the golden bowerbird (Sericulus aureus) have persisted on not a single land-bridge island, not even the largest, whose area is 7800 km^2. At the other extreme, the frilled monarch (Monarcha telescophthalmus) has survived on every single land-bridge island larger than 260 km^2. This differential survival on land-bridge islands since the Pleistocene is a model for the differential survival that we are now observing and may expect in the future in our natural reserves, where man himself has severed the 'land-bridges' of natural habitat by his agricultural, logging, and mining activities. These actual land-bridge studies can be used as a guide to predict which species will be most prone to disappear as isolated populations in natural reserves.

Lessons in management: three case studies

I conclude with three case studies to bridge the gap between these discussions of species diversity drawn from the ecological research literature and the practical problems faced by reserve managers. Each of these case studies involves catastrophic losses of species diversity explicable in terms of the factors discussed in this paper.

The first case study is drawn from the New Zealand region. Isolated by the thousand-mile-wide Tasman Sea from Australia, New Zealand evolved a unique avifauna. At least 34 bird species, including all the moas, disappeared following the first human colonization of New Zealand, that by Polynesians in the first millennium after Christ. Following the arrival of Europeans in the early nineteenth century, nearly two dozen more species have become extinct, rare, or confined to offshore islands. Correlated with the extinctions, exotic bird species introduced from Europe have become established in New Zealand, are now overwhelmingly dominant in open habitats, and account for a significant fraction of all bird individuals even in climax forest. While the reasons for the post-European extinctions and introductions have been subject to much debate, a dominant role of predation and altered habitat structure mediated by mammals introduced by Europeans is strongly suggested by comparison of the New Zealand mainland with an offshore island, Little Barrier Island (Diamond and Veitch 1980). Uniquely among the large offshore islands near New Zealand, Little Barrier is entirely without introduced mammalian browsers, mustelids, and European rats. One native New Zealand bird species that was exterminated from the New Zealand mainland following European colonization now survives only on Little Barrier; the native bird species common to Little Barrier and the New Zealand mainland have very different relative abundances on island and mainland; and introduced European bird species that arrive on Little Barrier are unable to establish themselves in the forest. Detailed consideration of these differences suggest the following interpretation of how much of New Zealand's unique avifauna became replaced by introduced species: introduced mammalian predators decimated native bird populations that had evolved in an environment free of non-volant mammals; mammalian browsers opened the forest structure and reduced the diversity of food plants important to native birds; finally, with the native avifauna reduced by these direct and indirect effects of introduced mammals, European bird species that would have been excluded from forest with an intact native avifauna were able to invade forest.

The second example, that of Barro Colorado Island, has already been discussed in this paper. In the past 60 years since it became an island, Barro Colorado has already lost at least 10 percent of its forest dwelling bird species, as well as its top predators. This island constitutes an exceptionally well-documented example to illustrate that, even on the short time scale of human lifetime, a small tropical rainforest reserve (17 km^2), no matter how completely protected, is unable to retain anything approaching an intact rainforest bird community.

The final example comes from the New Guinea land-bridge islands. About 10 000 years ago, just before the Pleistocene land bridges were severed, these islands were part of an enlarged New Guinea. One can approximate their number of lowland bird species at that time by the lowland species on modern New Guinea (Diamond 1972), or, better, by the number in an equivalent area on modern New Guinea (Diamond and Gilpin 1982). Today, even the largest of these islands, with an area of 7800 km^2, has lost about half of its original calculated avifauna. On land-bridge islands smaller than 130 km^2, virtually the entire original avifauna has disappeared and been replaced by overwater colonists. The exterminations that took some unknown fraction of 10 000 years on a 7800 km^2 island are expected to occur more rapidly, the smaller the island area. These and other land-bridge islands are instances in which nature, through the post-Pleistocene rise in sea levels, created natural reserves, and then demonstrated that in the long run even the largest of these reserves was inadequate and the smaller ones totally useless for conservation purposes.

It is hoped that such studies of how long different species actually survive on islands of different areas may motivate reserve planners to seek reserves that will provide adequate areas rather than futile token gestures, and will provide biologists with the detailed factual arguments essential for convincing political leaders that small is not enough.

SUMMARY

A goal of reserve management is to maximize the number of species whose populations can sustain themselves within reserve boundaries and that would be threatened with extinction in the absence of reserves. Hence this chapter reviews environmental determinants of species diversity.

Species diversity increases with complexity of habitat structure, habitat diversity, and area; decreases with isolation; is maximal at intermediate values of predation pressure, disturbance, and productivity; and is affected by history.

The correlation of species diversity with area has many causes. These include: territory size requirements of animals; the inverse relation between population size and risk of extinction; the correlation between habitat diversity and area, because many species are habitat specialists and others require multiple habitats; shifting population patches; and trophic cascades, by which extinctions of some species resulting from any of these causes tends to lead to extinctions of further species.

Extinctions among birds of New Zealand, Barro Colorado Island, and New Guinea land-bridge islands illustrate catastrophic losses of species diversity understandable in these terms.

CHAPTER 6 SELECTING TERRESTRIAL HABITATS FOR CONSERVATION

Kenton R Miller

INTRODUCTION

The management of selected wild and semi-wild areas for conservation purposes is recognized to form an element of overall conservation and ecologically sound development. The record of national parks and other types of reserves throughout the world suggests that protected areas form a viable approach to the in situ maintenance of species and ecosystems. While the national park is the most widely employed type of protected area, others have been developed to provide the capacity to meet a broad spectrum of objectives where careful management of wild ecosystems is required. While considerable progress has been made in the technology of area planning and management during the past 20 years, procedures for the selection of areas have only recently been explored in a scientific way. Habitats key to the maintenance of living wild resources will be irreversibly altered in the course of the two coming decades. The urgent identification and appropriate management will require the cooperative efforts of scientists and managers to develop the necessary knowledge and techniques.

BACKGROUND

The establishment of Yellowstone National Park in the USA in 1872 is considered generally to mark the beginning of conservation area management in modern times. The area was '...reserved and withdrawn from settlement, occupancy or sale ... and dedicated and set apart as a public park or pleasuring-ground for the benefit and enjoyment of the people ...' (US Department of the Interior 1933). Shortly thereafter, other countries established conservation areas dedicated to similar purposes, including Canada in 1885, New Zealand in 1894, and Australia, Mexico and South Africa in 1898 (IUCN 1975).

During the 20th Century, conservation areas have been established worldwide for an array of purposes, reflecting variations of culture and language and the relationship between peoples and their natural resources. In a review of the nomenclature in use at the time of the First World Conference on National Parks, held in Seattle, USA, in 1962, Brockman noted over 100 different names for conservation areas (Brockman 1962).

In the early decades, the purposes of conservation areas were expected to be achieved principally by the application of regulations. Protection and control of wild plants and animals and of human visitors were the main ways by which the administration of these areas was to be exercised. As with other natural resources, however, concepts for the administration of conservation areas evolved, focusing evermore explicitly upon goals and means for attaining them.

In contrast to the administration of conservation areas by regulations, the management of nature involves the articulation of specific goals, the design and comparison of alternative means, the selection of the best means according to established criteria, and the implementation of the chosen means in the field. The line of action to be followed in addressing a specified goal may require a small or large degree of manipulation of species or habitats, the construction of roads or buildings, and the reduction or expansion of visitation, research or other activities.

Parallel to the changing attitudes and approaches to the management of nature within the boundaries of conservation areas, there is a growing tendency to relate nature conservation to the surrounding regional context. Increasing rates of change in the use of land for more intensive agriculture and domestic animal husbandry, expanding urban centres and infrastructure and growing human populations are among the factors which bring national parks and other reserves directly into contact with cultured landscapes.

While to some this is a time of conflict, confrontation and litigation between two sides: the one espousing nature preservation and the other development of natural resources to meet 'basic human needs', the need for an integral approach to 'development <u>with</u> conservation' has become apparent to many. A major step forward was taken by Maurice Strong, the first Executive Director of the United Nations Environment Programme. Ecodevelopment is based upon the concept that ... 'Development at regional and local levels, should be consistent with the potentials of the area involved, with attention given to the adequate and rational use of the natural resources, and to the application of the technological styles (innovation and assimilation) and organizational forms that respect the natural ecosystems and local socio-cultural patterns' (UNEP 1976).

The 1970's brought an awareness of the interdependence of humans and the environment, of ecological systems, of the uniqueness of planet Earth and the urgency of caring for the thin living mantle - the biosphere. Some of the often myopic attention given by conservationists to individual species and sites was shifted to more-overriding issues. The fact that more species were destined to extinction in the 80's and 90's than at any time since the Ice Ages became a cause for growing concern (Myers 1979). Problems, such as the clearing of rainforests, destruction of mangroves, harvesting of krill, acid rainfall and desertification could no longer be addressed with tactical tools alone; strategic orientation was required.

The World Conservation Strategy (WCS) was prepared by the International Union for Conservation of Nature and Natural Resources (IUCN) with the support of the World Wildlife Fund (WWF) and the United Nations Environment Programme (UNEP), and the endorsement of the Food and Agriculture Organization of the United Nations (FAO) and the United Nations Educational, Scientific and Cultural Organization (UNESCO). Scientists, conservationists, resource managers, and political leaders from around the world participated in its drafting. The WCS provides a framework for selecting objectives, choosing steps for action, monitoring the status of living natural resources and preparing programmes of work and related budgets. The strategic approach recognizes the importance of tactical action to protect individual species and sites, and provides a rationale which serves to relate systematically the conservation of nature and human social and economic well-being. It related conservation to the need for expanding the welfare of this generation while maintaining open options for those to come (IUCN 1980a).

Through the explicit presentation of objectives, conservation can be shown to form an integral part of ecologically sustainable development. By prying open the term 'conservation', and by explaining the linkages between human needs and natural resources, eco-development can take on practical meaning. An expanded set of conservation objectives has been suggested (Miller 1974, 1975, 1980; FAO 1974):

1. Maintain large areas as representative samples of each major biological region of the nation in its natural unaltered state to insure the continuity of evolutionary processes, including animal migration and gene flow.

2. Maintain examples of the different characteristics of each type of natural community, landscape and land form to protect the representative as well as the unique diversity of the nation, particularly to insure the role of natural diversity in the regulation of the environment.

3. Maintain all genetic materials as elements of natural communities, and avoid the loss of plant and animal species.

4. Provide facilities and opportunities in natural areas for purposes of formal and informal education, research, and the study and monitoring of the environment.

5. Maintain and manage watersheds to insure an adequate quality and flow of fresh water.

6. Control and avoid erosion and sedimentation, especially where they are directly related to down-stream investments which depend upon water for transportation, irrigation, agriculture, fisheries, and recreation, and for the protection of natural areas.

7. Maintain and manage fish and wildlife resources for their vital role in environmental regulation, for the production of protein, and as the base for industrial, sport and recreational activities.

8. Provide opportunities for healthy and constructive outdoor recreation for local residents and foreign visitors, and to serve as poles for tourism development based upon the outstanding natural and cultural characteristics of the nation.

9. Manage and improve timber resources for their role in environmental regulation and to provide a sustainable production of wood products for the construction of housing and other uses of high national priority.

10. Protect and make available all cultural, historic and archaeological objects, structures and sites for public visitation and research purposes as elements of the cultural heritage of the nation.

11. Protect and manage scenic resources to insure the quality of the environment near towns and cities, highways and rivers, and surrounding recreation and tourism areas.

12. Maintain and manage vast areas of land under flexible land-use methods, which conserve natural processes to insure open options for future changes in land use as well as the incorporation of new technologies, to meet new human requirements, and to initiate new conservation practices as research makes them available.

13. Finally, focus and organize all activities to support the integrated development of rural lands, giving particular attention to the conservation and utilization of marginal areas and to the provision of stable rural employment opportunities.

A theoretical framework for the management of conservation areas has been proposed as shown in Table 6. In the matrix, the objectives of conservation are related to various categories of management. The model suggests that, given an objective, several alternative approaches to management may be followed. From a technical standpoint, the pursuit of each objective usually may be combined compatibly with others, depending upon the biophysical relationships among variables. The model also suggests that if the entire array of objectives is to be sought, then several types or categories of conservation areas are required.

The Commission on National Parks and Protected Areas (CNPPA) of IUCN developed a policy paper regarding the classification of 'protected areas' (IUCN 1978b). Individual areas dedicated to conservation purposes are classified by the stated and observed objectives of management. Ten categories are described and defined to serve as a guide for orienting the choice of management approach according to the objectives being pursued. The emphasis thereby is placed upon the ends; the means are to be designed and implemented to meet those ends.

Methods and techniques have been developed for planning conservation areas. Strategic and tactical considerations are organized by hierarchical levels and all activities are oriented to explicit objectives. National-level strategy plans provide a framework with which priorities for action can be determined. Plans for systems of protected areas orient the selection, management and development of national parks and other protected areas. Plans for the management of particular areas give the framework for action at the conservation unit level, providing details for key management programmes including resource management, protection, research, public use, among others. Finally, the development of physical facilities and institutional and human capacity is oriented by detailed plans designed to fit within the more strategic statements and meet higher-level goals.

The body of tools and procedures for conservation action, what can be called correctly 'the technology of conservation', is considerable if barely commensurate with the tasks on the agenda for the 1980's. However, increasing the knowledge upon which decisions must be based, 'the science of conservation', is receiving explicit attention only recently. In the volume entitled 'Conservation Biology', based upon the papers presented at the Conservation Biology Conference held at the University of California, San Diego and the San Diego Wild Animal Park in September 1978, important contributions are made to support the selection, management and development of areas for conservation purposes (Soulé and Wilcox 1980).

Thus, the emergence of conservation management signifies the systematic and orderly preservation, protection, utilization and manipulation of nature towards stated goals. The initiation of conservation biology signals the search for, and development of, information and principles to orient and evaluate management.

PRINCIPLES FOR THE SELECTION OF HABITATS FOR CONSERVATION

The selection of habitats for conservation can be guided by twelve principles and procedures which integrate ecological, social, political and economic aspects. Areas are identified and defined which have the biological and physical capacity to meet these objectives. Then physical facilities, institutional and monitoring aspects are considered.

First, macro-scale biogeographic mapping systems, such as that proposed by Udvardy (1975), are used to establish a general framework for the characteristics of a network of protected areas to cover the representative biological and physical features of the country (or region or continent). Locally prepared maps of vegetation, biogeography, forest types and geomorphology guide micro-scale choices within biogeographic provinces. Later, once specific protected areas are proposed, both macro and micro-scale classification systems serve to test the coverage of the network and to catalogue protected areas.

A first approximation of the content of each prospective protected area is stated, in terms of key species and their habitat requirements, migrations and successional patterns. Ecological processes are then added to ensure protection of water movements, plant succession and nutrient and energy flows. The parameters for environmental stability are checked to ensure maximum possible continuity, free of water and air contamination, chemical pesticides, conflicting uses and the exclusion of requirements of the ecosystems to be protected.

Genetic diversity factors are then considered. The range of species, identification of sub-populations and variation serve to suggest further definition of areas. Questions of short-term fitness, long-term adaptation and the continued opportunity for evolution of species are analyzed (Soulé 1980). More extensive areas are required by species which are thinly dispersed, such as some of the large herbivores, larger carnivores, scavengers and trees. Inbreeding depressions can possibly be avoided where populations of these and other species are maintained at levels greater than 500 individuals (Franklin 1980).

Multiple reserves, giving several protected areas will be required for each biological province. For genetic reasons, it is preferable to maintain several populations of particular species. This reduces the chances of accidental extinction due to disease or other catastrophe and permits opportunities for local adaptation which will increase chances for ultimate survival (Franklin 1980). Multiple reserves are also necessary for the maintenance of biological diversity. A range of situations can be incorporated into the network by including areas which are undisturbed, semi-wild and altered. Furthermore, plant successional stages are critical for inclusion, particularly in relation to species which have patchy distributions (Diamond 1980). Multiple reserves provide for the transitory nature of patches (Foster 1980), the replication needed for research and the capacity in the network to survive large natural or man-induced disturbances.

'Benign neglect' is not sufficient to insure the maintenance of diversity. Various types and amounts of manipulation of habitats will generally be required to hold or foster succession. With a series of reserves within each biogeographic province, some areas can be maintained in their undisturbed, natural dynamic state while others are allowed or encouraged to evolve more rapidly, thereby covering the various options considered to be desirable.

The size of each individual protected area will depend upon the species to be included, the space involved in meeting the species' requirements, and the ecological processes which need to be provided specially managed to insure their permanent contribution to the area. Basically whole ecosystems should be included in the protected area, with sufficient territory to include a large number of the least-dense species. Large undisturbed reserves in the tropics may require from 200 000 to one million or more hectares, while the multiple smaller undisturbed and altered areas may require a minimum of 50 000 to 100 000 hectares.

The shape of protected areas is critical in avoiding insularization effects, the ideal reserve being relatively round. Serrations, peninsulas and salients tend to lose species representative of the undisturbed core. They may be replaced by species from the zone external to the reserve. Evolved predator-prey relationships are disrupted and local extinctions occur. Therefore, within any biological province, protected areas should be large in size, round in shape, manifold in numbers and dispersed. Such a network of reserves will focus specifically upon the first three objectives noted above for conservation areas: the maintenance of representative samples, ecological diversity and genetic resources.

After covering these objectives, others can be considered. Ideally, several categories of conservation areas are analyzed and selected simultaneously as part of an integrated planning exercise. Often, particular prospective protected areas can be designed to yield several kinds of benefits for little additional cost or territory. Society can perceive itself the recipient of a wide array of goods and services fromits parks and reserves. That is, from the network of protected areas, of the several categories taken together, many or all of the suggested objectives of conservation for eco-development can be met. This decision can be oriented by Table 6. Within any given context of natural resources, some objectives (outputs) can be sought compatibly while others compete for resources

Table 6. Decision making guide to the alternative categories for the management of wildlands to support ecodevelopment

OBJECTIVES FOR CONSERVATION AND DEVELOPMENT	ALTERNATIVE MANAGEMENT CATEGORIES											
	A	B	C	D	E	F	G	H	I	J	K	L
Maintain sample ecosystems in natural state	(1)	(1)	2	(1)	-	2	4	4	4	4	4	4
Maintain ecological diversity and environmental regulation	(1)	(1)	(1)	(1)	(1)	(1)	(3)	(3)	(3)	(3)	3	3
Conserve genetic resources	(1)	(1)	3	(1)	-	3	3	3	3	3	3	2
Provide education, research and environmental monitoring	(2)	(2)	(1)	(2)	-	2	4	4	2	4	2	2
Conserve production of water from watersheds	3	3	3	3	-	(2)	3	(1)	3	3	4	(1)
Control erosion, sediment and protect downstream investments	3	3	3	3	-	(1)	3	(1)	3	3	4	(1)
Produce protein from wildlife: sport hunting and fishing	-	-	-	-	-	(2)	(1)	-	-	-	-	2
Provide for recreation and tourism	(2)	4	-	4	-	(2)	2	-	(1)	3	4	2
Produce timber on a sustained yield basis	-	-	-	-	-	(2)	-	4	-	-	-	2
Protect sites and objects of cultural, historical, archaeological heritage	(1)	4	-	-	-	4	-	-	4	-	(1)	2
Protect scenic beauty and green-belts	(1)	(1)	3	3	-	3	3	3	(1)	(1)	4	3
Maintain open options through multi-purpose management	-	-	-	-	(1)	(1)	-	3	3	3	-	(1)
Support rural development through rational use of marginal lands and provision of suitable employment opportunities	(3)	(3)	(3)	(3)	(4)	(1)	(1)	(3)	(1)	(3)	(3)	(1)

Key

A = National Park B = Natural Monument C = Scientific or biological reserve D = Wildlife sanctuary
E = Resource Reserve F = National Forest G = Game reserves, farms and ranches H = Protection zones
I = Recreation areas J = Scenic easements and rights of way K = Cultural monuments L = Watershed programmes or river valley corporations

1 : The objective dominates the management of the entire area
2 : The objective dominates portions of the area through "zoning"
3 : The objective is accomplished throughout portions or all of the area, in association with other management objectives
4 : The objective may or may not be applicable depending upon treatment of other management objectives, and upon characteristics of other resources
(): Major purposes for employing management systems
- : Not applicable

Note: In the case of the watershed programmes or river valley corporations, the areas normally include towns, agriculture and other land-uses.

Sources: Miller, Kenton R 1975. Guidelines for the Management and Development of National Parks and Reserves in the American Humid Tropics. In: The Use of Ecological Guidelines for Development in the American Humid Tropics. Proceedings of IUCN Meeting, Caracas, 1974.

(inputs). The reasons for complementarity or competitiveness are biological, physical and technological; they can be described and analyzed for each area. The prospective protected areas will then be modified in their size and shape to incorporate additional lands for watersheds, recreation resources, scenic features, archaeological sites, timber or range resources, erosion-prone areas and sites important for environmental monitoring.

Management plans are prepared for each protected area. Details are elaborated for specific objectives, zoning and boundaries, action programmes, man-made developments and the scheduling of activities. Based upon the management plan, operational and budgetary documents are prepared and implementation takes place in an orderly fashion (Deshler 1973; Moseley, Thelen and Miller 1974; Miller 1980).

A draft management plan provides the model for examining the feasibility of a prospective protected area. Biologists, economists, community leaders and general conservationists and interest groups can challenge the plan according to their various criteria and perspectives, and analyze the capability of the area, were it to be managed and developed as stated. Conflicts can be defined and classified through dialogue and re-design. Mistakes can be avoided or the damage minimized through the 'simulation' of problems and threats prior to actual implementation. Plans are then accepted or rejected by the political and legal mechanisms of the sovereign nation. They may also involve a proposal for association with the World Heritage Convention (UNESCO 1972), the world-wide network of Biosphere Reserves of the Man and Biosphere Programme (UNESCO 1973, 1974; IUCN 1978a), the UN List of Protected Areas (ECOSOC 1959; IUCN 1980b), the Global Environmental Monitoring System (UNEP 1975) and other international programmes.

To these biological and physical resources must then be added the necessary facilities and installations in support of the activities to be realized in the reserves. Man-made 'additives' typically include roads, trails, ranger stations, research laboratories, dormitories, communications and monitoring instrumentation. Other facilities will be required to meet the needs of recreation, tourism, education and the other objectives which may be included in the management of particular reserves. The prospective protected areas may have to be increased in size and altered in shape to accommodate these installations.

Given a set of proposed protected areas which have the planned biological and physical capacity and necessary installations to conserve nature and possibly meet other objectives as well, concerns for the perpetuity of the reserves arise. Future respect for and integrity of the areas will depend upon the understanding and support of society. This usually involves broad participation in planning and clear perceptions of the benefits to be received. It requires an expanded concept of the Yellowstone goals, (USA Department of the Interior 1933) so that 'the benefit and enjoyment of the people' means not only direct on-site visitation, or abstract pleasure from the idea of wilderness, but also an appreciation for water resources; crop and pharmaceutical genetic materials; environmental regulation, fishery, wood and wild meat production; and the importance of research, monitoring and education in wild areas. Perpetuity also depends upon the development of professional management organizations, with strong legal commitments and financial backing of governments.

Finally, a monitoring programme is established for each protected area, ideally prior to the implementation stage. Monitoring can provide several functions including the development of base-line information for the ecosystems, systematic and periodic evaluation of the status of the ecosystems, insurance that the size, shape and boundaries of the area are appropriate, and provision of information to management staff on the response of nature to current activities and practices.

EXAMPLES FROM LATIN AMERICA AND THE CARIBBEAN

Field experience in Latin America and the Caribbean has demonstrated the usefulness and importance (and perhaps the necessity) of linking (a) the process of selection of habitats for conservation, (b) the process of planning the management for the areas, and (c) the training of local managers and scientists in the knowledge and methods of selection, management and planning.

Management plans have been prepared for more than 80 protected areas in Latin America and the Caribbean since the first attempts in 1962. The majority of these plans have been for the national parks category, including Volcan Poas in Costa Rica (Boza 1968) and Torres del Paine in Chile (FAO 1974). While the earlier plans were made by individual experts, the more recent work in the Caribbean, Central America, Chile, Brazil and Ecuador has been realized by teams of local professionals, usually including area managers. Some experience has been accumulated in the planning of the wildlife reserves category, especially the case of Pampa Galeras National Vicuna Reserve in Peru (Direccion General Forestal y de Fauna 1977), and several current exercises in Costa Rica.

Planning methods and procedures have been synthesized into principles and flexible methodology prepared (Miller 1980). In this approach, which is deduced from field experience, the first step of management zoning is to 'identify areas where the natural and cultural resources relate to the individual park objectives', the first three such kinds of area are: '(a) the representative sample of biological provinces; (b) the ecological transitions, lake and river shores, swamps, coastlines and places related to ecological diversity; (c) the places related to endemic, unique or rare species and their habitats; ...' (Miller 1980). In virtually all of the protected areas which have been planned, a major portion of the area has been assigned as an 'Intangible or scientific zone' - dedicated primarily to those objectives related to scientific research, environmental monitoring, ecosystem and genetic resource protection, and specifically excluded from this zone are roads, motorized vehicles and tourism. Alternatively, a Primitive Zone is established which also excludes roads and vehicles and is dedicated to preserve the natural environment; however, this zone does provide for environmental interpretation and education and primitive-style recreation.

Training workshops for university professors of wildland management, protected area managers and scientists have been held under field conditions throughout the region. Each workshop covered the aspects of selection, management and planning, and included field team exercises to plan actual areas.

The selection of a network of areas to cover a nation's biogeographic provinces or life zones involves a complex exercise which integrates all of the steps suggested above (in the previous section of this paper). Starting with an ecological map, a study team of scientists and managers typically examines aerial photographs, land use studies and other literature to determine the actual status of wild and semi-wild lands. Existing protected areas are examined and evaluated to test whether in fact they cover a representative sample. New areas are sought in the field which are capable of covering ecosystem types not currently protected. Plans of management are outlined for the new areas to be proposed. The systems-planning methodology has evolved through direct field trials in Peru, Chile, Ecuador and Brazil (Miller 1980).

In Peru during the mid-1960's, a conceptual framework for the selection of protected areas was prepared prior to the establishment of parks and reserves. The fundamental idea was to begin with a large wild area in each of the three principal biomes of the country: costa, sierra and selva. This criterion guided the selection and establishment of Paracas National Reserve, Huascaran and Manu National Parks. Subsequently, some 15 additional protected areas have been established to cover various life zones and unique areas in the country.

By 1973, Chile had a network of 50 national parks. A cooperative study was initiated between the National Forestry Corporation and FAO to evaluate the network and suggest the modifications necessary to insure adequate coverage of the nation's extremely diverse life zones. Following two years of intensive field work, the team suggested that efforts be concentrated on 17 major parks. Three new parks were proposed, several areas were consolidated to form larger units, and many areas were suggested for transfer to other management categories which in some cases implied assignment to other public agencies (Thelen and Miller 1975).

The experience of Ecuador during the 1974-76 period followed four main steps: national inventory of remaining wildlands; study of alternative management categories; elaboration of a preliminary strategy; and the integration of the strategy into the national planning process. Following the design of a conceptual framework and methodology for the study, a seminar was held for the field managers and scientists who would participate in the study. Several workshop exercises were held to illustrate methods and procedures and stimulate dialogue among office and field personnel and individuals of various participating institutions. Ninety protected areas were nominated under four categories: national park, ecological reserve, fauna production reserve and national recreation area. These nominations were screened against criteria related to the importance of the resources, potential use and administrative factors. Areas were also screened to insure coverage of the nation's six major biotic provinces (IUCN 1974) and marine and coastal environments (Ray 1975), to provide recreation and environmental education services to the three major cities and to cover the four management categories to insure that potentially all objectives are met. A 'minimum system of outstanding wildlands' suggests nine areas for highest priority implementation; 29 additional sites are recommended for action subsequently (Putney 1974, 1976).

The Brazilian Institute for Forestry Development (IBDF) and the national FAO project, with support from the Brazilian Foundation for Nature Conservation (FBCN), initiated work on a system of national parks in 1975 in response to the mandates of the Second National Development Plan (1975-1979) and the POLAMAZONIA decree. The conservation problems of the entire nation were reviewed and a conceptual framework was given for a major effort to examine the Amazon basin as a single unit (Wetterberg 1976a). A second study focused on the Amazon and Orinocan region including neighbouring countries (Wetterberg 1976b). Six objectives guided the work:

1. To synthesize the published works of various Amazon specialists into a common format from which biologically significant nature conservation priorities can be tentatively identified.

2. To identify and locate the existing and planned nature conservation units in the Amazon.

3. To analyze the potential compatibility or incompatibilities between the Brazilian POLAMAZONIA priority development poles and the preservation of biologically significant areas.

4. To propose a general outline of an Amazon nature conservation programme which gives due consideration to the diversity of that region, permits identification of key areas to be preserved, yet is flexible enough to adapt to future scientific discoveries.

5. To permit those public agencies responsible for national parks and equivalent reserves to gain an offensive position from which an Amazon conservation policy can be actively pursued, prior to the elimination of this option by other developments.

6. To contribute, in the particular case of Brazil, towards the development of a National Park System Plan.

Existing and planned conservation units were examined in terms of the objectives being pursued and phytogeographic coverage (Prance 1973). The analysis showed where gaps existed and demonstrated the need for more detailed classification to insure adequate coverage of the diversity of the region.

Vegetation maps were refined to locate areas of biological diversity. Particular attention was given to the areas that may have provided refuge-habitats during the Pleistocene (Haffer 1969, 1974; Vanzolini 1970; Prance 1973; Wing 1973; Brown 1975). Information on birds, lizards, butterflies and various plants was synthesized. Maps were prepared on vegetative formations and likely Pleistocene refuges. A first draft system of proposed areas resulted from overlaying these maps to determine where Pleistocene refugia for two or more plant or animal taxa overlapped. These areas were then examined in terms of their relationship to the proposed development poles. Three criteria were utilized to select priority areas for the proposed system of reserves (Wetterberg 1976b). First priority areas were defined as those which two or more authors have identified as likely Pleistocene refuges. While these sites may not represent the places of greatest plant and animal diversity at the present time, they probably were the centres of evolutionary dispersion. Consideration was given to sites between the refuges where inter-breeding must have occurred among organisms from two or more refuges. Second priority was assigned to areas which contain samples of several vegetative formations and perhaps also a refuge.

Third priority was given to all other specific sites recommended by individual scientists or organizations, but not yet covered by the first two criteria.

The document which proposed the framework for a system of reserves in the Amazon (Wetterberg 1976b) was distributed to authorities in each Amazonian country as well as national planning bodies, universities, research institutes and individual scientists both in Brazil and abroad, requesting critical evaluation. The results of the critical review, and an update on progress towards implementation, were presented to the Second Meeting of the Inter-governmental Technical Committee for the Protection of Amazonian Flora and Fauna (Wetterberg 1977). A training workshop was held in 1978 for senior management personnel on planningthe management of conservation areas, and the IBDF interdisciplinary planning team proceeded to prepare management plans for areas in the Amazon and elsewhere in the country. A national strategy plan was published in 1979 (Jorge Padua 1979). Between June 1979 and July 1980, more than five million hectares were added to the Brazilian park and reserve system, mostly in the Amazon basin.

Early drafts of the World Conservation Strategy identified the Caribbean as a high-priority region warranting conservation planning, particularly in relation to marine resources. Two simultaneous and cooperative IUCN/WWF projects were implemented in 1978 through the Critical Marine Habitats team of the Johns Hopkins University and the Wildland Management team of the University of Michigan. Information on biophysical, socio-economic and political-jurisdictional variables was mapped on individual sheets for the wider Caribbean region. The citations and data were filed systematically. The individual maps were analyzed, overlay fashion, to identify areas of high concentrations of resources, critical habitats and related ecological processes. Areas of potential threat from human activities were noted. Seven 'hot spots' were selected for field study by interdisciplinary teams. General, strategic-level recommendations were made for the seven areas for:

(a) site-specific action to establish protected or management programmes of various types ranging from marine national parks to fishery zones;

(b) resource-specific action to address particular species or resources which transcend national boundaries and territorial waters, including marine turtle conservation, and

(c) theme-specific activities concerning topics of common interest to several countries, such as, environmental legislation and training of field rangers, among others (Putney 1978).

The Caribbean study provided a series of important tools and established the basis for continuing conservation action in the region. The Systems Analytic Mapping technique developed by James Dobbin, Toronto, Canada in cooperation with the Critical Marine Habitats Team of Johns Hopkins University was further perfected as a tool to help identify areas requiring high-priority attention. A data atlas for the major variables in the region was published (IUCN 1979c). A procedure for continuous conservation-strategy planning in the region was proposed (Miller and Ray 1979).

Local conservation organizations have initiated and expanded activities, to select and implement conservation-area projects.

The Eastern Caribbean Natural Areas Management Programme (ECNAMP), a joint programme of the Caribbean Conservation Association and the School of Natural Resources, University of Michigan, has worked with resource managers on 23 islands of the Eastern Caribbean to develop conservation strategies. Specific sites requiring conservation action are identified through a procedure similar to that used previously at the regional level. At the local level, detailed work is possible and recommendations relate directly to public agencies and individuals. Data atlases and strategies for each cooperating island-nation or territory were presented to the General Annual Meeting of CCA in August 1980.

The Caribbean example is one of the first cases of conservation planning which begins at the strategic-overview level, following considerable previous field experience in the region; proceeds down into the tactical details of planning individual sites, resource and theme-focused activities; and then returns to the level of strategic planning in an operational form appropriate to the region. This involved scientists and managers working as teams. Methods and techniques were developed or further defined. Abstract theoretical analysis and practical field work were carried out at various stages of the process. International specialists, local managers and regional conservation bodies collaborated. Significant was the need to combine research and development, science and technology, training workshops, and intensive field work. This multifaceted process appears to offer a productive way to ensure that the appropriate selection and management of habitats for conservation purposes becomes an integral element of sustainable economic and social development.

CONCLUSION

The procedure outlined in this chapter forms a scientific basis for the selection of natural habitats for conservation and for their management and monitoring. Developed from many sources, they have proved effective in numerous cases in Latin America and the Caribbean, and should be of general value elsewhere.

In particular, it would be important for conservation planners to review their own regional programmes in the light of the objectives, principles, procedures and examples in this chapter. This can apply to a range from nascent to well-developed conservation programmes. Even in well-conserved areas, there may be room for improvement, especially as nature reserves, more often than not, have arisen as patches in the land-use mosaic that accidents of planning have somehow left undeveloped. Conservation planning, equipped with recently acquired theory, can now be a far more objective process than even two or three decades ago.

SUMMARY

The background is outlined for the objectives, principles and procedures for the selection of habitats for conservation. Great progress has been made in conservation planning in the past twenty years, especially recently, in reaction to expanding human pressures steadily closing the options to preserve representative samples of natural ecosystems.

A set of objectives for conservation programmes is listed: this gives a kind of basic charter for the actions and procedures that follow. They allow the rational definition of principles for the selection of habitats for conservation, as well as the basis on which nature can be systematically managed to meet the objectives.

The selection procedures include initial macro-scale biogeographic mapping and survey; genetic and functional diversity-analysis; studies of the size, shape and layout of areas; and the provision of management and monitoring plans and related installations for achieving conservation in perpetuity, matching the great time-scales of evolutionary development.

Examples are given of the application of these principles in the selection of networks of areas in Latin America and the Caribbean.

CHAPTER 7 CONSERVATION OF MARINE HABITATS AND THEIR BIOTA

G Carleton Ray

INTRODUCTION

The title of this book is provocative. The term 'threatened habitats' is defined elsewhere in this volume, but it is one thing to arrive at a definition, quite another to identify such habitats. The nature of threat, particularly within the three-dimensional space of the sea, is even more difficult to determine. Therefore, I ask: on what basis can we circumscribe marine threatened habitats? Are not all habitats threatened, taking interconnecting ecological processes into account? On what basis may management proceed? Finally, how does the concept of habitat relate to the broader entity of the ecosystem, which has lately come to be recognized as the objective unit for management?

Clearly, there is a need for conservationists to define better how habitats may be selected for protection. I will attempt this chore for marine ecosystems and their biota by focusing attention on critical habitats. But at the outset, I must draw attention to the obvious fact that decisions about conservation and resource use will most often be made well in advance of acquisition of data necessary to predict the impacts of human activities. For example, a primary goal of conservation is the long-term maintenance of resources and their ecological support systems. This immediately and inevitably involves value judgements on at least three levels - individual preferences, social norms, and ecological functions (Andrews and Waits 1978). First, judgements must be made about what elements of the environment we may choose to identify as resources. Then, the threats to those identified elements must be determined, their habitats delineated, and management practices established. Obviously, conservation of a climax ecosystem-resource will involve different management practices from a sub-climax ecosystem resource; one manages habitats for caribou andmoose quite differently. Equally obviously, management practices will be in conflict if different values are judged to be of equal merit within the same geographical area. The nature of threat, thus, directly emanates from priorities for conservation - ie threat to what?

Living resource protection and the identification of threat are, certainly, not simple tasks. Geist (1978) points out that: 'We need to conserve resources in order that economic activities may continue. Alas, this is a false start. Resources are always defined by a given economic system, and only it determines what is not a resource.

Therefore, conserving resources implies only the perpetuation of the appropriate economic system.... We have to start, therefore, at a more basic level'. In my opinion, this should be the level of ecological process and evolutionary adaptation. This is especially important for marine conservation. In the first place, the definition of marine resources mostly revolves around what is commercially exploited. Secondly, economics dominate marine resource-use to a far greater extent than for terrestrial resources. These facts strongly alter the essence of conservation in the sea compared with that of the land. For example, conservation action in the sea often is restricted to limitations on commercial take, and little else. The fact that marine fishes also need resources, both food and space, hardly enters the picture.

Any definition of conservation involves the interaction of human society, as a whole, with resources and their habitats. Conservation, thus, refers to an entire scope of activities ranging from natural resource development to strict protection and includes research, ecological assessment, legislation, value judgements, habitat acquisition and restoration, etc. Holt and Talbot (1978) point out '... the need for conservation arises essentially because any group of users usually will give relatively greater weight to present values with respect to future values, than does the larger group of which the user group is a part'. Thus, conservation should be a means for adjusting short-term uses and needs so as not to jeopardize longer-term values and future options. Holt and Talbot have provided a summary of a workshop that concerned both marine and terrestrial resources and that evolved the following principles:

'The privilege of utilizing a resource carried with it the obligation to adhere to the following four general principles:

1. The ecosystem should be maintained in a desirable state such that:

   a. consumptive and non-consumptive values could be maximized on a continuing basis;

   b. present and future options are ensured; and

   c. risk of irreversible change or long-term adverse effects as a result of use is minimized.

2. Management decisions should include a safety factor to allow for the fact that knowledge is limited and institutions are imperfect.

3. Measures to conserve a wild living resource should be formulated and applied so as to avoid wasteful use of other resources.

4. Survey or monitoring, analysis, and assessment should precede planned use and accompany actual use of wild living resources. The results should be made available promptly for critical public review.

The workshop did not go beyond principles into strategies or tactics specifically, but the implications of these principles are very far-reaching. It is significant that much legislation and several international agreements agree with these principles, at least in part.

Examples include conventions for Antarctica and use of many ocean resources, as well as national park and fisheries legislation of many states. However, it is also significant that few government bureaus or other institutions are ecologic or integrative by nature. Most are limited to specific issues, making difficult or impossible the task of living resource long-term protection in the face of interacting, diverse, and often subtle threats to sustainability.

This paper is concerned with the applicability of such principles, as are quoted above, to the seas and their resources. It will examine a strategic approach toward marine conservation and present a method - that of 'critical habitats' - for the identification of resource values and the threats to them. In order to do so, however, we must first examine the essential nature of the sea itself, and our approach to it.

THE MARINE DIFFERENCE

Reichle et al (1975) state, in considering the characteristics of ecosystems, that: 'A system is a complex of interacting subsystems which persists through time due to the interaction of its components. The system possesses a definable organization, temporal continuity, and functional properties which can be viewed as distinctive to the system rather than its components... The ecosystem possesses a definite organization in its trophic structure and, indeed, this structure remains relatively constant in spite of disturbances.'

Reichle et al also point out that essential to the function and persistence of ecosystems are:

1. Establishment of an energy base,
2. Development of an energy reservoir,
3. Recycling of elements, and
4. Regulation of rates.

Further, ecosystems evolve towards 'maximum persistent biomass'. Material cycling, energy transfer, and other ecological processes are thus dependent upon the biota.

With these considerations kept in mind, it should be obvious to those familiar with ecological processes that marine ecosystems are quite different from terrestrial ones, and their management must, consequently, be so adjusted. Also consider approaches towards preservation of species diversity. At the species level, the land is about 4 times as diverse as the sea, but at the class level, it is some 20 times less so. This represents a striking difference in both perception and analysis, which will have major management consequences.

Ray and Norris (1972) emphasized that 'the human view of the sea is, in general, the top of it'. They contrast aquatic and terrestrial habitats as follows: '... while rather little life exists in the atmosphere, the hydrosphere contains the major variety of mass of life on this planet. Instead of there being a skim of life as we find on land, usually less than a few metres thick, in the sea life occupies the whole water column, in addition to forming a skim on the sea bottom. This is true whether there is light or not, and most of the sea is utterly black, except for occasional flashes of biological light'.

'While the winds of the atmosphere sweep around the earth, they carry rather little with them; dust, aerosols; a few insects and spiders and some birds, all of which utilize the atmosphere only for transport. The air is not an ecosystem; there is no nutrient recycling there. Even populations of airborne micro-organisms are attenuated in the atmosphere by rain. The sea is the opposite. It's a bouillabaise of animals and plants, of uncountable microscopic organisms, of nutrients, of degradation products of life, of inorganic contributions from land, from chemical precipitation, and of dust from the atmosphere. Its 'winds', which are the ocean currents, move at all levels from the surface to the deepest sea where water generally creeps northward from the Antarctic Convergence. With them move nutrients and life and clouds of reproductive products, and of larvae, so that no part of the sea is ever free of the replenishing supply of life suited to it, save those places where man has so altered the conditions of life that occupancy is not possible'.

Foremost, in the sea, the resource use situation is very different from that on land where man has learned to harvest (the gathering of a cultivated crop) living resources. There is very little true harvest or aquaculture that includes habitat management) in the sea; rather, humans are still largely hunter-gatherers of living marine resources, relying on the natural productivity of marine and coastal ecosystems for food and other living products. Advanced technology for the increasing use of ocean and coastal resources is developing rapidly, but institutional and legal frameworks for management of habitats have not yet matured. This paradoxical situation is a striking component of what I earlier termed the 'marine revolution' (Ray 1970).

Second, the need is obviously great for addressing conservation problems on the scale at which they occur. For most marine conservation needs, even many coastal ones, the most appropriate scale is regional or multi-national in order to reflect both the wide distribution of species populations and the effects of man's use on those areas. The eventual goal, therefore, is no less than the understanding of coastal and ocean ecosystems and the effects of human activities on them as a whole.

This matter of the huge scale of marine ecosystems has led, in fact, to statements that marine ecosystems differ from those on land by their lack of boundaries. The sea's habitats and ecosystems are no less encompassed than terrestrial ones; their boundaries are simply less discernible and less geographically stable than those of the land. Isotherms, water masses, salinity differences, etc, are true barriers, but are indeed difficult for terrestrially-oriented mentalities and land-derived legal and management systems to deal with. The sea's habitats differ from those on land largely due to relative inconstancy in space and time. A tropical forest doesn't move much; water masses vary not only seasonally, but also among years, often quite unpredictably.

For example, the sea ice of the boreal and austral seas is largely seasonal. The movements of krill, whales, seals, and walruses are dominated by it. Even primary productivity varies in a major way in accord with its extent, type, and percent of ocean that it covers. Yet, from year to year, the sea ice may display large differences in all these respects, in accord with meteorologic and oceanic processes. Predicting where and when biota may be most abundant is akin to predicting the weather! For temperate, inshore seas, the seasonal and temporal variations are notorious. Of course, some habitats - coral reefs, for example - are relatively stable. The point is that all habitats vary in time and space, but the scale is very different between marine habitats and terrestrial ones. The result is that both science and management must be placed on similarly different scales. This very often presents formidable problems for managers, in particular those that deal with habitat 'protected areas'.

Finally, most of the world's people, variously estimated at between 50 and 70 percent of the total billions, live in what is termed the coastal zone - at once the most peopled, most productive, and most polluted and perturbed biome of our planet. The coastal zone is a true ecotone, or transition zone, which includes the ocean zone over the continental shelf. Such transition zones are among the most dynamic and most difficult to comprehend in all the natural world. In the sense used here, the coastal zone includes the entire continental margin, ie the area of land and sea where terrestrial and oceanic processes strongly interact, both now and into the recent glacial past. Ray et al (1980) define it as follows: 'The coastal zone is a broad band of land and water where ecological processes - such as biological production, consumption, and the exchange of materials - occur at very high rates. Human activities on land directly and strongly influence these processes in the marine environment and vice versa. The landward boundary can be defined in several ways because of the inland influences of the marine environment. The seaward boundary is also variable because of the changing influences of human activities and terrestrial processes in the marine environment'.

Obviously, it is necessary in defining this zone to consider both national policy and international law; that is, a purely biophysical definition is not complete for management purposes. The coastal zone includes many of our most immediate marine conservation problems. A serious consideration concerns whether to treat it as a separate entity - neither land nor sea, but with characteristics of both.

The general tendency has been to treat the coastal zone as an extension of land and from a local perspective, but this surely is an oversimplification. For example, would one treat a terrestrial watershed as a province of forestry or of hydrology? Or can one treat estuarine species apart from the seas where they may live the greater portions of their lives? Obviously, there is no simple answer. About all we can do is to combat a disciplinary approach in favour of integrating ecological processes, and with great sensitivity for the similarities of habitats, as well as for their differences.

A STRATEGIC APPROACH THROUGH CRITICAL HABITAT ANALYSIS

It is especially true in the sea - and along our coasts - that we are still largely ignorant about the structure and dynamics of natural systems and the effects of our activities upon them. This not only makes very difficult the task of predicting consequences of threat, but also the perpetuation of what is 'desirable'. It is becoming increasingly apparent that human activities often result in unexpected and far more extensive consequences than anticipated, due to 'cascade' effects or 'residuals' that may result from seemingly innocuous activities. Therefore, human activities must be better planned and managed so as to protect the natural systems of which humans are a part and on which they heavily depend. Moreover, most resource management and conservation decisions are made on single issues (eg single species), for single sites (eg a threatened area), often on an ad hoc basis which ignores the cumulative, synergistic, and regional consequences of human activities and which does not result from any analytical process. Single-issue or site-specific decisions often lead to inefficient, incomplete and ineffectual results. Thus, there is a need to re-orient the tactics of single-issue, site-specific decisions towards comprehensive strategies for regions as a whole. This is no less true for management or development than for conservation.

The World Conservation Strategy (IUCN-UNEP-WWF 1980) states three main objectives:

- To maintain essential ecological processes and life-support systems
- To preserve genetic diversity; and
- To ensure the sustainable utilization of species and ecosystems'.

The second of these objectives has had the overwhelming attention of conservationists; the other two are still relatively neglected. Yet, these other two are at the heart of marine conservation. It is my belief, in fact, that over-concentration on species preservation, which is not as great a problem by sea as by land, save for certain higher vertebrates, has actually distracted attention from the overwhelming need to launch a meaningful marine conservation effort based on ecological processes and habitat maintenance, recognizing sustainable utilization. But whatever our individual perceptions, the need should be clear for a strategic approach as contrasted with the ad hoc emphasis of the past.

What is strategy?

Dasmann et al (in prep) summarized strategy by stating that its goal: '... is to provide a systematic overview that can help guide and complement present and future ... 'tactical' actions. Strategic assessment is useful for short-term decisions, but is essential for long-term planning, especially where it is desired that conservation and development accompany one another. Strategic assessment should result in a synthesis of presently available information that may be used, for example, to:

1. Identify potential conflicts and compatibilities among economic development projects and natural resource sustainability ...
2. Reveal the residual and cumulative or synergistic effects of a wide array of human activities ...
3. Select 'core' and 'buffer' areas for special management status ...
4. Identify research needs, data gaps, and monitoring requirements in order better to safeguard natural resources through an increasing data base; and

5. Allow wider participation in decision-making through explicit analyses and syntheses of data.

At the outset, it must be recognized that strategic assessment can be extremely cost-effective, as it can reveal ways to avoid costly duplication and it can predict where future problems are likely to occur. Furthermore, strategic assessments ... are highly 'adaptive; that is, they are dynamic allowing for adjustments to be made according to altered circumstances, rather than being static and fixed in time and space.'

The last point is important; Holling (1978) presents an especially useful treatment of the concepts and methods of adaptive environmental assessment and management.

Critical habitat analysis

The critical habitat approach is a strategic attempt to cut through the problem of making decisions about areas which require special protection, even though we may be largely in ignorance of the details of species biology or ecosystem function, as is all too often the case in the sea. It is designed specifically to show relationships among diverse sets of information, including gaps in data that must be addressed as a matter of high priority. Analysis of habitats, biota, and threats to them must often be based upon the best use of available data in advance of engendering large-scale research and monitoring schemes which usually cannot influence decision-making from the start. At the very least, it highlights areas within regions deserving special protection status. It also directs research towards the highest priority needs. At best, it helps direct our attention towards the cumulative, pervasive, long-range effects of our actions and to integrative ways and means that can help resolve conflicts between living resources and the demands that human activities place upon them.

There are several aspects to critical habitats analysis, incorporating two basic processes - that of identifying highest priority habitats and that of selecting, from the identified areas, those for immediate conservation action. I will now review each briefly, leaving the detail of methods to the references cited.

Classification: The first task is to place habitats within a regional context, that is, to make an effort towards regional classification and characterization. Every marine or coastal habitat may be placed within an oceanic realm or specific coastal zone. The continental United States, for example, falls between the eastern North Atlantic and western North Pacific Realms. Alaska's northern coasts are within the Arctic-Boreal Realm. The Gulf of Mexico is a sub-province of the West Indian region. Each of these units has its own peculiar features, which may be revealed by 'characterization', for which resource use conflicts are often quite specific. There is not adequate space here to go into detail on characterization; suffice it to say that there are several multivariate techniques (eg principal component analysis or biotic analyses of various sorts) capable of pointing out the principal covariant features of an environment. Such analysis is capable of revealing how the basic realms of the seas or coasts are subdivided. For example, for the USA continental coastal zone five basic regions have been identified. These are: 1. East Coast, 2. Gulf Coast, West Coast 4. Gulf of Alaska - North Pacific, and 5. Alaskan Ice-stressed Coasts.

Each of these may, in turn, be sub-divided into subregions, eg the East Coast's boreal-Acadian, north temperate-Virginian, south temperate-Carolinian, and West Indian-Floridian. The biota of each of these has its own central features and may react to human perturbation quite differently for physiological, behavioural, or ecological reasons; that is, temperature changes have quite different effects in cold versus warm habitats. The result of 'characterization' is a classification scheme to which the criteria of 'representativeness' or 'uniqueness' may be applied (see the Selection Process, below).

The terrestrial 'biotic province' scheme of Udvardy (1975) is primarily based on analysis of floristic components. There is no strictly analogous system for the sea, principally because rooted vegetation does not occur in much of the sea (exceptions are sea-grasses, estuarine 'pond weeds', mangroves, and algal beds). The classic work of Ekman (1953) has been modified by Briggs (1974) and Ray (1975), but the basis is zoogeographic. Hayden et al (in prep) are attempting a biophysical marine and coastal classification which incorporates these zoogeographic schemes with physical features of coasts and seas. The point to be emphasized is that without any classification, a systematic approach to habitats on a world or regional scale is not possible, and no banking of representative habitats - threatened or not - can be accomplished. A classification, based on characterization, thus allows discrete and defensible ecological units to be addressed.

Species for analysis: As the term habitat is preferable to species, by definition, it is essential to examine species which have aspects of being indicators of the specific habitat types that fall within the regions and subregions of the classification scheme. However, our state of knowledge of the sea, and the great variety of taxa involved, often makes choices difficult. For example, certain commercial species of great economic importance may be indicators of specific subregions (eg the Atlantic lobster, Homarus, of boreal waters). Others migrate widely throughout regions, or even over whole oceans (eg swordfish, tuna, etc). Although a strategic approach should be based upon the characteristics of regions, their subregions, and identification of indicator species which are representative of these, we are immediately confronted by questions such as: 'indicators of what?' or 'on what habitat does a species really depend?'. Therefore, as a practical matter, species should be chosen for analysis if they meet most of the following criteria: 1. economically important, 2. depleted, 3. ecologically important, 4. regionally representative, and 5. adequate of data.

The first two criteria identify species for which society ascribes some economic or aesthetic value. The third criterion is most important, but often most difficult to apply; forage species (eg those lower on the food chain that are eaten by commercial species) are an example. The fourth refers back to the classification scheme. The last is simply a matter of assuring that there is some minimum data level for analysis.

Two forms of data sets should now be compiled. The first is a data compendium that treats each species in terms of its life history and other essential information. Table 7 presents a format. The second is a map, drawn from the compendium, that treats the spatial aspects of life history. Ray et al (1980) have presented an example of this second aspect, in atlas form for a specific region, but which, regretably, did not include supporting compendia. However, the literature abounds with examples of this 'natural history' treatment. The purposes of this exercise are twofold. First, a list of species is created which is broad enough to be representative of a region or subregion, as derived from a classification, and for which data are compatible both in form and content. Second, the choice of species and information gathered is such that ecosystem relationships and habitat analysis may realistically proceed. For example, Ray (1981) has proposed the following points as essential for determining the ecological role of such large organisms as marine mammals: 1. food and feeding as an ecological process, 2. social behaviour, 3. reproductive rates and strategies, and 4. distribution in terms of ecosystem maturity and stability.

On these bases, it is possible to relate species functions to oceanographic, meteorological, coastal, food web, benthic, and ice-dynamics habitat features, once data described in the following section are compiled. Without such an approach, the determination of threat to the species' habitat, and especially the formulation of an ecologically realistic management scheme, would be impossible. Such a statement is, perhaps, obvious to those familiar with terrestrial game management; it is far from the practice for marine species.

Supporting data: The species level is most basic, as it is directly referable to habitat. But it is only one of five categories of information that are required. The categories are:

1. Species; described above;

2. Physical factors, comprising data of ecological importance which determine the distributions of species (eg oceánic currents, water temperature, salinity, bathymetry, storms, tides, etc);

3. Biotic factors, comprising such factors as distributions of coral reefs, sea grass beds, mangroves, wetland types, productivity, etc;

4. Economic and social factors, comprising the human activities that affect species and environments (eg pollution, shipping, fisheries, etc); and

5. Legal and jurisdictional factors, comprising various responsibilities for regulation and management from public health restrictions to various forms of environmental use and protected areas, to law of the sea.

The elements of these categories are important for the analysis of habitats and threats. Their scope is imposing, but in actuality, the number of elements is not large; experience with strategic assessments of the coastal zone (covering both land and sea portions) has shown that 100-200 elements might be involved for any region (cf Ray et al 1980). With respect to all categories, data compendia and maps must be developed. Table 8 suggests a format for categories 2 and 3. Finally, included with the data compendia, for species as well, should be 'evaluations'; this exercise assesses data and should be held discrete from the data themselves as it is a judgement of data relevance and adequacy. Table 9 suggests how evaluations of data might be composed.

Table 7. Species compendium format

1. CATEGORY: (Fish, Birds, Invertebrates, Mammals, etc)

2. CLASSIFICATION: Class: Order: Family: Subfamily

3. NAME: Common name(s): scientific names

4. LEGAL STATUS: International protection: Federal protection; State protection

5. RANGE:
   a. Worldwide: General geographic range of the species
   b. Region of Concern: The general geographic range of a particular region of concern

6. DISTRIBUTION:
   a. Discrete Populations: General location of recognized discrete populations
   b. Concentrations:
      i. Natural: Locations of large aggregates of a species found as year round residents or as seasonal visitors (include dates)

      ii. Commercial: Locations where commercial concentrations of a species are harvested (include tonnage)

7. HABITAT:
   a. Type: General habitat type(s) the species prefers, eg marsh, benthic, littoral, pelagic
   b. Physical/Chemical: Specific tolerances of the species, including water depth, temperature, salinity, sunlight, turbulence, shelter needs

8. LIFE HISTORY
   a. Social Behaviour: Characteristic behaviour of the species, eg solitary or colonial, diurnal or nocturnal, secretive, adaptable or intolerant of change or human encroachment
   b. Biological Association: Dependence on species associations for survival
   c. Nutrition:
      i. Feeding Type: General class of feeding, eg predator, scavenger, filter feeder, carnivore, omnivore
      ii. Food: Preferred to tolerable food for adults and young, including seasonal foods and requirements
      iii. Feeding Behaviour: Special conditions or characteristics of feeding, eg food size, stimulus, group or solitary
      iv. Feeding Location: Where the animal feeds, eg coastal benthic, pelagic, etc

Table 7 continued

d. Reproduction:
   i. Mode: Manner in which reproduction occurs, eg sexual or asexual, internal or external fertilization, dioecious or monoecious
   ii. Location: Geographic and habitat location specific to mating, nesting, or courting areas
   iii. Behaviour: Important aspects of the reproductive process, eg pair bonds, territorial defence, colonial or solitary breeding or nesting, promiscuous or monogamous, special requirements, tolerance for humans
   iv. Biology: Important considerations of reproductive biology, eg stimuli conditions, seasonal time and duration

e. Development: Important aspects in the development and maturation of young, the degree of parental care, environmental needs of the developing young, age of maturity, stages of growth (eg larvae, juvenile, etc), and nursery areas

f. Growth: Rate of growth, size and weight of adults, life span

g. Movements: Migratory routes, date, duration and critical aspects, including important resting areas and seasonal areas outside of the region of concern

9. FACTORS INFLUENCING POPULATIONS:
   a. Natural: Environmental and community interactions that would increase or decrease species abundance, eg predators of young and adults, weather conditions
   b. Man-Related: Human activities that threaten or enhance a species or a population, eg habitat destruction or alteration, food availability, chemical or pollution intolerances
   c. Potential: Known threats that have yet to occur that will affect species abundance, eg lack of proper management, potential use of known carcinogens or intoxicants, synergisms, etc

10. POPULATION SIZE: Estimates or counts of species in the region of concern; worldwide population status, including historical and future trends in the poplation size and structure

11. MANAGEMENT: Present and proposed management, highlighting particularly sensitive aspects

12. PERSONS CONSULTED: Name and address of person(s) reviewing information

13. REFERENCES: Sources consulted in preparing this compendium

14. SUPPLEMENTARY READING: References for greater depth in understanding the species

Table 8. Environmental data compendium format

1. ELEMENT NUMBER

2. CATEGORY: eg "physical oceanography", "habitat"

3. ELEMENT NAME: eg "currents", "wetlands"

4. GEOGRAPHIC DISTRIBUTION: General statement of distribution of element

5. DESCRIPTION:
   a. Characteristics:
      i. Physical/chemical
      ii. Biological
   b. Processes:
      i. Physical/chemical
      ii. Biological

6. VARIABILITY: ie the dynamics related to the element
   a. Spatial
   b. Temporal

7. INFLUENCING FACTORS:
   a. Natural
   b. Man-Related
   c. Potential

8. PERSONS CONTACTED

9. SOURCES: ie referenced

10. SUGGESTED READING: ie not referenced but useful for further information

Critical habitat identification

The data compendia and supporting maps form the basis for habitat analysis, critical habitat identification, and at least an initial evaluation of threat. The evaluations indicate state of the art and point toward further needs; as such, they are especially important from the strategic point of view. The immediate purpose is to identify where each of the indicator species' critical habitats occur so that areas in need of species protection status can be at least initially identified. First, critical habitat must be further defined. The USA Endangered Species Act of 1973 is the only USA legislation that mentions critical habitat specifically:

> 'The purposes of this act are to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved.... Federal departments and agencies shall... insure that actions, authorized, funded, or carried out by them do not jeopardize the continued existence of such... species or result in the destruction or modification of habitat of such... species determined... to be critical.'

Critical marine habitat was defined by Ray (1976) as those identifiable areas which are vital to the survival of a marine species at some phase in its life cycle, or of a marine habitat, community, or ecosystem, because of the ecological processes that occur within it. Emphasis was given to ecological processes due to downstream effects, which are of such importance on a regional level. At about the same time, the USA Fish and Wildlife Service and the National Oceanic and Atmospheric Administration adopted the following operational definition (Federal Register, 50 Code of Federal Regulations Sec. 424.02 (c)):

> 'Critical habitat means
>
> (1) The specific area occupied by a species, at the time it is listed (as endangered or threatened)... on which are found those physical or biological features
>
> (i) Essential to the conservation of the species and
>
> (ii) Which may require special management consideration or protection; and
>
> (2) Specific areas outside the geographical area occupied by a species... upon a determination... that such areas are essential for the conservation of the species.'

However, as for the principles elucidated by Holt and Talbot (see above) methods were not included with any of these definitions. Consequently, the USA Marine Mammal Commission supported an attempt to develop such a method (Ray, Dobbin and Salm 1978, 1981; Ray, Salm and Dobbin 1979). The species chosen to exemplify the method was the Pacific Walrus, Odobenus rosmarus. The study required examination of:

1. The species' vulnerability in terms of functions such as breeding, feeding, etc;

2. The ecological processes necessary for habitat maintenance; and

3. The threats to species directly (biologically) or indirectly (ecologically).

The result of the study was a regional, graphic representation of the complex interactions between human activities and the biology and ecology of an important species which is representative not only of its environment, but also of other species and of human conflicts with living resources occuring in the region. That is to say, the walrus is important for itself alone, but also represents regional living resource management problems in the Beringian ecosystem in general. Ray and Miller (1982) have

Table 9. Evaluation format

1. WHAT DATA AND MAP SHOW: single source, compiled, new?

2. JUSTIFICATION:

   a. Value: of subject matter, of itself and for analyses
   b. Choice: of data mapped - why presented as it is

3. COMPLETENESS AND QUALITY OF DATA:

   a. Mapped Data: result of comprehensive analysis, partial, etc
   b. Scale: adequate for element, too generalized, etc
   c. Confidence: poor - excellent, obvious data needs
   d. Problems Encountered: data availability, form

4. NEED FOR ADDITIONAL STUDY:

   a. As a part of this analysis:
      i. Specific sites and/or problems
      ii. Specific data gaps
   b. As a consequence of this project
      i. Specific sites and/or problems
      ii. Specific data gaps

5. RELATIONSHIPS TO OTHER CATEGORIES:

   a. For analysis and/or synthesis:
      i. Possible conflict and/or compatibility
      ii. cumulative and/or synergetic effects
   b. Seasonal needs or problems
   c. Other

6. REFERENCES

re-examined this case. Their analysis is as follows:

'The walrus is a gregarious animal. Its distribution appears to be determined principally by bathymetry, sea ice dynamics and benthic food supply. Winter concentrations occur in the north central and south-eastern Bering Sea; summer concentrations occur in the north-western and north-eastern Chukchi Sea. Most of the northward migrants are females, sub-adults, and young; most males occur on or near land haulouts in the Bering Sea.

The walrus is polygynous, mating in mid-winter, and the males are hierarchical and probably semi-territorial. Pregnancy lasts 15 months and birth occurs just before and during the spring migration. Nursing lasts for up to two years (occasionally longer). Females in late pregnancy and during nursing can be presumed to feed heavily. The walrus is a benthic feeder; it locates food by rooting on the bottom with its muzzle, mostly for soft-bodied invertebrates.

These features of walrus natural history suggest that the greatest vulnerability of the walrus population occurs when both reproduction and least food supply occur together. That is when the animals are concentrated in winter and engaged in reproductive activity, with many females near term and feeding heavily, walruses might be subject to severe stress if food supply was low. Areas of low benthic biomass occur within walrus winter concentration areas.

The Pacific walrus exhibits features of K-selection (low reproductive rate, moderately long life, etc), but it is moderately facultative in selection of food. It is not an endangered species. In fact, there is evidence that its population may be near carrying capacities. It occupies all of its former range and may now be having a strong impact on its food supply, some components of which may themselves be K-selected. In addition, recent data indicate that population productivity declined during the late 1970's. Crude birth rates were about 14-17% from the 1950's to the early 1970's, contrasting with estimates of a third as much from the mid 1970's to 1981. In this regard, it is important to note that subsistence hunting by Alaskan natives may not have made a measurable impact on the population. Also, it is not correct that the walrus is considered a 'pest' because of possible conflict with proposed fisheries; quite the contrary, there is concern among natives of Alaska and elsewhere about the health of the population and its habitat.

It is apparent that consideration of the ecological processes responsible for walrus concentrations is essential to any consideration of this species' critical habitat. Unfortunately, very little is known about processes responsible for food supply. For example, it is possible that walrus bioturbation of the benthos during feeding induces 'feedbacks'; that is, walrus rooting patterns in sediments might release nutrients to the water column in significant quantities. Thus, walruses might actually enhance local productivity. A corollary is that a reduction in walrus numbers could result in lowered ecosystem productivity, either generally or locally, with unforeseen - but quite possibly extensive - consequences. The distribution of walruses is also strongly influenced by sea ice dynamics ...'

Even if the walrus population is near carrying capacity, there is little likelihood that it will undergo severe oscillations under natural conditions. That is, it is probably not out of equilibrium with its ecosystem, as its food supply has not been exploited by man. Future human-caused impacts within walrus habitat are related principally to possible exploitation of shellfish on which the walrus feeds, and to oil and gas exploration. Disturbance to food supply could have disastrous consequences, by analogy to the case of the elephant.

We see from this description that there are three levels of critical habitat:

1. Areas where species are biologically vulnerable, whether the species are depleted or not;

2. Areas which contribute ecological support processes; and

3. Either of the above sorts of areas that are threatened by human activities. Separating these three allows analytical procedures to be used, rather than intuitive guesses, on any of these levels or on all three together, as a synthesis. There is, however, one cautionary restraint that deserves mention. The walrus critical habitat analysis for the USA Marine Mammal Commission (referenced above) was presented in simplistic, graphic, 'overlay' terms which has obvious shortcomings. Population ecology is much more complex than graphics alone can show; it tends to highlight spatial correlations at the expense of functional ones, and can lead to false conclusions. Careful interpretation by biologists and ecologists thoroughly familiar with the species and area involved, is necessary to avoid the many pitfalls involved.

The community/ecosystem level

It is possible and instructive to combine species information so that a composite or community representation of the region and its subregions is achieved. For this purpose, the critical habitats for several important indicator species should be combined. For example, selected and important species' habitats, as defined by their breeding and nursery areas, in comparison with environmental and economic data, will indicate areas of very high priority that should be considered critical on each or all of the three levels described above. Also, one would suspect that there is a hierarchy of areas, some more critical than others. For example, core areas may be derived from a species biology approach. Buffer areas could be derived from an ecological approach. Highest priority habitats may be those of endangered species, of great species richness or productivity, or in particular need of relief from human perturbation. It is important that analysis towards these ends be performed on as objective a basis as possible. Unfortunately, identification of critical habitat is as often highly prejudiced as not. A problem lies in acquiring sufficient quantitative data for the purpose.

The approach here, through identification of critical habitats of a few species only, rests on the assumption that data for a few representative and relatively well-known species will yield as much, or even more, insight into environmental conflicts than will analysis of data for a great many species, some of which are bound to be poorly understood.

The rationale for this is that niche variety is expressed well enough by a few selected species, in the absence of detailed information on a great number of species, to determine major habitat patterns and the threats to them. Also, one would wish to avoid undertaking complete inventories as they rarely reveal a level of information that justifies the expenditure of time and effort involved.

THE SELECTION PROCESS

If the process described above for identification of areas of special significance is followed, many critical habitats will inevitably emerge. Further, a diversity of critical habitat types and threats will require an equal diversity of objectives for conservation, eg resource sustainability, continuance of species diversity, assurance of appropriate biological productivity, pollution abatement, maintenance of ecological processes, strict protection of breeding areas, etc. Strategic decisions for living resource conservation of large assemblages of critical marine habitats will most often have to be made in the context of multiple use, particularly given the size of marine ecosystems. For example, both commercial and endangered species may inhabit the same or adjacent areas; utilization of commercial species, restoration of habitats, and strict protection of depleted species at the same time and within the same region or subregion requires multiple management objectives, as well as sophisticated techniques that are subject to continued improvement, as indicated by scientific study and management experience.

Priorities for conserving critical habitats will vary according to the perceived value of the habitat, its ecological importance, and the amount of human caused threat. A comprehensive set of priorities has been developed for selection of a regional system of protected areas for the Mediterranean by IUCN (1980); these criteria are listed in Table 10. A method for employing the criteria was implicitly suggested, but how criteria may be applied is still a subject of considerable debate. The point is that a great variety of factors must be considered and that priorities will vary accordingly. Also worthy of note is that there are two levels of criteria, the generic and the specific. This implies that ratings are to be made on each of these levels, separately. That is, ratings are first made for specific criteria, then separately at generic levels, ie all ecological criteria are assessed first and an overall ecological rating stated. Then, the generic levels are assessed together, ie the ecological compared with the economic or cultural. Obviously, various levels of value judgements, some quantitative and some qualitative will be involved.

Characteristics of some criteria must be pointed out. First, 'naturalness' is often troubling. There are almost no completely natural areas; even recreational fishing is a perturbation. This means that a degree of perturbation will involve highly intuitive judgements. Second, for some criteria, such as diversity, a more quantitative approach is possible. Nevertheless, even here, difficulties are encountered. I have already pointed out that the fundamental approach to diversity is quite different on land and in sea (= species vs higher taxa). But 'diversity' also refers to habitats. Further, non-diverse areas are often highly productive, so that lack of diversity is not necessarily negative. Third, the set of criteria lumped generically under 'social and economic benefit' is exceedingly difficult to assess or to apply. A considerable political influence is often evident. This is made more complex by the fact that economics is a social science, and despite its promise, has not shown itself capable of ranking social and aesthetic benefits satisfactorilv; cost-benefit analysis has reached a state of great apparent sophistication, but doubts about the long range wisdom of the technique are widespread. The history of civil engineering projects, in particular some of those of the USA Army Corps of Engineers or of foreign aid agencies that have conceived of port development on estuaries and the damming or re-routing of rivers - are cases in point. The sensitivity to social and economic consequences of such projects lags far behind the mathematics!

Fourth, landscape and cultural criteria are only slightly less difficult to deal with than economics. The first often involves inter-relationships between land and sea, on an ecological basis. Seashore roads, marinas, jetties, and such developments may improve access, but may also interrupt ecological patterns (drainage, inshore current structure) that are responsible for the landscape (or seascape) value for which the area was given a high rating in the first place. As for cultural values, judgement is often in the eye of the beholder. The value of the criterion, from the habitat point of view, may lie in the fact that cultural sites are often located in biologically rich or unique areas; preservation of cultural values on the site often means preservation of biological values as well. Examples abound of cultures that hold dear certain biological values. New Guinea peoples who value, use, and protect the much depleted dugong is an example. Also, sea-faring cultures, both ancient and extinct, developed uses and traditions on sites of high ecological value and often placed their villages in close proximity to these areas (cf Dasmann et al, in prep).

Finally, the concept of productivity needs some clarification. It is mentioned under ecological criteria and implicit in several other criteria. Productivity expresses a rate; it is not the same as production, which expresses a quantity. Very often, high productivity is associated with organic pollution and eutrophy. Therefore, primary productivity should be appropriate to the ecosystem so that high productivity (resulting in production) of valuable commercial or aesthetic resources will result. Fisheries models are excellent examples of the relationship between productivity and production.

As a result of the application of these criteria, priorities among the identified critical habitats should be achieved and the management objectives for each should be made clear. For some areas, strict protection of resources or of ecological processes (eg productivity) will be necessary and for others, specification of fisheries zone wherein sustainable take is emphasized will emerge. For still others, monitoring and research on the effects of pollution will be the major objectives. For yet others, human recreation will be paramount. However, each of these objectives tends to fall within the purview of different agencies. Protection of areas of substantial size implies multiple agency management and the multiple use concept. A significant problem is the blending of the exploiting fisheries agencies with the protective parks or sanctuaries agencies, and this can only be solved on a case- or site-specific basis.

DISCUSSION

Dasmann et al (in prep) make the point that: 'There is no easy solution and there is no one solution, but at least there can be a systematic approach to decisions'. This is especially important when considering threats to marine habitats, as they are so poorly known compared with terrestrial ones - much more out of sight and out of mind to all but a very few. There are, indeed, only two basic approaches to identification of threatened habitats - intuitive and analytical. Inevitably, resource-use decisions almost always fall between these two extremes, but intuitive judgements about terrestrial habitats are likely to be an order of magnitude better than such judgements about marine habitats. Of course, this situation is rapidly changing as the 'Marine Revolution' (Ray 1970) proceeds, but the point remains. Therefore, it appears that the identification of areas requiring special protection, especially on a regional basis, can be appropriately approached by analysis of critical habitats through selected,

Table 10. Selection criteria (slightly modified from IUCN, 1980)

1. ECOLOGICAL CRITERIA: these relate to values of ecosystems and the species within them:
   a. Dependency: the degree to which a species depends on the area, or the degree to which an ecosystem depends upon ecological processes occurring in the area. If an area is critical to more than one species (or process), it should have high rating.
   b. Naturalness: the degree of perturbation of the area. Undisturbed areas should have higher rating.
   c. Representativeness: the degree to which the area is representative of a habitat type, ecological process, biological community, physiographic feature, or other natural characteristic. If no area of the type is protected, it should have high rating. NOTE: a classification system for coastal and marine areas is necessary for the application of this criterion.
   d. Uniqueness: the degree to which an area is "one-of-a-kind"; habitats of endangered species which occur in only one area are an example. These should have high rating. NOTE: a classification system for coastal and marine areas is necessary for the application of this criterion.
   e. Diversity: the degree of ecosystem, community and species variety or richness. Areas having the greatest variety should receive priority. NOTE: this criterion may not apply to simplified ecosystems, such as some pioneer or climax communities, or areas subject to disruptive forces such as shores exposed to high energy wave action.
   f. Integrity: the degree to which the area is a functional unit, that is, an effective, self-sustaining ecological entity. The more ecologically self-contained the area is, the more likely it is that its values can be effectively protected, and so higher rating should be given to such areas.
   g. Productivity: the degree to which productive processes within the area contribute to species or to human values. Productive areas which contribute most to ecosystem sustainment should receive high rating. NOTE: Exceptions are eutrophic areas where high productivity may have a deleterious effect.

2. SCIENTIFIC AND EDUCATIONAL CRITERIA: these primarily concern areas for research and monitoring. Such areas may be natural or perturbed, and may accommodate training or educational programmes:
   a. Proximity: the degree to which the area is accessible to those wishing to do research in it. Greater proximity should receive high rating.
   b. Benchmark: the degree to which the area may serve as a "control" in the scientific sense, ie as a non-manipulative area against which to measure change occurring elsewhere. Such benchmark areas are essential to the conduct of an ecological monitoring programme and should receive a higher rating.
   c. Demonstration: the degree to which the area can serve to exemplify techniques or scientiic methods. Such areas should receive higher rating.

Table 10 continued

d. Process Relationship: the degree to which the area represents ecological characteristics of regional value susceptible to research and study; these should receive a high rating.

3. SOCIAL AND ECONOMICAL BENEFIT CRITERIA: these consider benefits to human welfare, measured in economic and social terms:
   a. Economic Benefit: the degree to which protection will affect the local economy in the long term. Initially, some protected areas may have a short-lived, disruptive economic effect. Those that have obvious positive effects should have a higher rating: eg protection of feeding areas of commercial fish, or of areas of recreational value.
   b. Social Acceptance: the degree to which support of local people is assured. Should an area already be protected by local tradition, custom or practice, this should be encouraged and the area should receive a higher rating; moreover, an "official" protected area designation may not be necessary if local support is high.
   c. Public Health: the degree to which the creation of a protected area may serve to diminish pollution or other disease agents that contribute to public health problems. For example, protective status for contaminated areas such as shellfish beds or bathing beaches may result in amelioration of pollution as the polluting source is recognized and controlled.
   d. Recreation: areas which benefit the local community by providing them with the opportunity to use, enjoy and learn about their local natural environment should receive high rating.
   e. Tourism: areas which lend themselves to forms of tourism which are compatible with the aims of conservation should receive high rating.

4. LANDSCAPE AND CULTURAL CRITERIA: these consider benefits which provide pleasure to people to enrich their appreciation of the natural or historic environment:
   a. Landscape: natural areas which also contain features of exceptional natural beauty should be given higher rating, since such areas depend upon the maintenance of the integrity of the coastal and adjacent marine systems.
   b. Cultural: natural areas which also contain important cultural, artistic or historic features should be given high rating.

5. REGIONAL CRITERIA: these criteria can best be applied if a regional approach is adopted so that it is possible to measure the contribution which an area may make to a network of protected areas:
   a. Regional significance: the degree to which the area represents a characteristic of the region - whether it be a natural feature, an ecological process or a cultural site. This involves an assessment of the role which the area plays by contributing materials, nutrients, or support for species (especially migratory ones) to the region as a whole. As both ecological processes and natural resources are shared among nations or regions, areas contributing towards maintenance of species or of ecosystems beyond national boundaries should have high rating.

Table 10 continued

b. Sub-regional Significance: within every region there are numerous sub-regions whose characteristics would be classified by a regional classification scheme. It is relevant, therefore, to determine whether an area fills a gap in the network from a sub-regional point of view. This may be done by comparing the distribution of protected areas with sub-regional characteristics. If a type of area is preserved in one sub-region, that type should also be protected in another sub-region.

c. Awareness: the degree to which monitoring, research, education, and/or training within the area can contribute knowledge and appreciation of regional values. Areas which can combine such activities as pollution monitoring and education should have high rating.

d. Conflict and Compatibility: the degree to which the area may help to resolve conflicts between natural resource values and human activities, or the degree to which compatibilities between them may be enhanced. If an area can be used to exemplify the resolution of conflicts elsewhere in the region, it should receive high rating. Protected areas which demonstrate the benefits, values or methods of protection and/or restoration should also have high rating.

6. PRAGMATIC CRITERIA: these consider whether protection can be accomplished or whether action is necessary:

a. Urgency: the degree to which immediate action must be taken, lest values within the area be transformed or lost. NOTE: lack of urgency should not necessarily be taken as low priority, however, as it is often best, and least costly, to protect well in advance of threat.

b. Opportunities: the degree to which existing conditions or actions already underway may justify further action. For example, an extension of an established protected area should have high rating.

c. Defensibility: the degree to which an area can be properly safeguarded or restored. Sites which are defensible should have high rating.

d. Availability: the degree to which the area is available foracquisition or can be managed satisfactorily by agreement; such areas should have high rating.

e. Accessibilty: the degree to which the area is accessible to those managing it or those doing research or other activities within it; such areas should have high rating. Indeed, areas of very low accessibility may be protected by that fact.

f. Restorability: the degree to which the area may be returned to its former natural state. Areas capable of having their productivity increased should receive high rating.

representative, indicator species. Obviously, such an approach can be used for any species, marine or not, depleted or not, but its use in the marine sphere is especially useful for the reasons mentioned above.

The critical habitat method involves understanding of indicator species' roles in their ecosystems. It may be presented graphically. Simplistic graphic overlay methods, particularly useful in landscape and town planning, must be taken with care, however. The totality of adaptations of species within ecosystems, expressed as an 'adaptive complex' (Bartholomew 1970) or 'bionomic strategy' (May 1978) is not easily represented by graphics. This is not to say that graphic techniques are not useful; for a first approximation or to emphasize strategic reconsiderations to a wide variety of users, graphic interpretations can be essential, in fact. The reverse side of the coin is that they can also be highly misleading and that interpretations by ecologists are essential. Nevertheless, this approach - graphic or otherwise - results in an array of justified critical habitat areas. Criteria for selection may then be applied so that, from this array, priorities for selecting and management may be established. These identification and selection processes are strategic by nature; that is they can avoid the ad hoc, issue specific, or intuitive methods which have, unfortunately, dominated conservation and development processes alike in the past.

I have not dealt with the analysis of threat which should be at the heart of this volume. In fact, the selection criterion 6(a) - urgency - should be a measure of threat. It is defined by one dictionary as 'an indication of impending danger or harm'. But how difficult assessing urgency is and how lost in the sea of criteria that I have suggested it appears to be! For example, the establishment of sanctuaries for many species is necessary, but how urgent is this and on what basis? The rationale for oceanic whale sanctuaries is presently not one of biological urgency - providing hunting is ceased - although it may be useful in other ways. On the other hand, the rationale for protection of many coastal habitats, such as mangroves, wetlands, estuaries, and coral reefs, is exceedingly urgent on biological, ecological, economic, and aesthetic bases. Use of the selection criteria should help us to achieve a better perception of why and for what purpose we must establish marine protected areas.

To illustrate how very difficult it is to perceive threats and urgency, consider the concept of residuals - ie the side effects of human activities. Human activities often affect the natural environment and, through feedback mechanisms and ecological interactions they also affect those same activities in return. For example, development associated with tourism and recreation may produce sewage, altered water circulation, discharge of solid wastes, noise, and artificial illumination. These, in turn, may affect the marine environment by causing turbidity, erosion, heavy metal pollution, and alteration of water temperature and aesthetic values. Such effects have impacts on fisheries and wildlife, as well as on tourism and recreation themselves. Thus, an analysis of the environmental threats posed by socioeconomic development involves not only conflicts among human activities and resource values, but also among those activities. Resolution of such problems involves consideration of the three value concepts mentioned at the outset of this paper - individual preferences, social norms, and ecological functions. It also involves thinking beyond single actions and single sites towards a wider ecosystem view.

It is obvious to the ecologist, but not well reflected in the generally piecemeal or bureaucratic approach to conservation and development, that our thinking and approach to environment must be integrative. This is especially necessary in the sea. Further, conservation and resolution of threat should be based upon principles which take on the role of general fundamentals of conduct. They should be planned by strategies and guidelines which indicate how policy should be carried out. Finally, they should be implemented through the application of clearly stated criteria which are standards on which implementation should be based. None of the above should, however, be rigid. They must only be clearly stated, so as to be subject to wide public participation.

Equally clear are three other factors. First, a complex array of factors controls species diversity and ecosystem function. Consequently, the critical habitats approach appears to over simplify, but I would emphasize that it involves quite complex concepts, some of which will not be readily apparent from the analysis itself. For example, the interdependence between species diversity and area size is one such valuable concept (cf J Diamond, this volume). It identifies a minimum requirement for protected areas. Whereas it emphasizes diversity, it is not so applicable to the 'other two' objectives of the World Conservation Strategy, ie ecological process maintenance and sustainable resource use. In fact, Salm (1980) has found that for coral reefs, the species-area relation may under-estimate minimum reserve size; the application of area-dependent survival probabilities may be more useful. Second, it is essential, for marine conservation, that one address both local and regional levels. Local perceptions must be placed within a regional perspective in order to grapple with insidious, cumulative alterations which may have regional consequences. It is a mistake to assume that only individual nations can take effective conservation action. As a matter of fact, the Antarctic treaty and several other regional and marine agreements of far reaching consequences (eg a whale sanctuary, recently established for the entire Indian Ocean that may not immediately affect whales, but could have other important conservation and research impacts). A regional approach to marine conservation is also required because each region has its own identity and also because shared species' movements and ecological interdependencies are inter-connected across national jurisdictions in the bouillabaisse of the sea. Further, a regional approach avoids duplication of effort and enhances information transfer. Third, habitat and ecosystem are not the same thing. Habitats may or may not be manageable functional units, by themselves alone. Threats to habitats, unless placed in an ecosystem or regional context, may not be resolvable. I do not wish to dwell on such an obvious point, but how easily and how often it is forgotten!

The 'marine difference' revisited

The objectives of the World Conservation Strategy emphasize differences in approach and perception that have influenced conservation of habitats between land and sea. The attention to species diversity and preserving endangered species and habitats has been overwhelming by land, but is limited with respect to marine conservation. One could only venture a guess that our comparative lack of attention to the coastal zone where, after all, most people live, is biased by the lack of endangered species there - at least in the marine portion. The principles summarized by Holt and Talbot are in accord with the World Conservation Strategy and call attention, appropriately to both consumptive and non-consumptive uses.

There are many similarities between land and sea and how their ecosystems function. However, I have attempted to point out significant differences. Among these are the relative weight that must be given to shared resources and a regional approach, the different nature of threat and the comparative difficulty in interpreting it, the different definition of resources, differences in ecosystem structure, and differences in both management objectives and bureaucratic responsibilities. The single fact that, for most marine systems, high primary productivity replaces the terrestrial pattern of high plant biomass, must lead forcefully to the conclusion that we are dealing with a different set of circumstances in the sea. In addition, the management of marine systems is dominated not by aerial responsibility - most agencies generally responsible for a piece of designated land - but by multi-layered jurisdiction in which a multitude of agencies are responsible for water quality, fisheries, public health, etc within the same area. Confusion often abounds when ecological process considerations are attacked.

Also apparent, from the ecological point of view, is that 'cores' will be less useful than 'buffers' for that segment of marine conservation that is concerned with protected areas. This is so for three reasons;

(1) sanctuaries or other protected areas can be established only for very small portions of the sea, simply for reasons of manageability,

(2) identified critical habitats are often of such size as to completely dwarf even the Serengeti (cf the walrus, above), and

(3) large expanses of the seas are so ecologically interconnected that devices other than protected areas may be more useful (eg control of pollution and fisheries).

To my knowledge, the extension of protected area concepts - those by which we often attempt to 'solve' threatened habitat problems by land - have not yet been satisfactorily attacked for the sea. The useful matrix of Miller (1975) which places objectives for management against alternative management categories might, with much modification, be made applicable to coastal and marine problems and the threats to them. However, Miller (cf this volume) does not address this nor has IUCN yet expanded its own protected area/objective matrix to cover most marine threatened habitat problems. Figure 9 expresses the problem that I perceive; land derived measures can go so far towards solutions within the 'grey area'. Further, this area is, in my opinion, that of the greatest need because it is mostly concerned with protection of the larger portion of the sea that cannot forseeably fall in a protected area category, as we usually define such matters. Clearly, filling this void on a conceptual basis should be a high priority during the Marine Revolution.

We must learn to think on a different level for marine issues, even as we stand on the ecotone of the shore, not fully appreciating that our footsteps could at any moment be marine. We must look towards regional networks of 'core' (= critical habitat) protected areas so that each will represent a link in the ecological processes which sustain species and ourselves. But, we must not neglect the bulk of the sea which supports and buffers such areas. It may be especially true of marine conservation that the critical habitat is the sea itself.

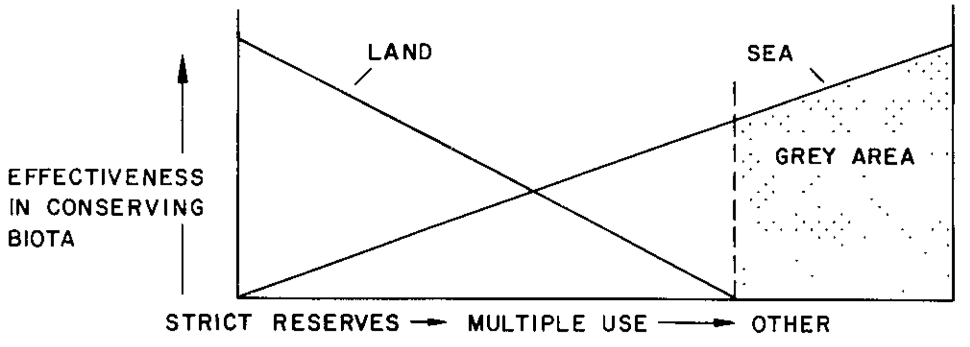


Figure 9. Effectiveness of protected area types in conserving biota. For meeting problems of threatened habitat protection, areas of many sorts may be established in which appropriate management may be undertaken. For the land, an array of protected area types has been developed and has been summarized by IUCN, from "strict" nature reserves to multiple use areas. All of these types are useful and applicable for marine habitat conservation, but their utility and effectiveness is in reverse order to the land. Further, there remains a "grey area" where land-derived methods and types are not easily applicable, if at all. This is often in direct contrast to the need to do so. Examples include such matters as pollution control, ocean dumping, and ecological process conservation, for which entire ecosystems, rather than habitats, must be treated.

SUMMARY

Land-based principles need to be adapted to the difficult problems of conservation in the sea. The sea differs from the land in having virtually invisible depths containing less species but which cover a considerably greater range of taxonomic forms. Resource-use by humanity is still almost entirely of the crude hunter-gatherer type, concentrated mainly in the coastal zone. Conservation is made more difficult by the lack of understanding of the structure and dynamics of marine systems, and the effects of human activities upon them: a serious aspect is that these systems may be linked, so that seemingly innocuous actions may have far more extensive consequences than might be expected from terrestrial management policies.

A strategic approach, linking many facets in a dynamic, holistic system, is needed. Such an approach is offered by critical habitat analysis in which the highest priority habitats are identified, and of these, those needing immediate conservation action are chosen by specifically designed methods. Habitats are classified using indicator species as the chief criteria. Other data come from physical components; biotic factors; economic and

social pressures; and legal and jurisdictional aspects. These data are combined using a graphic overlay method, showing where critical areas exist for

1. Places where species are biologically vulnerable;

2. Sites which contribute ecological support processes; and,

3. Either of these which are threatened by human activities.

Care must be taken with the overlay method not to overlook the complex linkages of biological systems, as exemplified by the adaptive factor complexes that are known to rule the population sizes of many species. Data from the community and ecosystem levels are included where known.

Selection of the critical habitats that deserve prior attention is based upon a comprehensive system of rated criteria.

Once identified, priority critical habitats must be conserved, and here a host of problems exists. One is the multi-agency nature of authority over the oceans. Another is the perception of threats in a remote environment that is essentially difficult to observe. The vast sizes of ocean areas needing conservation is a further problem. There is a good case for providing a marine version of the matrix of objectives versus kinds of conservation-area, that is used for terrestrial reserve planning.

CHAPTER 8 THE CONSERVATION AND RATIONAL EXPLOITATION OF THE BIOTA OF AFRICA'S GREAT LAKES

Geoffrey Fryer

INTRODUCTION

This chapter is concerned mainly with the sometimes conflicting wishes of those who, quite rightly, seek to exploit a major natural resource, the Great Lakes of Africa, and those who, with equal justification, wish to conserve the remarkable faunas found in several of these lakes. Some of the threats to the well-being of these faunas are indirect, and could have serious consequences for the lakes as a whole. Others are the direct result of fishing practices, some of which have already had deleterious effects. In the long run, damage to fish stocks is detrimental not only to the fishes but also to the beneficiary of their exploitation, humanity. It is therefore in the mutual interest of both the exploiters and the conservators jointly to seek reconciliation of their wishes, making concessions and compromises where necessary, and always taking into account the needs of those most likely to benefit or suffer from the consequences of their decisions, the local populace. The problems in achieving reconciliation provide a case study that reflects much that has been said in earlier chapters.

THE DYNAMISM AND RESILIENCE OF ENVIRONMENTS

Like other natural systems lakes are dynamic, ever changing, and, in geological terms, purely transient features of the environment. This transience they exemplify perhaps better than any other natural system. Thus most of the vast number of north-temperate lakes originated only at the close of the Pleistocene glaciations and, in their short histories, have often undergone various vicissitudes. Some have already suffered the ultimate fate of all lakes: they have become extinct.

More ancient lakes such as those of East and Central Africa (Figure 10) are the exception rather than the rule, and are all the more precious for that, for time is an essential ingredient in the processes of adaptation, differentiation and speciation of plants and animals, and it is only in lakes where continuity has been long sustained that diverse and species-rich faunas and floras can evolve. Although we have evidence of rapid evolution in some of these African lakes there is no doubt that their long persistence has been an important contributory factor to the faunal diversity of lakes such as Tanganyika and Malawi. There has just not been time

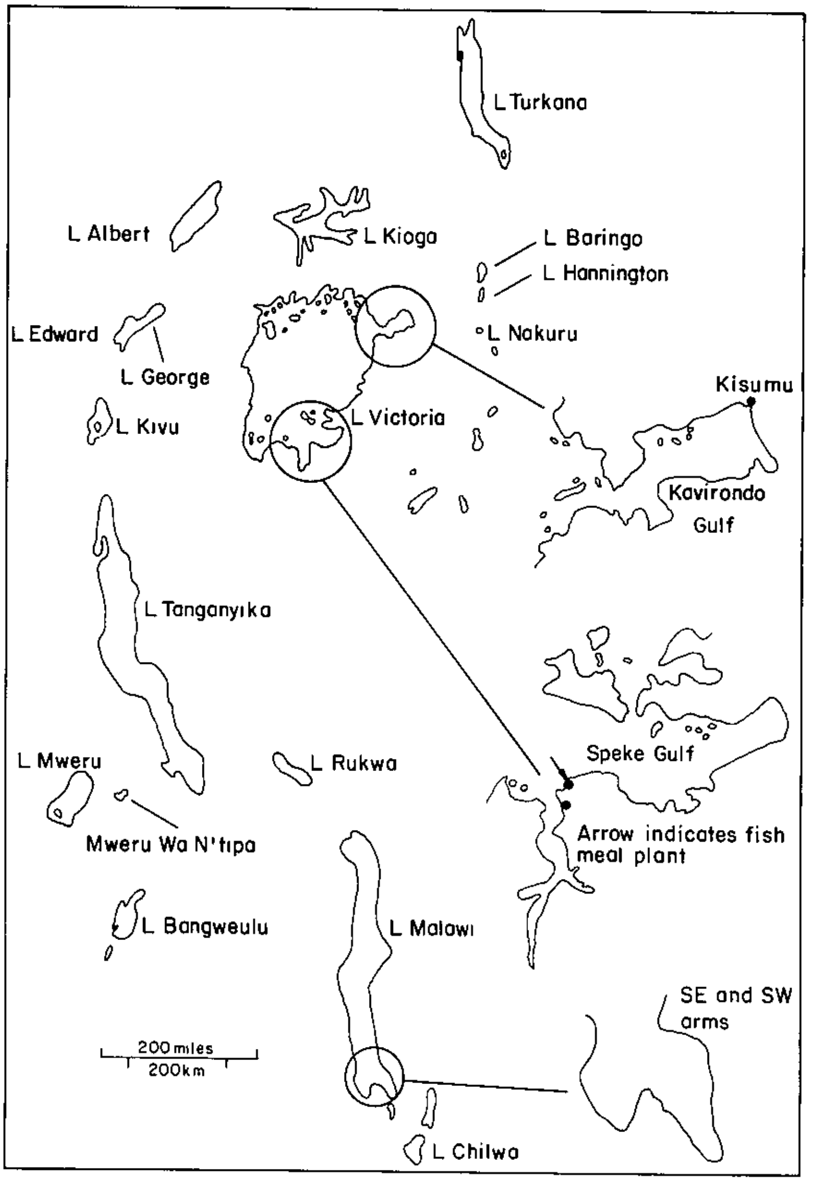


Figure 10. The Lakes of East and Central Africa.

for such diversification in post-glacial north temperate lakes - even if other factors had been favourable.

The evolutionary exuberance of some of the animals in African lakes clearly reveals the dynamic nature of their communities in the temporal sense, but we should not think that such dynamism is lacking elsewhere. While individual organisms, such as lung fishes and crocodiles, may display apparent evolutionary stagnation and conservatism, ecosystems are continuously changing. They also often display remarkable resilience. This is relevant to the conservationist who, while rightly drawing attention to threats to the environment, perhaps sometimes underestimates the ability of habitats to recover from apparent catastrophes. The Pleistocene glaciations physically obliterated most organic life from vast areas of land yet on the whole the affected areas of the Holarctic region recovered with great rapidity, as studies of lake sediments and peat deposits have shown in considerable detail. Further, while some extinction of mammals occurred, work on organisms as diverse as angiosperms and beetles suggests that these glaciations were responsible for surprisingly little extermination of species and that, in the face of changing climates, beetles for example, showed great morphological, and apparently physiological, stability, migrating with their habitat as the ice ebbed and flowed rather than adapting to prevailing climatic conditions. Empty niches led to new opportunities as the ice retreated. African vegetation which, although not exposed to glaciation, was subject to drastic changes at that time, did likewise, as the thermal equator was displaced southward, wind and rainfall patterns were changed, and temperatures fell. Enormous shifts in the distribution of humid tropical forest, grassland and areas of semi-desert took place - to be reversed during what were interglacial periods in the north (van Zinderen Bakker 1978). Here again we see the dynamic element, the ability of nature to adapt, given time. By contrast man-made changes, such as the felling of forests or the pollution of lakes, may give the biota little, or no, opportunity to move elsewhere.

In Africa one is all too familiar with natural ecological catastrophes, such as droughts and the depredations of locusts. However, devastating as they may be at the time, these are really no more than minor perturbations and often have scant effect in the long term. Recovery is often rapid provided a reservoir of the plants and animals involved remains. Lacustrine examples are provided by Lakes Rukwa, Chilwa and Mweru Wa N'tipa, all of which are subject to droughts that sometimes have catastrophic effects on their relatively sparse faunas yet, so long as a remnant of the population of certain fishes, especially the local representative of the cichlid Tilapia remains, multiplication and recovery of these species is sometimes amazingly swift. (For convenience in citing earlier work the name Tilapia is used throughout, though many species formerly assigned to this genus are now referred to as Sarotherodon). It is important to recognize, however, that these fishes are generally strategists whose attributes - good colonizing ability, rapid development, ability to breed at an early age - are well suited to such recovery. That they are capable of these feats should not beguile one into thinking that the many undoubted K strategists of the Great Lakes can do likewise. We already know that they cannot. Here is an excellent example of the need for the conservationist to know the biological (as well as the purely demographic) attributes of the animals he seeks to preserve, or to exploit rationally. To assume that a mathematical model that treats a species from Lake Chilwa in exactly the same way as a different, but perhaps closely related species from the adjacent Lake Malawi, can explain a situation, is inadequate. Theoretical models are important but without a biological input can be disastrous in practice.

A dramatic change of a different kind is provided by Lake Nakuru where, within about six months, the blue-green Spirulina platensis lost its previous dominance in the phytoplankton to tiny single-celled cyanophytes which were accompanied by algae rarely seen previously, such as species of Anabaenopsis and certain diatoms. There was also a marked decline in algal biomass (Vareschi 1978). Although associated with increasing salinities, the full explanation of these changes is not understood. A striking effect, however, was a reduction in the formerly large flamingo population. Flamingoes are filter feeders and the algae now present are too small to be filtered by the sieves in their beaks. As a result these birds have largely deserted Lake Nakuru for Lake Hannington. As the flamingoes were a prime attraction of the Nakuru National Park this is relevant to the tourist trade.

Incidentally, the best means of exploiting Lake Nakuru when in its Spirulina phase (and similar East African soda lakes) might be to crop Spirulina directly. This alga is collected by primitive means from Lake Chad and used as human food, and offers prospects as such and as animal feedstock.

While natural events can be catastrophic, as in the case of volcanic outbursts - some of the fishes of Lake Edward were certainly eliminated by volcanic activity that took place in the area some 8000 years ago - often even these events include a constructive element. New or empty niches may be provided and speciation stimulated by the isolation that sometimes results. Indeed the formation of all African lakes involved an element of catastrophe. The ponding back of rivers and subsequent flooding in the case of Lakes Victoria and Kioga, the tectonic events that gave rise to Lakes Tanganyika and Malawi, and the damming by the Bufumbiro Volcanoes that led to the formation of Lake Kivu are among the more dramatic examples. If one wishes to maintain a balanced view the conservationist must bear the destructive element of natural events in mind and remember that nature exterminates individual species - yet must appreciate that natural catastrophes usually have side benefits and that natural extermination generally involves replacement and is accompanied by the creative process of speciation. Man tends merely to eradicate.

THE AFRICAN LAKES : A BACKGROUND FOR THE CONSERVATIONIST AND THE EXPLOITER

That changes can take place with frightening rapidity even in large, and until recently remote, water bodies is now all too apparent in the great Lakes of Africa. These are the repositories of some of the world's richest lacustrine faunas: a richness associated with a degree of endemism rivalled only in Lake Baikal. Furthermore, as areas where one can study the processes that gave rise to these situations, the Great Lakes have few rivals. Among the end products are species-flocks of crabs, prawns and harpacticoid copepods, a host of gastropod molluscs whose habits and achievements remain largely unknown, a caddis fly that as an adult behaves like a pond skater, a curious bug representing an endemic sub-family and, in different lakes, species-flocks of parasitic copepods of the genus Lernaea and branchiurans of the genus Argulus that have utilized the opportunity presented by the radiating fishes with which they have clearly evolved in parallel. And then of course there are the fishes. Besides the most exciting group of all, the cichlids, there are many interesting examples of adaptive radiation species-flocks of clariids in Lake Malawi and of bagrids, mastacembelids, centropomids and others in Tanganyika. But it is the cichlids that show the most spectacular radiation and diversity. It is difficult to give an accurate figure for the number of species involved as new discoveries continue to be made, especially as habitats formerly difficult of access, such as the deep waters, are explored, but certainly Victoria and Malawi each have well over 200 endemic species and the totals may well eventually reach 300. Additional scientific interest stems from the fact that such radiation and speciation has taken place in more than one lake. Comparisons, always useful in biology, are possible and can be very illuminating. For example a comparison of speciation in Lakes Victoria and Malawi, which differ strikingly in genesis, history, morphology, hydrology, biogeographic affinities and biological productivity, can help to focus on features common to the process in very different situations, and equally to show that what might have seemed to be essential elements of it are not so. Such things are relevant to the conservationist for the argument is bound to be advanced that there are several lakes and it will be sufficient to ensure that the fauna of one of them is protected. This might have some weight if these lakes as it were duplicated each other; but they do not.

Besides exemplifying local speciation phenomena some of these fishes are of extreme scientific interest in their own right. They display a fascinating range of attributes and abilities, in morphology, ecology and behaviour, and many of them are very beautiful. Furthermore, some of them are an important source of human food. In a hungry world who can argue that this is not their most valuable attribute? It is the reconciliation of the scientific and aesthetic claims of these fishes with the desire to exploit them as a valuable source of protein that presents the conservationist with a serious challenge.

In seeking both to conserve and to exploit these resources one must understand the biology of the fishes - their ecological preferences, where they live, what they eat, their rates of growth, reproduction and mortality and what factors influence such - yet many of these things are poorly understood. But this is not enough. One should also understand things like hydrology. Two examples from Lake Malawi, one relevant to the wellbeing of the fauna as a whole, the other of direct relevance to an important fishery, make this clear.

As is well known, because of their depth, the configuration of their basins and tropical climate, Lakes Tanganyika, Malawi and Kivu have a relatively thin layer of oxygenated water overlying an enormous sink of oxygenless, and therefore azoic, water, and that, because of the reduced capacity of water to retain oxygen as temperature increases, the absolute amount of oxygen per unit volume is less than in temperate lakes. Furthermore because profundal temperatures are high (22°C or more in Malawi and Tanganyika) decomposition, a reducing process, is promoted. As Ruttner (1963) put it, the profundal of a tropical lake functions as an incubator; that of a temperate lake as an ice box. Thus they have a much smaller capacity for dealing with oxygen demanding pollution than their enormous size suggests. Furthermore, because evaporation is great, outflows are small, and renewal times are very long. Thus the discharge of toxic, oxygen consuming wastes into these lakes - as from a pulp mill planned for Lake Malawi - could lead to a catastrophe of enormous proportions, which for practical purposes would be irreversible. While one hopes that extreme care will be exercised, the possibility of such a discharge - there is nowhere else for waste to go - poses a threat whose importance can scarcely be exaggerated. Long renewal times are also relevant to the accumulation of pesticides used in the catchment areas of lakes in disease control and crop protection, and directly in rivers in the control of Simulium, the vector of onchocerciasis. Already considerable amounts of organochlorine insecticides have been found in important food fishes in Lake Tanganyika (Deelstra 1979). Likewise the Edward-George basin acts as a sink for copper wastes emanating from the Kilembe copper mines (Bugenyi 1979).

The other example concerns the influence of hydrology on the fertility of the waters of the south-east arm of Lake Malawi. Because the long axis of the lake lies in more or less the same direction as the trade winds that blow between March and September these are funnelled up the rift valley, push the waters of the epilimnion towards the northern end, and there depress the thermocline, thereby causing a tilt that causes upwelling of deeper nutrient rich waters at the south end. This leads to enhanced phytoplankton growth that sustains cichlids of the genus Tilapia that feed directly on algae (Fryer and Iles 1972). Thus is a fishery directly dependent on hydrological phenomena.

FISHERIES IN THE GREAT LAKES: THE HOPE AND THE REALITY

The utilization and conservation of fish stocks calls for accurate information on their make up and their response to exploitation, both in gross terms (numbers and biomass) and, more important in the long run, in biological terms. Unfortunately the information produced (which is admittedly not easy to obtain) is often woefully inadequate, simple principles are ignored and short term gains are put before long term prospects. The results are overfishing, falling yields, wasted investment and damaged resources. All these statements can unfortunately be substantiated. Furthermore the damage has not been done in a lake like Victoria because 'the fishery has recently been unregulated' (Jackson 1979) but because it has been consistently mismanaged for 20 years or more by those who were unwilling, or unable, to recognize what was taking place, though there was abundant published evidence. The same 'policies' - a free for all with no mesh size regulations or serious restraints on fishing - have long been in force.

To give one example, a statement made in 1972 that 'already the rewards for fishing in Lake Victoria have been drastically reduced' (Fryer 1972) was denied (Jackson 1973) and it was claimed that Tilapia stocks were 'far healthier' than had been thought (Stoneman et al 1973): however their decline became obvious and subsequently continued, in some cases virtually to extinction. (See subsequent remarks on T esculenta in the Kavirondo Gulf). A possible justification for such a claim was the establishment of stocks of the introduced T nilotica which, for a time, made a significant contribution to yields in Ugandan waters (but not elsewhere) and which have since declined - by a factor of eight times between 1975 and 1979 if recently acquired figures can be relied upon. Some of the claims that all was well came from an institute that was at the same time publishing information on the decline of various species - a decline unequivocally attributed to overfishing (Kudhongania et al (1972), Kudhongania et al (1972).

It is not easy to get an accurate picture of what has been happening in a lake such as Victoria, nor to reconcile certain statements with such data as are available. According to some, total yield is steadily increasing, for example from 85 000 tonnes in 1964 to 110 000 t in 1971 (Jackson 1973), an increase of about 29%. Even more optimistic is an estimate (FAO 1973) of the yield, probably for 1971 though this is not explicitly stated, of 125 000 t, though another estimate (FAO 1973) given in the same issue of the same journal, was some 19% less - only 101 500 t. Unfortunately the derivation of such figures is not stated. It is of course possible for production to increase in a lake suffering from overfishing and mismanagement if effort is increasing and small meshed nets are used. Under such conditions increased yields are to be viewed not with satisfaction but with alarm. Furthermore, total yields, which do not necessarily indicate the health of the stock, are influenced by such things as social and economic factors. Nevertheless, in view of unreliable figures given in the past, some scepticism is justified. This scepticism is strengthened by such reliable data as come to hand. Thus Benda (1979) gives figures for the weight of fish brought to nine landings in Kenya representative of the Kenya waters of Lake Victoria as a whole for the years 1968 to 1976, and these show a decline of about half over that period (Figure 11), a decline that would have been greater but for increased catches of Engraulicypris, a fish subject to large and as yet unpredictable fluctuations in population size - a known characteristic of short-lived species. Individual species or groups, including Tilapia which had been in rapid decline since the mid 1960s, show the same trend (Figure 12). Indeed Benda states that 'stocks of Tilapia sculenta, T nilotica, T variabilis, Labeo victorianus, Barbus altianalis, Mormyrus kannume and Schilbe mystus have nearly disappeared from the (Kavirondo) Gulf'. Incidentally most of these are short foodchain fishes and therefore particularly well suited to exploitation for man's benefit.

The same picture emerges for landings in Uganda. At Masese in the early 1970s catches (by number) of T variabilis (Figure 13) and of Bagrus docmac were roughly 10% of those made 10 years earlier (Marten and Guluka 1975) and, as individual fishes were smaller, the weight landed must have declined even more. One is therefore suspicious of claims of increase total yield. If such occurred there must have been enormous increases in landings of several species in many areas, and of this no evidence has been seen. Enquiries both to Africa and to FAO have elicited no response.

More recently Benda (1981) has also given details of catch rates made in trawls in 1976 in the Kenyan waters of Lake Victoria and compared them with those made in 1969-70 by Kudhongania and Cordone (1974). Seven 10 m depth zones were investigated. Catches at all depths were lower in 1976 than in 1969-70, often frighteningly so, the reductions in each depth zone, shallow to deep, being 6,8, 6,1, 3,9, 6,2, 1,5, 2,9 and 5,9 times respectively.

Muller and Benda (1981) have also recently given details of trawl catches made in the Kavirondo Gulf in 1977 and compared them with those made by trawling in earlier years. A reduction in mean stock densities over a seven year period (the factor of reduction being given in each case) was shown by Bagrus docmac (6,4), Clarias mossambicus (4,8), Haplochromis spp (1,3). Protopterus aethiopicus (14,6), Schilbe mystus (5,0) and Synodontis spp (4,5). Although both the indigenous Tilapia variabilis and the introduced T niloticus showed an increase in density (though both were present in very small numbers) Muller & Benda believe this to be an artifact as previous surveys could trawl only in water more than 4 m deep whereas they were able to do so in water as shallow as 1 m, and landings of Tilapia in fact steadily declined over the period in question. Not a single individual of Tilapia esculenta (once the mainstay of the fishery) or of Mormyrus kannume was found in 167 trawl hauls. Ironically the only species to show a genuine increase was the introduced predator Lates niloticus, not present in 1969/70: a species whose presence is to be deplored on biological grounds and whose effect is to reduce that proportion of the stock that can be harvested by man.

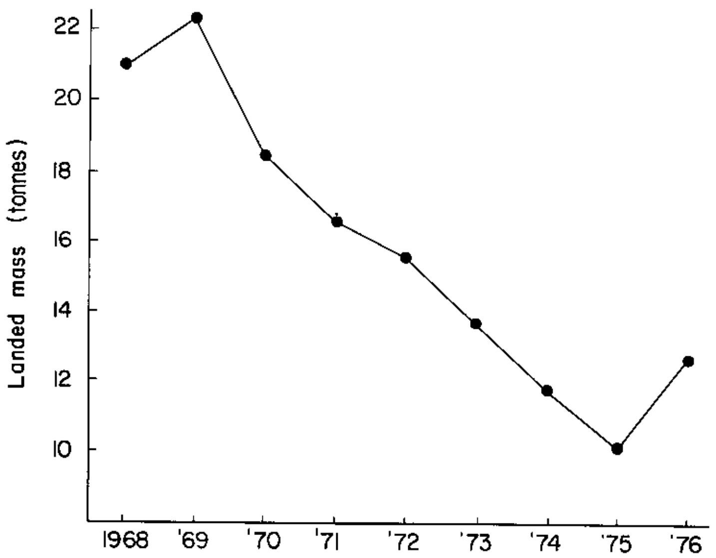


Figure 11. Values for the mass of fish brought to nine landings in Kenya for the years 1968-1976.

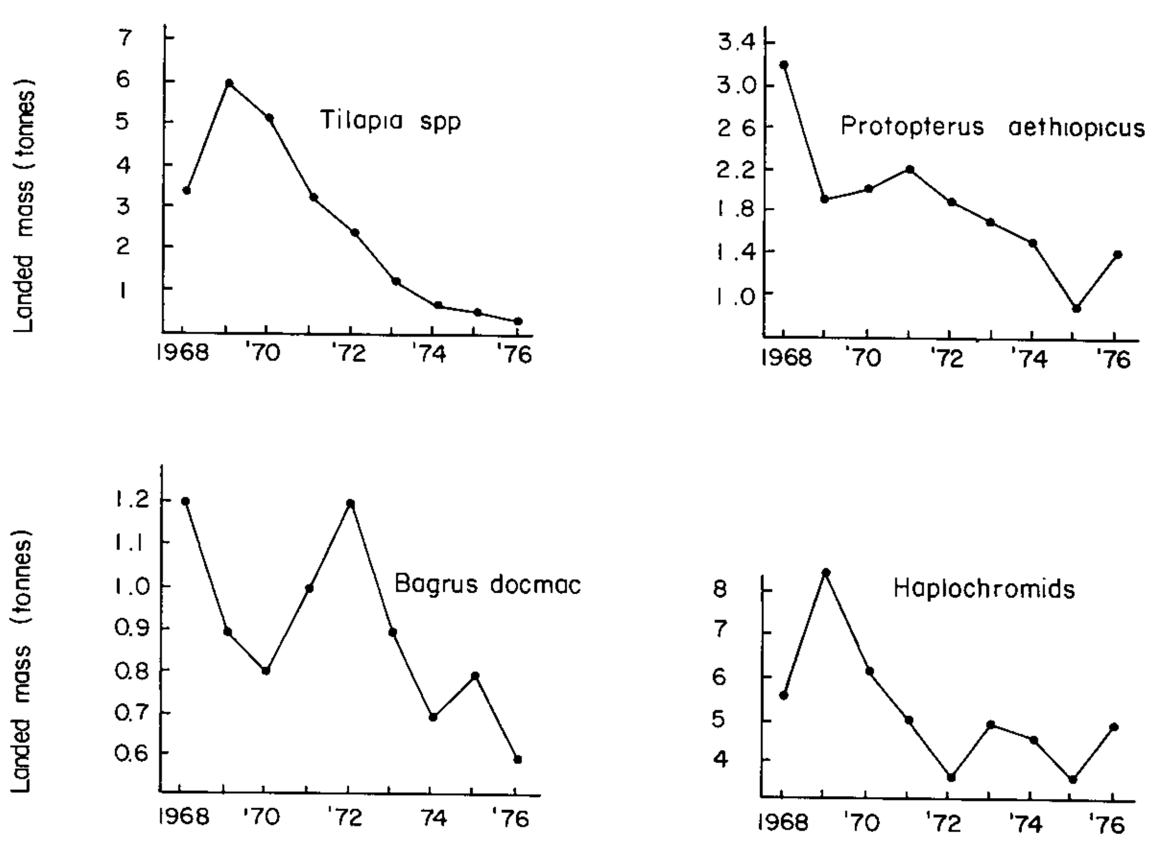


Figure 12. Trends for individual species groups over the period 1968-1976.

There is no need to re-document the destruction of the T esculenta stocks in the Kavirondo Gulf of Lake Victoria (see Fryer 1972), but it may be noted that the process has now continued virtually to the point of extinction. Thus during extensive trawling in 1976 and 1977 (Benda 1981; Muller and Benda 1981) not a single T esculenta was caught. Catches of Tilapia (now consisting of a mixed bag of indigenous and indiscriminately introduced species) as a whole have diminished and the fisheries are in a parlous state. Instead let us concentrate on more recent happenings in Lakes Malawi and Victoria that give cause for anxiety.

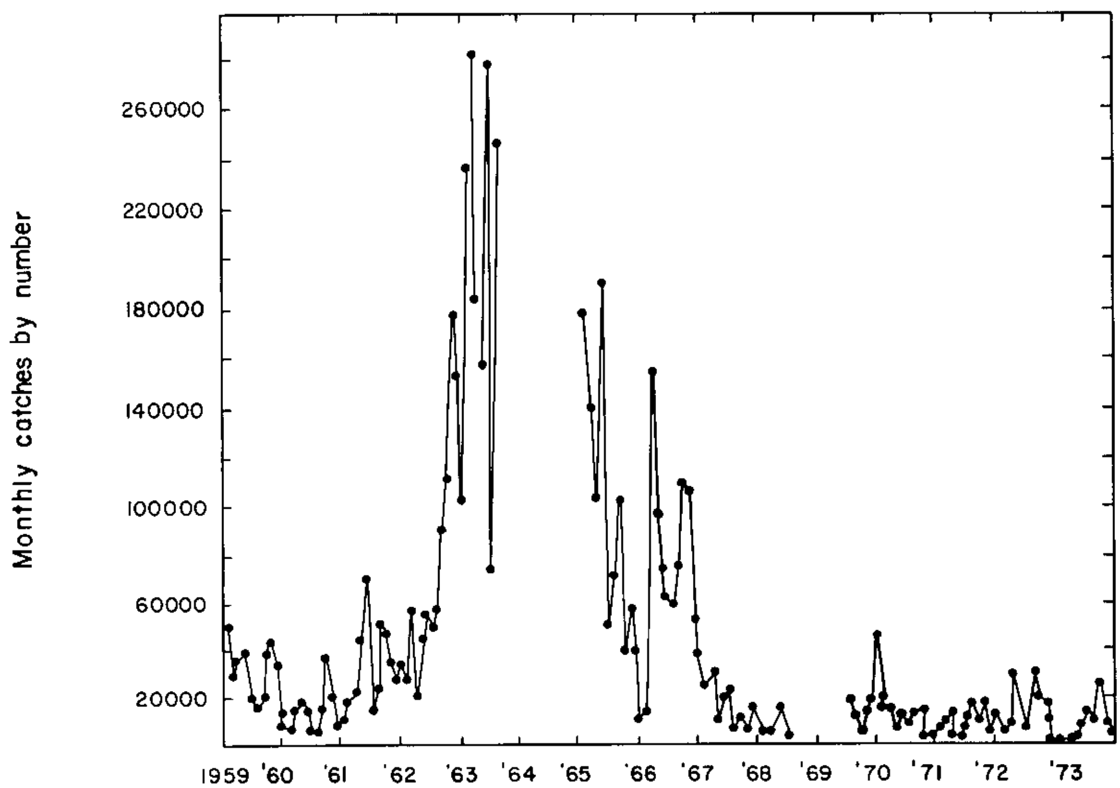


Figure 13. Numbers of fish landed in Uganda for the period 1959-1973.

At the south end of Lake Malawi a trawl fishery is now in operation (Turner 1977a, 1977b). Here over a seven year period the composition of the catch, which included over 160 species, predominantly cichlids, has changed from one dominated by large species of Haplochromis and Lethrinops to one dominated by small species. Fishes over 20 cm in length have suffered heavy mortality and show few signs of recruitment; somewhat smaller species (18-20 cm) have also suffered heavy mortality and show limited recruitment, while smaller fishes (14-18 cm) have suffered less mortality and show excellent recruitment. Equally frightening is the fact that the number of species caught has declined by over 20% and it is only a partial comfort to know that the surviving common species seem to be expanding their range to take their place.

It is not surprising that Bagrus meridionalis, which does not become sexually mature until it reaches a length of 37 cm, and of which large

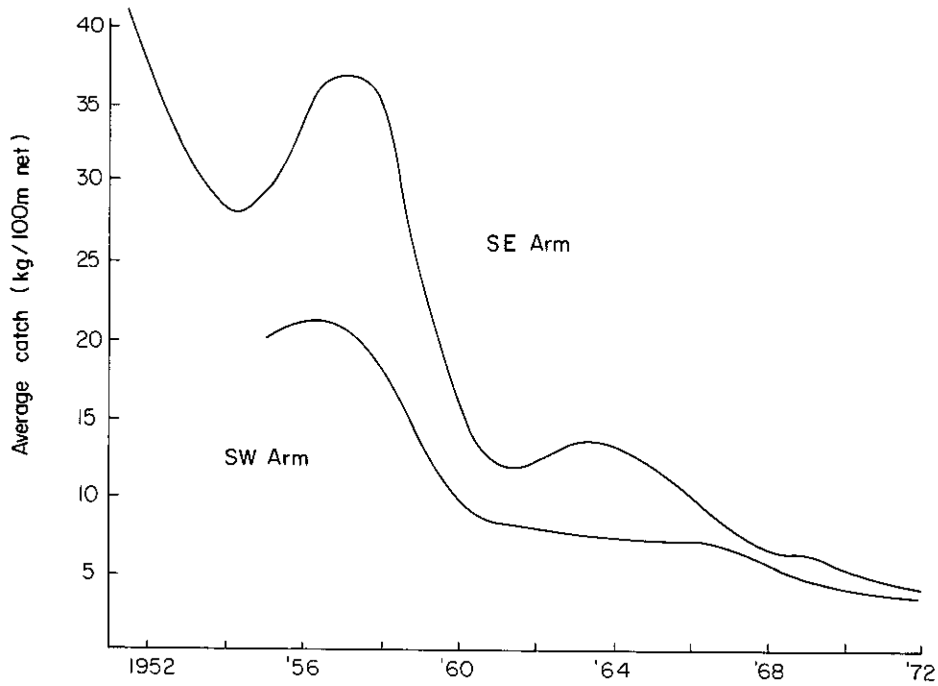


Figure 14. Summary of average catches for the period 1952-1972 in the two southern arms of Lake Malawi.

numbers of immatures have been caught in the trawls, has declined, and the same applies to all the clariid catfishes of the lake. These catfishes were already in decline - probably as a result of fishing pressure - when trawling began. These are the facts, made at this stage without comment, and summarized in Figure 14. Catches of the important genus Labeo have also declined markedly, possibly, as happened in Lake Victoria (Fryer 1973), because of overexploitation of the vulnerable spawners (Turner 1970).

Let us turn now to Lake Victoria. Here attention has recently been directed particularly at the most remarkable end points of evolution within its basin, the haplochromids. Various estimates have put the standing stock of these fishes as being between c 550 000 and 605 019 t (Kitaka et al 1971; Jackson 1971; Kudhongania 1973; Kudhongania and Cordone 1974), the figures for the Tanzanian waters alone being estimated at some 321 000 t (Kudhongania and Cordone 1974). Yields of 200 000 t per annum for the whole lake (Kudhongania 1973) and more than 114 000 t for the Tanzanian sector (Kudhongania and Cordone 1974a) were confidently predicted and the belief expressed that even higher yields could probably be sustained. Such yields were to be based largely on trawling though other methods of capture are also employed.

It is not the intention to snipe at these figures, though their exactitude engenders suspicion. Lake Victoria is bigger than Switzerland yet it was stated precisely that it had a standing stock of 605 019 t of haplochromids

(Jackson 1971). Even more precise were estimates of stock between certain depths. For example Tanzanian waters between 10 and 19 m deep were estimated to carry a stock of 68 931,2 t of haplochromids (Kudhongania and Cordone 1974) and figures were given with similarly spurious precision for other depths. Figures rounded to the nearest 1000 tonnes and estimated to within + 10% would have evinced admiration from those familiar with the problems involved. A salutory account of how wrong one can be even when using modern methods of assessment on a 1 ha pond (Stott and Russell 1979) puts such estimates in perspective.

Anticipated yields were also optimistic. While small, early maturing species sometimes offer splendid prospects for a fishery - the pelagic clupeids Limnothrissa and Stolothrissa of Lake Tanganyika being an excellent example from African lakes (Coulter 1977) - this is not necessarily so. Thus, according to Balon (in Balon and Coche 1974), although Haplochromis darlingi has much the highest biomass of any fish of Lake Kariba, the available yield is inconsequential, a matter probably not without relevance to the situation in Lake Victoria (Fryer 1975).

Recent developments reveal a very different picture from that predicted. First Kukowski (1978) has shown that, among other things, the gape of the trawl on which the estimates were based was not 9 but 16 m. This, plus additional data on catch rates, reduced the estimated biomass to about 248 000 t, or considerably less than half the least optimistic of those just cited and not much more than 40% of the most optimistic. Likewise estimates of yield have had to be downgraded.

Tanzanian waters, from which 114 000 t were predicted, are now suggested as having a potential of about 50 000 t. However, as officially at least, trawlers are excluded from waters less than 20 m deep, some 34% of this yield is not available to these vessels and a further 15% is located in water over 60 m deep where fishing is uneconomic. The realisable yield, if the figures are correct, is thus reduced to some 25 000 t · with no guarantee that it can be sustained.

The practical consequences are already apparent. Trawling is taking place in the Speke Gulf and a fishmeal factory with a capacity of 60 t/day has been constructed to cope with the catches. Conservationists will deplore the conversion of these fishes to meal that is fed to pigs and poultry: it represents a loss of perhaps as much as 80% of the protein that could have been consumed directly by man, is an energy demanding process, and required capital investment. Be that as it may the trawlers have been unable to supply the estimated 60 t but seem to be supplying between 10 and 20 t per day (van Oijen 1979) - and this in spite of the fact that a virgin stock (which will inevitably give an initial yield higher than that which can be sustained) is being exploited with small meshed cod ends. Indeed if we take the now anticipated yield from trawling the Tanzanian waters (25 000 t) and think of the weight of protein reaching the human consumer at the end of the chain now set up, we come up with a figure of 5 000 t - a far cry from the 114 000 t regarded as a conservative estimate! There is no guarantee that even this amount, little more than 4% of that anticipated, can be sustained, and it will have been obtained at much expense in vessels, gear, fishmeal plant, fuel and transport.

All estimates considered so far are on the basis of sustained yields and take little or no account of the biology of the fishes concerned, which in most cases is unknown. The indications are that even the revised, lower, estimates cannot be sustained. Thus over the period October 1976 to March 1978 in the two areas chiefly trawled, both the hourly catch rate and the mean catch per trip declined. In one area the catch rate declined by 38% in one year - from March 1977 to March 1978 - even though catches removed less than originally estimated (Kukowski 1978). The decline was probably more serious than the figures indicate because, although officially forbidden to trawl in less than 20 m of water, vessels frequently do so - to the detriment of the inshore fishermen, their nets, and the fishes themselves.

Heavy exploitation of the haplochromids will inevitably have other deleterious consequences. Experience in the Kavirondo Gulf shows that intensive fishing with small meshed nets, here mostly seines, has led to a sharp decline in average lengths over a period of some 10 years. The average length in heavily fished areas is now less than half that in lightly fished areas (Marten 1979; Wanjala and Marten 1975). This implies the virtual disappearance of large species in the face of intensive fishing - exactly as in the Lake Malawi trawl fishery. The same process is indeed already taking place in the Lake Victoria trawl fishery (Kukowski 1978). This is a predictable response, known since at least the early years of this century when, for example, the size of plaice landed from the North Sea declined year by year. Those responsible for giving advice years ago need have looked no further than Lake George where the average weight of each Tilapia nilotica landed declined from c. 0,9 kg in 1950 to c. 0,4 kg in 1970 (Gwahaba 1973). The same is true in Lake Baringo where within no more than 5 years the length of individual T nilotica passing through the filleting plant fell from 18 cm to 12 cm (Kudhongania and Cordone 1974) and the catch per unit effort was falling (Ssentongo 1974). As the length at first maturity is 18 cm the consequences of cropping at 12 cm needs no comment. Furthermore, small-meshed nets catch many immature haplochromids - 35% of the commercial catch in the South Nyanza region of the Gulf was made up of such, including large numbers of individuals as small as 6 cm in length (Wanjala & Marten 1975). As in the Malawi trawling operations such fishing also catches large numbers of immature individuals of important larger species such as Tilapia, both indigenous and introduced (Wanjala and Marten 1975) - or did until these were drastically reduced or, in some cases, virtually wiped out (see Benda 1979; Muller and Benda 1981) - the effects of which can be disastrous. For example, T esculenta, once the mainstay of the fishery in the Gulf - more than two million fishes per year were railed from Kisumu to Nairobi alone in the mid 1950s - had virtually disappeared by the mid 1970s.

Exactly the same happens in the trawl in the Mwanza region where a 20 mm mesh cod-end (which is too small) is used. There is a terrible inevitability in the response to falling catches with size selective gear: a reduction in mesh size. Already, to quote van Oijen (1979), 'there seem to be plans to start fishing with 10 mm mesh cod-ends', the effect of which, as he says, would be disastrous. Exactly the oppositeresponse is called for, and Witte (1981) has recently advocated an increase in the size of the cod-end meshes employed. At the south end of Lake Malawi two cod-end mesh sizes, 25 and 36 mm, are in use and recommendations have been made that only the larger of the two should be used (Turner 1977a).

The effects of such fishing have thus far mostly been considered in terms of yields and changes in length, but there are other biological consequences. Trawling is carried out in complete ignorance of its effects on the substrata on which demersal haplochromids rely for food and dwelling places. Sheer disturbance may be important, but no account is taken of the fact that, if we can extrapolate from species for which information is available, all these are fishes whose breeding habits involve the establishment of a territory and, generally, the making of a nest. Some of them may also establish arenas. The effects of trawling on these activities is easy to imagine. Furthermore, these fishes are female mouthbrooders, so trawling inevitably destroys many young that would have escaped from the nets had their parents not evolved this, ironically, protective device, which is no protection against trawls. Some species may also frequent brooding grounds which, if trawled, could result in damage to the stock out of all proportion to the numbers caught. Furthermore many species appear to be bound to a particular type of substratum or to have a restricted vertical distribution (eg see Greenwood (1974) for summaries of data from his earlier papers). Such restriction is proving to be more stringent for many species than originally suspected (Witte 1981) and personal communication). Because of this there is no guarantee that a depleted region can easily be recolonized. Alternatively it may be occupied by species with more generalized preferences, whose other attributes may be less desirable to the exploiter than those of the species originally present. Here our ignorance is profound.

There is also the vexed question of stock and recruitment. Mouth brooding is related to the production of few offspring and, if these are destroyed by trawling, recruitment will inevitably suffer more than in free-spawning species which, is now generally agreed, can be reduced tonumbers below which recruitment is impaired.

Work that ignores the biology of the fishes involved is not confined to Lake Victoria. In a recent paper on the Bangweula area (a lake in Zambia), Toews and Griffith (1979) estimate yields of mostly unnamed species by several methods (with a 3,5 fold difference between maximum and minimum estimates). This work used refined statistical techniques on inadequate data.

What can the conservationist do when faced with a situation such as prevails in Lake Victoria? It is easy to be critical but the problems are immense, as they would be even without the complications caused by overfishing and lack of management. The population dynamics of species which, like many of these fishes, have continuous recruitment, are far from simple (eg Argentesi et al 1978b). Further not only are the interrelations of such a complex array of species extremely complicated but they are not even stable because fishing pressure has repercussions not only on the species cropped (in this case numerous) but indirectly on other species, and changes in fishing pressure can alter these relations, via such things as compensatory shifts in population densities, enhanced survival if predators are heavily cropped, and in other ways. Economic and social factors, such as the activities of the numerous fishermen, are also involved. A theoretical background for efficient management is scarcely developed. The population dynamics of a single species can be complex (eg Argentesi et al 1978a) and only recently have models for multi-species

Table 11. Actual and optimal catches in inshore waters of Lake Victoria (after Marten 1979a).

	1972-3	OPTIMUM
Tilapia	15	41
Bagrus	12	16
Clarias	15	10
Protopterus	26	32
Haplochromis	22	0
Synodontis	2	0

fisheries begun to be worked out, and these are generally specific to one area. We are still only groping towards the understanding of general principles, some of which have recently been enunciated in a simple way by May (1979) and others.

While there are advantages in harvesting small, fast-growing species which may be more efficient converters than larger species - and some of them convert phytoplankton and detritus directly to fish flesh - this in no way justifies the destruction of fishes such as Tilapia, the two indigenous species of which do likewise. These, or their herbivorous but less palatable relatives that have unfortunately been introduced into the lake, should take pride of place in any rational scheme of exploitation. It is therefore pleasing to see that such is the case in some new thinking (Marten 1979a) that advocates a fishery for the inshore waters based exclusively on gill nets and hooks, that would ban seines completely, and that, contrary to all recent aims to exploit the haplochromids, would exclude these and Synodontis entirely in order to obtain optimal yields of Tilapia, Bagrus and Protopterus. Clearly some haplochromids would be caught but these would be only incidental. According to Marten's model the optimum Tilapia catch is almost treble the 1972-73 catch (Table 11) and efficient exploitation of these fishes would more than offset the loss of haplochromids.

Marten (1979a) developed equations that show the contributions of mixes of gill nets of four sizes, of hooks and of seines (Table 12) needed to maximize production of individual species, and also the mixes of gear that would give the best yields both by weight and by cash value (Table 13). The equations reveal that in some cases small meshed gill nets and seines make a negative contribution to yields.

A comparison of optimal yields for weight and value is instructive. The optimum mix for the latter includes some small-meshed nets, simply because, as catches become less, fish prices rise in accordance with the law of supply and demand, so the fishery continues to be economic even when output has declined. This may be good economics but it is very bad biology. Economic pressures are well known to the conservationist when developers wish to make inroads into some interesting habitat. They are equally at work in the exploitation of renewable resources.

Marten (1979a) also suggests that, although the lake is overfished, a partial remedy may lie in an increased fishing effort, provided this is directed against predators. It is ironical that what was obvious at the time of the Nile perch debate (Fryer 1960) has been recognized almost

20 years too late to prevent the irresponsible introduction of that predator. The stepping up of hook fishing and the banning of seines and small meshed gill nets would be welcome measures. If, as one hopes, the scheme is tried, only time will tell whether the biological attributes of the species cropped will enable the hoped for yields to be met at what, for some size groups, is an increased fishing pressure.

This still leaves the vexed question of trawling in offshore waters. It has not taken long to show the claims such as those of Stoneman et al (1973) - 'that sustained catches of previously unexploited stocks can be made' are misleading, nor for it to become apparent that it is not easy to enforce legislation that prohibits trawling in certain areas. Trawling in shallow waters that are officially out of bounds occurs almost daily (van Oijen 1979). Here the catch includes juveniles of valuable food fishes. The trawlers exist and will doubtless be used so long as it is economical to do so. It is tragic that those who supported their introduction have to fall back on the argument that fishing will cease at this point. By then it may be too late. It is even more tragic that, in order to feed the ill-conceived fishmeal plant, there is agitation to obtain additional trawlers that can range more widely than the existing vessels.

The situation is already becoming a microcosm of the tragedy that has been enacted in the seas of South East Asia where the introduction of trawlers, which use nets of too small a mesh and which completely ignore a ban on fishing in inshore waters, is jeopardising the livelihood of no fewer than 6 million small scale fishermen, and has led to overfishing in the space of a few years (Peng 1980). In Malaysia, where trawling began in 1965, by 1972 individual trawlers were catching only about one sixth of what they were in 1966, and the catch is declining in quality. 'Trash' fish now make up 57% of the trawler catch in Malaysia and 71% in Thailand, and is converted to animal feed and fertilizer. Fish traditionally supplied for local consumption by small-scale fishermen is becoming scarce. The amount available in local markets in Malaysia dropped by a third between 1967 and 1975. It is scarcely surprising that violent clashes - resulting in deaths - have occurred between small-scale fishermen and trawlers. Similar trawling ventures are planned for the South China Sea. As Peng says "It took less than 10 years for the effects of overfishing by relatively unsophisticated trawlers to be felt in the Straits of Malacca and the Gulf of Thailand. Local fishermen are now asking how long will it take in the South China Sea?" Those concerned with Lake Victoria might ask a similar question with reference to the local situation.

So far as the Lake Victoria trawlers are concerned one can unfortunately do no more than plead for a re-think before an expansion of the fleet is sanctioned, and for the activities of the existing trawlers to be rigorously controlled and for severe penalties to be imposed for fishing inshore. Careful monitoring of catches and effort and the possibility of imposing strict quotas, or banning vessels from certain areas from time to time, will be needed, and the economic needs of the fish meal plant should play no part in determining yields. As much of the catch as possible should be sold fresh (ice would help) and fish meal made only from what would otherwise be wasted - which would doubtless render the existing plant uneconomic. If those who financed its construction could be prevailed upon to study the disastrous effects on a herring stock of such a plant and its

Table 12. Equipment needed to maximize catches of individual species

	Optimum gear densities (per km^2)				Yields ($kg/km^2/day$)				
	3,8-5,1 cm gill nets	6,4-9,5 cm gill nets	10-12 cm gill nets	13-20 cm gill nets	Hooks	Seines	Current average	Opti- mum	Multiple correlation*
Current average	90	12	100	68	1 240	0,65			
Maximum occurring	383	120	400	240	2 420	7,72			
Optimum for each kind of fish									
Tilapia	0	0	450	0	2 300	0	40	240	0,85
Bagrus	0	0	400	0	0	0	33	96	0,74
Clarias	0	0	0	150	3 700	0	40	150	0,89
Protopterus	0	0	0	0	6 800	0	70	390	0,87
Haplochromids	0	0	0	0	8 100	4,2	58	300	0,88
Synodontis	400	120	0	0	0	0	5,8	81	0,83

*This pertains to the regression equation used for optimization

Table 13. Equipment needed to maximize yields by mass and by cash value

	Optimum gear densities (per km^2)				Yields $kg/mg^2/day$				
	3,8-5,1 cm	6,4-9,5 cm	10-12 cm	13-20 cm	Hooks	Seines	Current average yield	Optimum yield	Multiple correlation*
Total wt	0	0	410	0	2850	0	270	460	0,94
Total value	190	0	170	170	4300	0	66	150	0,95

*This pertains to the regression equation used for optimization supporting fishery that were backed by the Norwegian government (see Korringa 1978) they may have the courage to close it down. By so doing, or by restricting its use to waste products, they would be rendering a real service. If the haplochromids are to be exploited it should not be beyond the wit of those concerned with the fishery to devise non-destructive means of doing so.

If the present activities (one can scarcely call them policies) are continued and expanded, the inevitable result will be a repeat of the process that destroyed the Tilapia fishery in the Kavirondo Gulf and led to the virtual extermination of other important food fishes in certain areas. The haplochromids - many of them certainly K strategists - are no less, and perhaps more, susceptible to cropping with small mesh nets than those species whose stocks have already been wrecked or seriously depleted by unscientific exploitation. With the now undeniable results of previous ill treatment all too evident, and admitted even by those who previously claimed that all was well, it is inconceivable that the danger inherent in the situation can be ignored.

One would have liked to have included Lake Kioga in this discussion, for here is a lake into which both herbivores (Tilapia spp) and a top predator (Lates niloticus) have been introduced and which, between them, have virtually eliminated seven major indigenous species (Twongo and Oguta-Ohwayo 1979). Had reliable data been available, which they are not, one might have considered whether the destruction of an ecosystem that had evolved by natural selection via the biological fitness of its individual components, and was therefore ecologically efficient, was justified by a resulting improvement in sustained yield. Introductions may be justified in essentially fishless lakes, but whether they have led to long term benefits in Lake Kioga only time will tell. Whatever its yield, however, there can be no logical justification for the introduction of Lates.

Lake Victoria has been subjected to the introduction not only of Lates but of herbivorous cichlids of the genus Tilapia, whose presence is now regretted. Apart from any deleterious consequences suffered by the indigenous species as a result of competition, some aspects of which were noted not long after the introduction of T zillii (Fryer 1961), the introduced species are in general less palatable than their indigenous relatives, and are disliked by the fishermen. The competitive interactions revealed by field work were, by their nature, unpredictable, as are most effects of introductions, and it is therefore profoundly disturbing from time to time to hear the mooting of suggestions that certain species might be introduced into the Great Rift lakes. Of all African lakes these are the ones in which fishes are most likely to have evolved to fill the available niches. If the 'academic' knowledge acquired concerning these lakes enables one prediction of practical value to be made it is that the effects of such introductions are likely to be deleterious rather than beneficial in terms of harvestable protein. The possible destruction of unique communities is a hazard to which these lakes should not be exposed by the irresponsible introduction of species whose effects are impossible to predict.

MAN AND THE LACUSTRINE ECOSYSTEM

The management of lakes is more complex than that of a national park in which man's activities are greatly restricted. Here not only is he the dominant animal of the ecosystem but his influence is enhanced by modern technology. Treated as the top predator he may be just an element in the equations. But he is more than that. He is a sentient being for whom, as well as for other components of the ecosystem, lakes should be managed. In the past conservation measures have tended to be imposed from above and decisions about the exploitation of fish stocks have sometimes been based on economic consideration rather than on the general welfare of large segments of the population. Even scientific judgements must consider the opinions, needs and desires of those directly involved, in this case not only the consumers but the fishermen and their families of whom there are many thousands on a lake like Victoria and who have sometimes lived in considerable harmony with their environment for centuries and evolved valuable cultures and traditions. Their lot can often be improved by science and technology and one hopes it will, but they may wish to develop according to their own cultural values which may not always harmonize easily with technological innovations or western ideas of economics. Some cultures embrace concepts like sharing of ownership and help within extended families and communities that differ much from the cultural norms of modern western societies with their emphasis on entrepreneurial skills, the profit motive, and their own kind of work ethic. Cultures can of course be changed. The making of large profits was for long anathema to European societies (eg see Tawney 1926) which have changed much since medieval times. Likewise one should not idealize the life of the fisherman. Gwahaba (1979) for instance mentions their misuse of long periods of leisure, often spent drinking alcohol, and the need for education in fishing communities. Nevertheless, on social grounds alone, traditional fisheries, enhanced by modern methods, have advantages over those based on a few large, mechanized units. Production should be for needs, not profits. Whatever one's political philosophy, experience unequivocally shows that in dealing with a biological resource it is folly to rely on economics, market forces and the profit motive. This has been clearly demonstrated by European marine fisheries (eg see Korringa 1978) which have, for example wrecked a herring fishery and are in a state of considerable disarray as a result of attempts to get immediate maximum returns with little thought for the future. Tropical forests tell a similar frightful tale. The Mwanza fish meal plant is likely to be another example, and the need to keep the Baringo filleting plant working has led to the processing of immature fishes.

Modern technology does not always bring the expected benefits. Even such an apparently beneficial thing as the plough has been a mixed blessing to tropical Africa and in some areas has had deleterious effects. Ironically it has recently been accepted that minimum tillage conserves moisture and soil structure and that what was sometimes referred to contemptuously as scratching the surface is often better than the deep ploughing often advocated. It is not unreasonable to compare the plough with the trawl. Both can be of immense benefit, but both can also be dangerous. African methods long deplored by experts - such as mixed cropping systems - are now also hailed as new discoveries and important breakthroughs in agricultural research. Such things are relevant to the conservationist.

Indeed it should not be assumed that the problems of lake management are necessarily always of the kind to which science alone can give a complete answer. Some of them are perhaps nearer to the category of what Hardin (1968) calls 'no technical solution problems', and certainly the freedom of the commons to which he refers, if indulged in without restrictions, can only have disastrous consequences. This does not mean that solutions should be devoid of a scientific input. Such is essential and should be of the highest quality, but it is not all. If solutions necessitate the imposition of restrictions on certain groups for the common good then so be it. The acceptance of such is the hallmark of a mature and caring society.

Large mechanized fisheries have certain advantages, and may be the only ones practicable in many maritime situations, but these may be outweighed by disadvantages in other circumstances, especially if the motive is profit rather than sustained production and conservation of stocks. Regulations do not always control human greed. Bearing in mind both the needs of conservation and the chronic unemployment in Africa it would probably be better to encourage large numbers of fishermen to use relatively simple gear on a lake such as Victoria, and let technology provide things like ice plants, fish smoking and drying facilities, efficient small boats and the wherewithal to distribute catches. Control of fishing effort and gear is easier on the Great Lakes than in the sea where many nations compete. Absolute control could be exercised by banning the import of nets and setting up local plants that could manufacture nets of both the number and mesh size deemed most suitable for the fishery. Net making, probably employing imported twine, is well suited to such local enterprise, and already takes place to some extent. It may also be possible to use locally produced materials for buoys, floats and sinkers, thereby providing additional employment. Of course such a system has its problems, but they are small compared with those now facing the fisheries. It could certainly lead to increased yields of the most palatable species and would at the same time preserve the biological (genetic) diversity that is one of the most priceless assets of these remarkable lakes.

SUMMARY

The remarkable endemic faunas of the Great Lakes of Africa include the world's richest assemblages of lacustrine fishes. These fishes are of immense scientific interest and are also valuable sources of palatable protein. Such properties engender conflicting attitudes between those who wish to exploit and those who wish to conserve them - both with good reason. An account is given of some of the difficulties inherent in the reconciliation of these two desires and of some of the deleterious effects of exploitation in the past, documented by concrete data for specific cases. Declining yields and overfishing are now acknowledged in several lakes even by the most optimistic would-be exploiters. Particular attention is drawn to the most recent development, the introduction of trawling, and to some of its effects, especially on the haplochromid cichlids of Lakes Malawi and Victoria. Possible means whereby the situation might in some cases be improved are discussed and the importance of taking into account not only the biological attributes of the fishes (all too often ignored) but the welfare and desires of those for whose needs their exploitation should be tailored, is emphasized.

POSTSCRIPT

In the three years that have elapsed since this paper was written various items of information have emerged, to some of which it has been possible to refer by updating the text, but one recent development demands particular attention. The introduced Nile perch, *Lates niloticus*, is now well established in Lake Victoria, at least in the north, and some remarkable changes, some of which could not have been anticipated, have taken place. In the Kavirondo Gulf almost all the indigenous fishes that were of commercial importance have not merely declined but have virtually disappeared. This applies even to the formerly abundant and diverse haplochromid cichlids. Thus at Kendu beach, where the Lake Victoria Fishery Service Report for 1950 showed a catch of over 650 000 haplochromids, not a single fish is recorded for 1982 in the Annual Statistical Report of the Kenya Fisheries Dept (1983). The 1950 catch of the two indigenous species of *Tilapia* (now *Sarotherodon*) was 33 787: the 1982 catch nil. The only cichlid recorded in 1982 was the introduced *T nilotica* (now *S niloticus*) of which 132 kg were caught. Other important food fishes - *Bagrus*, *Clarias*, *Synodontis* and large *Barbus* - are represented in the records by 4 kg of *Clarias*! On the other hand there has been a great increase in *Lates* since 1980 and very large catches are recorded. This immediately raises the question of what these predators, which in the early years of colonization consumed many haplochromids, are now eating. The answer is partly given by work of Hughes who finds that 80% of the diet of *Lates* less than 45 cm in length is made up by the prawn *Caridina nilotica*, a food source apparently relatively little utilized by the indigenous fish fauna (N Hughes, personal communication). In the Kavirondo Gulf even *Lates* up to 100 cm in length are now feeding on *Caridina*. Small *Lates* are the predominant fish prey of large individuals!

Many problems present themselves. One wonders whether the *Lates* are still living on the expanded capital of now eliminated fishes, and whether prawn production can sustain the present level of abundance of this predator. One also inevitably contemplates the further spread of *Lates* and its effects, - a process which merits serious investigation. Whatever the outcome, it is already evident that the ecology of at least the Kavirondo Gulf has been irreparably upset by the introduction of *Lates*. This is not a matter of mere academic interest but one that affects the lives of large numbers of local people. Already the situation reveals how unpredictable the results of such irresponsible introductions can be.

Hughes notes further that *Lates* is not liked as a food by the local people, that prices are low, and that because of its large size it cannot be sun-dried and has to be smoked, which is leading to the denudation of certain islands as trees are felled to produce firewood. I am grateful to Mr N Hughes for information obtained by him on *Lates* in the Kavirondo Gulf and for permission to cite it.

CHAPTER 9 SAFEGUARDING PLANT DIVERSITY IN THREATENED NATURAL HABITATS

S K Jain and A R K Sastry

INTRODUCTION

Plants play fundamental roles in the environment of most organisms. They are the main acceptors of solar energy, holding it as chemical bonds. This energy can then be taken up as food by other organisms. Plants largely define the shape and structure of micro-habitats of terrestrial organisms, through the sheer dominance of vegetation and its height, density, cover, litter and chemical features. In marine and freshwater environments, phytoplankton and macrophytes may play vital roles both in supporting ecosystems and in providing habitat characteristics. Coral reefs are partly an exception: their structure is animal dominated, but their survival as living ecosystems depends ultimately upon the food input from plants. Allen (this volume, chapter 2) defines a habitat in terms of species, communities and the places where they live. The plant element in any such habitat is of major importance and must be a prime target for conservation.

Many organisms are closely interdependent with plants for specific micro-environments. If an aim of conservation is to maximize the chances of survival of organisms, the target should be not just for plant life *per se*, but also for an adequate diversity of plant species, so as to provide for these interdependencies.

There are two basic approaches for safeguarding plant diversity in threatened natural habitats. In *ex situ* conservation, the safety of individual, critically important plants may be aided by holding living samples of them in places away from the habitat. Populations may be kept for a while in botanic gardens; seeds may be stored for periods at optimal conditions in a seed-bank; or, as in the case of ornamentals, plants may be released through nurseries to the public, for general horticulture or other practical uses (Synge and Townsend 1979). *In situ* conservation is the major purview of this chapter. This is defined as the conservation of species and ecosystems in the places where they probably existed in the pristine condition, or where they have become established over an extended period.

In view of the increasing human populations and their rising demands on land-uses, conservation has to be confined to selected areas. The conservation may be intensive, along the lines of nature reserves; or it may be extensive, with advice to landowners to follow certain rules in looking after important habitats on their properties.

Priorities for this can be suggested along two lines. Conservation may be directed towards the entire habitat and its total biological richness of plants and animals; or, it may aim to conserve one or more selected taxa.

Conserving selected taxa is more difficult than it may seem: some may in fact not survive without the complex support functions of their original, natural habitats, or at least comparable places with similar features. If no such places are left, one may try *ex situ* conservation, said by some to be the only hope for the survival of species in many areas because of the intense pressures of land uses by humanity, especially in developing countries. However, *ex situ* conservation suffers from severe limitations. The cost of conserving even one species over a long period in a botanic garden or a seed-bank may be enormous. The populations may have to be large to remain viable over a long period. Space in botanic gardens is already so limited that custodians are finding it difficult to maintain even the existing collections. As research commitments widen, the limited land in botanic gardens has to be used for laboratories, offices, and even sometimes residences for workers. As in the case of animals, the long-term conservation of even a small sample of the world's living organisms by such *ex situ* methods seems to be quite impracticable, although for short-term bridging operations they may be of great value (Synge and Townsend 1979).

SOME REASONS FOR SAFEGUARDING PLANT DIVERSITY

Why are attempts made to safeguard biological diversity in threatened habitats? Among the many reasons usually given in support of this, the following are more significant in the present context.

Diversity implies variety. Each living being contributes to this variety by being a unique biological entity. Not only does each species have a different genetic constitution from any other, but every individual differs to a greater or lesser degree. Experience has shown that, more or less unpredictably, some of these variants have certain unique traits or attributes, which can be of immense value in programmes for improving the genetic stocks of the plants and animals to be utilized by humanity today or in the future. It is a function of the conservation of plant resources to ensure the survival of as many of these variants as possible for meeting this utilization.

The second reason comes from the fact that biological evolution is a process that relies upon the continuity of genetic lines. If one or more lines are destroyed, evolution is at best retarded but may eventually continue on its former course. The loss of local lines may cause evolution to be deflected on to a more or less different pathway. At worst, the lines leading to greater diversity in the taxon may be irretrievably broken, with unknown consequences for humanity or other interdependent species, other than greater biological poverty.

The third reason for conserving diversity comes from the importance to humanity of the chemicals produced by plants. Today's technologies have been able to synthesize relatively few of these compounds and it is unlikely that economic processes will be found for this in the future.

Finally, the interactions between organisms in an ecosystem are too little understood for allowing diversity, particularly of plants, to decline. Raven (1976) has pointedly remarked that the extinction of one species of plant is on average accompanied by á ten to thirty-fold loss among other organisms.

THE SPECIAL LIMITATIONS OF PLANTS FOR CONSERVATION

The conservation of the world's remaining stocks of larger animals often steals attention from the equally pressing need to conserve plant life and habitats in general. With this in mind, it is of value to consider the limitations peculiar to plant conservation.

The most significant limitation compared with larger animals is that most plants are attached to their substrate and immobile. They suffer the bondage of being fixed in place, in contrast to the facility of being able to flee at the time of danger. Seen from the eye of a hunter, an animal facing the danger of being shot at or trapped could run for its life and perhaps save itself. A rooted plant cannot do this.

Rooted plants need their vectors to come to their habitats; their pollens as well as their seeds would otherwise be shed only in their vicinity, so they must depend upon external agencies for dispersal. When such vectors are absent, plants are genetically isolated by their immobility: this may have serious consequences for their long-term viability, as it may reduce the out-breeding that is so valuable in producing new forms for coping with the challenges of the environment.

Another disadvantage of being a rooted entity is the inescapable linkage to the single, local microclimate that surrounds the plant. This linkage may develop into such close dependence that it may be impossible to establish the plant at some new locality where the microclimate seems only slightly different. Larger animals are by comparison more easily translocated, provided of course that major climatic factors such as temperature and rainfall are comparable between the new and former habitats. For example, the populations of the one-horned rhino in India are presently confined to the Assam Valley in Eastern India. Studies have been made to find similar habitat conditions in other parts of the country, and Dudhwa National Park, 1200 km to the north west in Uttar Pradesh, has been found to be equally suitable in terms of habitat, and may turn out to be a perfectly adequate translocation site (Hajra and Shukla 1982).

By comparison, the only insectivorous pitcher plant in India, *Nepenthes khasiana*, is endemic in the State of Meghalaya in Eastern India. It grows in only a few spots. Efforts to grow it at other places in the country have met mostly with failure, or with very little success. Compared with animals, a host of extra factors may be critical in plant habitats, such as soil-types and associated micro-organisms, or details of micro-environments such as local, diurnal fluctuations in temperature and humidity.

Such characteristics of rooted plants may result in rather dense populations covering limited areas. This may make them prone to at least local extinction by quite localized pressures. Major damage can occur to localized plants during fire, landslides, flooding or submergence by dam-waters. An example is the imminent danger to certain taxa in the region of a proposed hydro-electric project in peninsular India. The following are some of the taxa that are likely to have their chief or only populations submerged by the waters of the proposed Silent Valley Dam (N C Nair, personal communication):

Antistrophe serratifolia:	Myrsinaceae
Cryptocarya wightiana:	Lauraceae
Hopea utilis:	Dipterocarpaceae
Kanjarum palghatensis:	Acanthaceae
Oberonia brachyphylla:	Orchidaceae
Poeciloneuron indicum:	Guttiferae
Smithsonia straminea:	Orchidaceae
Stylocoryne nilagirica:	Rubiaceae

PRIORITIES BETWEEN PLANT AND ANIMAL CONSERVATION

While many habitats are singled out for attention because they are the abode of some particular endangered animal, this happens seldom where a plant is threatened. Most often it is the habitat's total floristic diversity which justifies its conservation. Exceptions are the reserves for some ornamental groups, such as the proposed Rhododendron Sanctuary in Sikkim and the Orchid Sanctuary in the Darjeeling Himalayas; and for some crop plants, such as the proposed Citrus Gene Sanctuary in Meghalaya.

None of these proposed or existing plant sanctuaries are being proposed as Biosphere Reserves, the scheme whereby the total habitat is conserved as a sample of a major biogeographical region. By 1979 this scheme had resulted in a total of 161 Biosphere Reserves, in 40 countries across the world, with programmes in hand to proclaim others. It is notable in the case of larger animals, some existing sanctuaries, like those for the tiger in Simplipal and Sundarbans, are being proposed for elevation to the status of Biosphere Reserves. Why is this not being done for important plants? It would seem that many conservationists consider wildlife synonymous with wild animals and simply forget or ignore wild plant life.

Usually, whatever natural habitats may be taken up for safeguarding the diversity of life, significant biomasses of both plant life and animal life would be involved. Few have conspicuous animal life but virtually no plant life, although for many the reverse is true. Plants have a unique self-sufficiency for food production through photosynthesis, giving them, in theory, the capacity to survive in habitats without any animals at all.

Co-evolutionary links between animals and plants demand a strictly holistic view to be taken in conserving either and in planning the conservation of their habitats. Not to do this is to prejudice the success of conservation in the long term.

For example, even many monoecious plants require cross-pollination with the help of insects and/or birds. Good examples are the yuccas that are pollinated by the moth Teqiticula (Pronunbo) yuccasella, which depends entirely on the yucca flowers for larval food; Ficus carica with its complicated pollination mechanism, always affected by the fig-wasp, Blastophaza psenes. Other cases are the insect-pollinated species of Arisaema (Araceae), and pollination by the bat Pteropus edulis in the genus Freycinetia (Pandanaceae). Other linkages are seen in the dispersal of seed by animals, even the aid given to germination by the erosion of the seed coat by the animal's digestive system. It is easy to overlook the vital joint functions of plants and animals in the soil: earthworms that increase soil fertility; fungi and bacteria that cause breakdown of litter; ants that bury seeds in the fire prone vegetation of South Africa and Australia, protecting them from heat; and plant roots that bind the soil, helping to prevent erosion. Finally, an item of increasing concern is the rising proportion of carbon dioxide in the atmosphere, perhaps associated with the destruction of plants on a huge scale, especially in the tropics, reducing their contribution to maintaining the oxygen-balance which is vitally important to most kinds of life on the planet.

One must conclude from this that there are sound reasons for making certain that the conservation of plant diversity is given emphasis in keeping with its fundamental importance to the biosphere. At present this emphasis is lacking in many areas, which is a problem that must be corrected.

PLANT DIVERSITY IN TROPICAL REGIONS

Most of the world's richest areas of plant diversity occur in the tropical regions. Raven (1976) estimated the numbers of flowering plant species in various regions of the world to be as follows.

Of the world's 240 000 species of flowering plants, 50 000 occur in the north temperate zone, including Mexico, north Africa and the Himalayas; 15 000 in temperate to arid Australia and New Zealand; 10 000 in the Cape region of South Africa and bordering arid zones; and about 10 000 in temperate South America. About 150 000 occur in tropical regions: of these, about 30 000 are in tropical and semi-arid Africa and Madagascar; at least 35 000 in tropical Asia including New Guinea and tropical Australia; and about 90 000 in South, Central and Tropical North America. Thus about two-thirds of the world's flowering plant species are chiefly tropical in distribution.

Raven (1976) also discussed the statistics of threatened plants. Of some 85 000 flowering plants of temperate regions and bordering arid zones, nearly 4500 are threatened. About a third of these threatened plants are in the Cape region of South Africa. The situation in the tropics appears to be much worse than this. Of about 155 000 tropical flowering plants, some 50 000 will reach threatened status or become extinct by the end of the century. Most of the threatened tropical species will be in Latin America.

The statistics for India show comparable relationships. Of about 15 000 species of flowering plants, about 5000 are endemic. More than 2000 are threatened or probably so. Work on the evaluation of their status, distribution, natural habitats and actions to conserve them are in hand (Jain and Sastry 1980, 1981a, 1981b, 1982).

Some rare plants grow at more than one distant location, such as the following Indian examples: *Coptis teeta*, *Podophyllum hexandrum*, *Valeriana* sp ined. and *Nardostachys jatamansi*. Any natural or unnatural damage to one habitat is not likely to exterminate the species. In many other cases, however, localization is so great that such damage poses a fatal threat to the species, for example *Frerea indica*, which is confined to a very small population in a single place in the Western Ghats.

In certain habitats, such as in island ecosystems, plant species may suffer certain additional handicaps. Being isolated from other land areas by long or short distances, such plants may be unable to have adequate flow of genes between their various populations. Even if the island populations are fairly large, founder effects and the lack of gene-flow may combine to lead to genetic erosion in the long term. A large number of candidates for this condition exist in the Andaman and Nicobar groups of islands. Although it has not been possible to monitor their genetic constitution, many are endemic, rare and confined to small populations. Examples are as follows:

Amorphophallus carnosus:	Araceae
Artabotrys nicobarianus:	Annonaceae
Calamus dilaceratus:	Arecaceae
Cyperus kurzii:	Cyperaceae
Garcinia cadelliana:	Clusiaceae
Hippocratea nicobarica:	Hippocrateaceae
Hypoestes andamanica:	Acanthaceae
Jasminum andamanicum:	Oleaceae
Pubistylis andamanensis:	Rubiaceae
Syzygium andamanicum:	Myrtaceae
Taeniophyllum andamanicum:	Orchidaceae

There are other aspects of island plant life that can be illustrated in the Andaman and Nicobar groups of islands. Situated in the Bay of Bengal, they are the largest chain of islands in the Indian region. Their combined area is about 8300 km^2. The flora is made up of about 2200 flowering plants, of which 210 are endemic to the islands (BalaKrishnan and Rao 1981, 1982). One may compare these data with those of a fairly well-studied area on the mainland, the Jaintia Hills (Jowai) in the State of Meghalaya. The area of this district is about 2000 km^2 and it has 1517 flowering plants (BalaKrishnan 1981). It is less than a quarter of the area of the Andaman and Nicobar Islands, but the species-content is relatively high. However, only six species are endemic to Jowai, far fewer than in the islands. This illustrates the point that islands often show less diversity than mainland areas, but have more species unique to them. The insular condition has inhibited the free flow of neighbouring species to the islands, which has resulted in proportionately less species-diversity, and at the same time restricted the distribution of its indigenous species to other regions due to the barrier of great stretches of open sea.

THREATS TO PLANT DIVERSITY

A general list of threats to natural habitats is given by Allen (this volume, chapter 2). The major threat to natural habitats of plants is the expansion of a variety of land uses. Chief among these are agriculture;

monocultural forestry; towns and related development such as roads and airfields; and mining and quarrying.

The natural plant diversity in an area can sometimes be reduced even without physical damage to the habitat. For example, invasive hardy weeds, particularly exotics, may not only disturb the relative frequency of species in a natural habitat, but sometimes may almost exterminate the local flora. There is an onslaught on the ground-flora in India by exotic species like Lantana camara var aculeata, Parthenium hysterophorus, Eupatorum odoratum, and Mikania scandens (which also damages arborescent plants). In aquatic habitats in India the damage to natural plant diversity by water-weeds such as Eichhornia crassipes has been a subject of much study for the last several decades. So far no satisfactory methods of extermination or large-scale utilization have been found.

India has about 749 000 km^2, or 22% of its land set aside as legally classified forest. Although 570 000 km^2 of this is considered to be effectively afforestable, only 260 000 km^2 are adequately forested (Champion and Seth 1968). These forests are made up of 21 040 km^2 of evergreen rainforest, 8340 km^2 of semi-evergreen rainforest, 102 000 km^2 of moist deciduous forest and 138 750 km^2 of dry deciduous forest. Shifting cultivation affects forests over an area of about 80 000 to 100 000 km^2 (Myers 1980a).

Atlases or maps can be deceptive in the data they give for the areas of forests. For example, Himachal Pradesh is one of the most forested states in India, yet of the area classified as 'forest', only 9% is in reserves and 26% is demarcated as Protected Forests. Only 34% of the area is actually covered by tree-growth, the remainder being scrubland, grassland, and even barren wastes (Singh 1979).

Destruction of forests by collection of timber and firewood is a major problem in India. It is estimated that every year about 211 million m^3 of wood are collected for firewood and commercial timber. The total standing crop of timber in India is estimated to be about 2 500 million m^3. Even if the annual production is estimated at 50 million this rate of collection could cause total deforestation in only about fifteen years' time (Baig 1980).

The destruction of forests is causing massive erosion of soils from mountains, particularly in the hilly states. This in turn is causing silting up of reservoirs: some are filling up with alluvium at a rate almost twice that of twenty years ago (Kayastha and Juyal 1979).

Shifting cultivation, or slash and burn agriculture, is more common in north eastern India than elsewhere in the country. It contributes to the destruction of plant habitats on a considerable scale in other tropical regions besides India. Ramakrishnan et al (1980, 1982) have made detailed studies in parts of north eastern India in the State of Meghalaya, where shifting cultivation, known as Jhum, is quite prevalent. Jhum cycles of cultivation, alternating with fallow, vary in length from 4-5 to up to 50 years. It has been shown that a Jhum cycle of 30 years or longer, as practised until recent times, was in harmony with the environment and sustainable on both ecological and economic grounds. The shortening of the Jhum cycle has been chiefly due to having to grow more food to meet the needs of greater numbers of people, on limited land that cannot be extended. Areas that are permanently infested with weeds are not suitable for cultivation: the reason given for this is that a short Jhum cycle of four to five years had been continuously imposed on the same site for many decades. This problem is widely repeated across the tropical regions of the world.

Scientifically interesting plant groups, such as carnivorous taxa, grow in specialized, local habitats such as marshes, sphagnum bogs and other aquatic environments. Carnivorous plants are adapted to soils lacking organic-derived nutrients. They are able to grow in such places through their ability to obtain these substances from the insects that they trap and digest. These specialized habitats are being subjected to various kinds of changes for forestry, agriculture, farming of aquatic habitats and other pressures, all of which are especially intense near human settlements. Carnivorous plants may catch fewer insects, and receive correspondingly less nutrients, when their marshland habitats are sprayed with insecticides to kill mosquito larvae.

Similarly, several members of the scientifically interesting family Podostemonaceae are adapted to grow only on rocky substrates that are partly submersed in swiftly flowing freshwater streams. Changes in water-flow caused by human impacts upstream have led to shrinkage of these habitats, resulting in the loss of many of the plants' populations.

BIOSPHERE RESERVES FOR PLANT DIVERSITY IN INDIA

The Biosphere Reserve scheme as defined by the IUCN (1980) offers a programme for the identification and setting aside of representative areas from the entire spectrum of ecosystems. The programme has to be highly selective: for a variety of reasons it will not be possible to conserve many present-day natural habitats. This can be illustrated by its application in India.

The IUCN (1980) has laid down the following criteria for the selection of Biosphere Reserves.

Firstly, each Biosphere should include one or more of the following features.

- Representative examples of natural biomes
- Unique communities or areas with unusual natural features of exceptional interest
- Examples of harmonious landscapes resulting from traditional patterns of land use
- Examples of modified or degraded ecosystems capable of being restored to more natural conditions.

Secondly, a Biosphere Reserve must have long-term legal protection. Thirdly, each should be large enough to be an effective conservation unit. Finally, each must be approved by the International Coordinating Council of the Man and the Biosphere Programme before it can be designated as a Biosphere Reserve.

The first step is to identify the natural biomes. In India, this has been done in studies that have mapped out the main biogeographical regions and provinces (Blanford 1901; Udvardy 1975; Gadgil and Meher-Homji 1982). This last study proposed sixteen biogeographical regions, each subdivided into units based upon the main vegetation types. The biogeographical regions were proposed as follows:

Wet evergreen forests of the West Coast and Western Ghats
Ecotone between wet evergreen forests and Teak forests
Teak zone
Transition zone between Teak and Sal
Sal zone
Hardwickia zone
Albizia amara zone
Anogeissus pendula zone
Deccan thorn forest
Transition zone between the Deccan and the Indian Desert
Indian Desert
North western Himalayas
Transitional North western Himalayas to Eastern Himalayas
Eastern Himalayas and North eastern India
Andaman and Nicobar Islands
Coastal zone

The Indian Committee for the Man and the Biosphere Programme has provisionally listed twelve areas as prospective Biosphere Reserves. Many factors were taken into account in the choice of the areas, in addition to those of the IUCN (1980) noted above.

For example, in a report on the situation in Himachal Pradesh, Gaston et al (1981) have suggested that within the western Himalayas one can distinguish ecological change along three principal axes. The first is a vertical axis determined by altitude, where ecological features are related to the effects of temperature variation. The second is a transverse axis cutting across the mountain chain, along which topographic features between the front ranges and the interior cause reduced annual precipitation and increasingly extreme temperature fluctuations. The third is a longitudinal axis paralleling the ranges, along which there is a trend of decreasing monsoon precipitation and greater winter snowfall, from south east to north west. It has been suggested that all three axes should be considered in selecting any areas for reserves and for conserving maximum biological diversity.

An example of one of the places proposed for designation as a Biosphere Reserve is the Tawang area, covering about 3765 km^2 in the Kameng District of Arunachal Pradesh. This adjoins Bhutan and Tibet and, rising from an altitude of 2000 m to 5000 m, has a climate and vegetation that varies from temperate to sub-alpine. A wide range of bryophytes, pteridophytes, gymnosperms and angiosperms appears in the flora. Among the gymnosperms are *Tsuga dumosa*, *Abies densa*, *A delauayi*, *Picea brachytyla*, *P spinulosa*, *Juniperus wallichiana* and *Larix griffithii*, which occur here but not in western Himalaya. *Pinus armandii* and two of the above, *Picea brachytyla* and *Abies delauayi* are outliers of Chinese populations not found elsewhere in the Himalayan region. The forests include several important evergreen trees and shrubs, frequent dominants being *Quercus griffithii*, *Q semiserrata*, *Q lamellosa*, *Magnolia campbellii*, *Castanopsis indica*, *Michelia doltsopa* and species of *Acer*, *Alnus* and *Terminalia*. The area abounds in a number of species of *Rhododendron*. The orchid flora is very rich and includes the very rare and interesting lady's slipper orchid, *Paphiopedilum fairieanum*. The area is also very rich in medicinal plant species, such as *Dioscorea prazeri*, *D deltoidea*, *Lycopodium clavatum*, *Nardostachys grandiflora*, *Orchis latifolia*, *Picrorhiza kurrooa*, *Podophyllum hexandrum* and *Swertia purpurascens*. Several wild relatives of cultivated plants are also found in the area. Along with its generally good representation of the biogeographical region and reasonably undamaged condition, it is clear that these properties qualify the area well for conservation as a Biosphere Reserve.

CONCLUSIONS

The large-scale conversion of natural habitats to human land-uses, especially in the tropical forest regions of the world, has been the major factor responsible for the depletion of wild plant resources. This has been accelerated by the rising need of fast growing human populations. The degradation of wild plant resources is feared in many areas to have gone beyond any possibility of restoration.

SUMMARY

Plants form such an essential supporting feature of the habitats for life that the conservation of locally adapted species forming the vegetation cover should always be an integral part of the management of natural areas.

Plant species of special value to humanity or to particular ecosystems should be conserved *in situ* in their natural habitat. *Ex situ* conservation in botanic gardens or seed-banks should be at best only a temporary bridging operation: at worst it may be the only option when the natural habitats have been destroyed.

Because of the value of particular plants in the functioning of ecosystems, and through this and in other ways to humanity, a plea is made for a better balance of effort between plant and animal conservation. The special problems of plant conservation are reviewed, with examples from the Indian subcontinent and islands. The seriousness of some of the threats is noted: as an example, it is predicted that all natural forests in India will disappear within fifteen years, due to commercial timber collecting and gathering of firewood.

The mapping of biogeographical provinces and the estabishment of Biosphere Reserves are valuable steps in the conservaion of samples of threatened natural habitats in the tropics. In India full attention is being given to plants in these programmes.

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