Conservation of Ecosystems: Theory and Practice

W R Siegfried and B R Davies

A report on a workshop meeting held at
Tsitsikama, South Africa, September 1980

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Editors' addresses

W R Siegfried
FitzPatrick Institute
University of Cape Town
RONDEBOSCH
7700

B R Davies
Zoology Department
University of Cape Town
RONDEBOSCH
7700

PREFACE

One of the main challenges facing mankind is to find answers to pressing problems attending the utilization of natural resources, while at the same time taking care not to create even greater problems in the future. In South Africa, a step towards meeting the challenge has been taken by the Council for Scientific and Industrial Research (CSIR) which has established mechanisms for sharing responsibilities for the planning, execution, synthesis and financing of scientific research of common interest.

The main thrust of the CSIR's nationally co-operative research is through an organizational structure known as Cooperative Scientific Programmes (CSP), which brings together scientists from different disciplines and institutions, and which aims mainly at finding solutions to environmental problems affecting the quality of man's existence. The role of CSP in promoting co-operative environmental research is channelled through its National Committee for Environmental Sciences which is the national body adhering to the international Scientific Committee on Problems of the Environment (SCOPE). SCOPE, the body set up in 1970 by the International Council for Scientific Unions (ICSU), seeks to encourage non-governmental international scientific activity for the benefit of mankind, and to develop means to enable individual scientists all over the world to join in these activities.

In furthering its role, CSP periodically sponsors and arranges international symposia and workshops to assess progress made in relevant research fields, and to identify key questions for future research in these fields. These conferences are designed to meet local needs, as well as the needs of research undertaken in South Africa as contributions to SCOPE and other international bodies.

During the last five years or so, South Africa has spent approximately R20 000 000 on research in the fields of wildlife management and nature conservation. Much of the research has involved studies of individual populations of plants and animals, especially those threatened locally with extinction. This state of affairs has persisted in spite of (or perhaps because of) a widespread recognition that ecosystem conservation still has many aspects that are poorly understood, even though such conservation is the key process in conserving threatened species.

Acting in response to a need for rationalization and improved co-ordination of the considerable body of research focused on threatened species, CSP set up a national committee of experts in 1979 to co-ordinate all research related to nature conservation in South Africa. One of the first acts of this committee was to convene, in association with the Southern African Nature Foundation, an international conference to consider the problems of identifying ecosystems for conservation, of delimiting them and of managing them. Contributors to the conference were asked to supply critical commentaries on: the viability of small habitat reserves in the time-scale of biological evolution; the critical minimum habitat of a threatened species; the layouts of optional core, peripheral and buffer zones which are minimal for threatened ecosystem conservation; the possibility of the development of a blueprint which could ensure long-term success rather than risking public funds in projects that eventually fail; the identification and restoration of threatened ecosystems; the time-scales on which conservation planning should be based; the development of public awareness of conservation problems; and so on. These and other pertinent matters were considered during a symposium held on 11 and 12 September 1980 at the University of Cape Town, under the title of "The Conservation of Threatened Natural Habitats" (soon corrupted to the acronym HABCON). Following the symposium, a workshop meeting was held during 14 - 17 September at the Tsitsikama Coastal National Park. (The names and addresses of the invited participants are listed as Appendix 1.) The workshop used the symposium papers together with a series of pre-workshop "background documents" as the basis for discussions, and this volume is the product of those discussions. The volume should be regarded as a joint effort, since all participants generously shared their experience, data and ideas, and many other colleagues read and criticized the original manuscript. The conveners of the groups of participants responsible for drafting each of the book's chapters also have enclaves of writing in other chapters. Thanks are due to one and all. Finally, this book would not have been possible without Brian Huntley's organizing ability, the generous hospitality of the National Parks Board, the financial support of the Southern African Nature Foundation and the assistance of Diana Banyard, Elize Auret, Marie Breitenbach, Margaret Orton, Suzanne Winkelman and Tisha Greyling.

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1. INTRODUCTION

> "Humans eat participants, not interactions; being relatively incompetent until quite recently, humans have by and large not generated cultural rules for the maintenance of interactions *per se*, but rather for the preservation of the participants."
>
> Daniel Janzen

By the turn of the nineteenth century, the original African wilderness and its populations of large animals had so shrunk and fragmented, due to the rapacious activities of man, that a need for "game reserves" was recognized. This led to the establishment of numerous "national parks" during the first half of the twentieth century, mainly in remote, unsettled areas, which were at that time, of marginal importance for agriculture. Science did not influence the location, size or shape of these reserves.

Today, much of the effort of nature conservationists is still directed at persuading national and local governments to establish nature reserves. Moreover, there is still a widely held, but mistaken, belief that nature conservation is largely a matter of setting aside special areas for the protection of mainly large, spectacular animals. The notion of nature conservation as something much more vital than an assortment of preserved areas or protected populations of plants and animals is only just beginning to impress public authorities. Even further behind is a proper appreciation and realization of the roles of science and economics as integral components of nature conservation. Indeed, it is something of a paradox that many bodies, either corporate or personal, public or private, which profess to advance nature conservation, are also poorly informed about the contributions which modern scientific theory and practice can make to their cause.

This state of affairs is hardly surprising, since the full significance of a dramatic transformation which has characterized the scientific discipline of ecology in the last couple of decades has scarcely been recognized by scientists, let alone laymen. The change, verging on a revolution, has seen ecology advance from a largely descriptive endeavour, bordering on natural history, to a predictive science of considerable import to nature conservation. This exciting, still emerging, development provides new dimensions for an evolutionary-ecological underpinning of practical, mission-orientated conservation.

This is not a textbook. Rather, the book consists of a series of short essays which are designed to highlight the use of the modern understanding of ecological principles, paradigms, theories and other information in furthering effective and practical nature conservation. In keeping with this intent and the need for brevity, the treatment of subject matter is deliberately elementary, much technical detail is omitted and several additional disciplines (such as economics and sociology) relevant to nature conservation are accorded only perfunctory recognition. This caveat is important. We have attempted, without doing the complexity of the subject too much violence, to make the book comprehensible to the reader who has not had a formal education in ecology. Special terms are explained in a glossary, and suggested reading guides the reader to further information on specialized subjects.

The book should be seen as a starting point for persons embarking on making themselves more effectual in the field of conservation. More particularly, the book's recommendations are offered to all who are not necessarily well versed in ecology, but who participate in local and regional decisions which affect planning and managing the conservation of natural resources, and especially sensitive and vulnerable ecosystems. Viewed pragmatically, these ecosystems are those which require special management for their conservation in a natural or near-natural condition. Thus, much of the text is somewhat evangelical; an important message for the uninitiated reader being that it is the grand-scale reduction of biological interactions that is promoting the accelerating degradation of ecosystems and their constituent species of plants and animals (and eventually life as we know it). Attempts to preserve individual species and their habitats offer little by way of preserving biological interactions and without preserving the interactions, species are lost, communities are impoverished and man's life-support systems are threatened. Hence, modern conservation has to do with saving as much biological diversity as possible, but especially those elements of diversity which through their interactions are the determinants of ecosystems and their renewable natural resources.

The book begins with two general chapters which emphasize some of the problems that must be faced, and the ways they can be solved if the modern version of the conservation movement is to gain sufficient acceptance and support for success. The question of interest is no longer whether the cause of nature conservation, and hence the quality of mankind's environment, is serious; it is to what extent, and for how much longer, the delay in the universal integration of ecological theory and practice in planning and managing the utilization of natural resources can be tolerated. The next two chapters provide an ecosystem perspective. This is a prerequisite to understanding a systems approach to nature conservation. Both chapters also stress the importance of prevention of breakdown and loss of dynamic ecological processes and patterns.

Clearly, the traditional wildlife management approach, largely aimed at maintaining individual populations of plants and animals or biotic associations at static levels, does not meet modern requirements. Not only does the traditional approach lead eventually to the decay of ecosystems, it also inhibits the recovery of degraded ecosystems. Indeed, it may be necessary to manage some ecosystems in such a way as to allow for maximum disturbance, so that early, intermediate and late stages of development of biotic communities can co-exist. This raises questions concerning the boundaries of ecosystems and the numbers of organisms associated with viable processes within ecosystems. These topics are taken up further in Chapters 6-8, where theoretical and practical applications of current ideas of ecological genetics and biogeography to the location and geometry of nature reserves are considered.

Increasingly, nature reserves are destined to become isolated "islands" and, in spite of intensive management, they will lose diversity and hence viability. The prognosis that nature reserves have no long-term future (here "long-term" is taken to mean a relatively short period of time, spanning only three or four human generations), unless they are integrated into a series of development programmes designed to promote the survival of man himself, is considered briefly in the final chapter of the book. Traditional conservation practices (e.g., the creation of reserves) must be expanded and rationalized if conservation itself is to continue, which of course, it must.

Throughout the volume, the human species is consistently regarded as an integral evolutionary force in many ecosystems. Only the scale of anthropogenic influence varies between ecosystems, but if present trends continue man could be responsible for the elimination, without any prospect of evolutionary replacement, of about 25% of the world's estimated 3-10 million species of plants and animals in the next 20 years. Bear in mind that this is a projection, not a prediction. Other projections indicate additional environmental devastation, including the expansion by up to 20% of the world's desert areas. But the gloomy prognostication for the year 2000 need not become a reality. According to one expert, this is an exciting time to be working for nature conservation, because so much can be saved and so much can be lost. In the final analysis, there is the need to keep the world a liveable place for our children. This can be achieved if a concerned citizenry can persuade the nations of the world to co-operate in long-range planning, policies and actions necessary for dealing with the major problems of population growth, use of natural resources, and threats to life-support systems.

2. GOALS OF ECOSYSTEM CONSERVATION

R Allen (convener)

A P Bowmaker, C K Brain, D Edwards, G Newman, R N Owen-Smith, A J Ribbink, R L Specht

INTRODUCTION

Man's attitude to plants and animals differs from culture to culture and changes over time. The meaning of nature conservation has, for example, changed from preservation of wildlife and "natural" areas, to something far more complex and comprehensive, namely: 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. Within this definition, which has been adopted officially by the International Union for the Conservation of Nature and Natural Resources (IUCN), lie three overall goals of conservation. They are: to ensure that the biosphere can continue to renew itself and provide the means for all life; to ensure human survival and well being; and, to keep options open.

The first goal is an acknowledgement that the human habitat is now the biosphere as a whole. Modern human societies draw on a wide range of ecosystems near and far for the resources that sustain them. Furthermore, human activities have global impact. Man's capacity to alter the biosphere greatly exceeds his current understanding of it, and in some instances (e.g., desertification) it seems likely that the productivity of the biosphere has been reduced permanently. The second goal of conservation is to maintain indefinitely the biosphere's capacity to produce the resources needed by people. Humanity's future needs are unpredictable. History suggests, however, that the needs of people a few generations hence could be very different from those of today. Thus, the third goal of conservation must be to keep open as many options as possible in order to meet these potential needs of future generations.

Conservation is for and about people. If there were no people, there would be no need for conservation. People are conservation's beneficiaries. But many people are also concerned with the survival of species of plants and animals for their own sake. Man's influence on the biosphere is now so great that he holds the fate of a great many species in his hands. This is an awesome responsibility for which human societies are poorly equipped in experience or, as yet, ethics (see Chapter 3). Three specific objectives need to be achieved to meet the general goals of conservation. These objectives are interdependent, but distinguishing them, as set out below, helps to define priorities and the actions to be taken.

OBJECTIVES OF NATURE CONSERVATION

1. Maintenance of essential ecological processes and life-support systems

Ecological processes keep the biosphere going; without them life would not be possible. They include the cycling of oxygen, carbon, phosphorus, nitrogen and other essential mineral elements including trace elements, the formation and protection of soil, the cleansing of air and waters, the disposal of wastes and the recycling of nutrients. They are the life-support systems of both the planet and man (see Chapter 4).

The action required to maintain these support systems depends on their scale. At one end of the spectrum are global processes, such as the cycling of essential mineral elements, and the regulation of the chemistry of the planet, so that it remains fit for life. Certain ecosystems may play a crucial role in these processes, but they have not yet been identified. Hence, important though they are, the manager can do little about them at this stage. There are, however, several intermediate processes, on which the productivity of agriculture, forestry, pastures and fisheries depend, and which the manager can influence. They include the production, regeneration and protection of soil, the regulation of water flow by watershed vegetation, the provision of nurseries for fishes by estuaries, lagoons and other coastal wetlands, and the concentration and fixing of nutrients dispersed in the sea by coral reefs. These processes are free services, the loss of which adds enormously to the cost of producing food and other necessities. Some of the support systems are for all practical purposes irreplaceable. For instance, it takes from 100 to 400 years or more to generate 10 millimetres of top soil. At the other end of the spectrum are local processes, such as pollination and seed dispersal. These processes are as important to relatively small areas (e.g., nature reserves) as are the global processes for the entire biosphere.

The prime use of the major part of the earth's land surface must be to supply food to support the human population, whatever success may be achieved by population control. Transformation of large parts of the earth's surface and significant modification of much of the remainder are therefore inevitable. The challenge for management is to ensure that such transformations and modifications do not create biological deserts - areas that are incapable of sustaining life-support processes in the long term, because of artificially accelerated soil erosion, siltation, pollution, and biotic extinctions.

2. Maintenance of biotic diversity

The biota (plants, animals, and other living organisms) are the building blocks of the biosphere and the raw material of evolution. There are, broadly speaking, two types of biotic diversity: species diversity and genetic variation within species. It is essential that both should be maintained. The maintenance of species diversity can be achieved by maintaining those ecological processes that occur through particular species (e.g., pollination by animals) or through ecosystems in which certain species or groups of species play key roles. Such key roles include maintenance of crop exploitation, for forest and wildlife (including fisheries) products, maintenance of medical, industrial and scientifically important species, as well as those species, or species groups, that may be needed in the future, and maintenance of cultural (including aesthetic and recreational) needs. The maintenance of genetic variation within species is particularly necessary with respect to crops, livestock and their wild relatives to provide a pool of different characteristics on which to draw, to help control pests and diseases, to increase yields, and to make other improvements. Finally, the resilience of the biosphere and its capacity to support life may also be to some extent a function of the number of species and of variation within those species.

Ecosystems may be identified by their constituent species. It is these species which are responsible for carrying out ecosystem processes, such as energy capture and transformation, nutrient cycling, and the regulation of these processes under fluctuating climatic, and edaphic and biotic conditions. Certain species may be much more important than others for these processes. Human societies draw on a wide range of wild species for food (e.g., fish), raw materials (e.g., timber, pharmaceuticals, hormones, gums, resins, alginates), and ideas (e.g., imitation of chemiluminescent processes). As many of these species as possible (and the genetic variation within them) need to be maintained, as well as other species for which uses may be found in the future. Since it is not possible to predict future needs or applications, what this requirement means is the conservation of as many species as possible, concentrating in the first instance on clusters of interdependent species which together constitute the biotic communities of ecosystems. People of many cultures have a great attachment to plants and animals, drawing on them for inspiration, art, poetry and song, dance, religion and ritual, recreation and refreshment. For example, certain animals serve as totems for particular tribal groups among people in different parts of the world. Frequently these animals are the major herbivores or top carnivores within their communities and, as such, they are dependent on the continued functioning of a whole host of associated organisms for their survival. As with material needs, human non-material needs change, and as many species as possible need to be safeguarded to meet those needs.

Most food production depends on relatively few crop species, but within those species there is variation as a result of their spreading far beyond their centres of origin. This pool of variation is the raw material which has enabled plant breeders to obtain substantial improvements in yield. The many cultivated varieties and their wild relatives need to be conserved to consolidate these improvements and achieve new ones. Botanical or zoological gardens may serve for the short-term preservation of small collections of wild species, but such remnant populations are deprived of the necessary range of environmental and genetic variation that might be needed (see Chapter 6). In the long term, wild species of plants and animals can be conserved only as members of the diverse biotic communities of which they form an integral part within functioning ecosystems.

3. Sustainable utilization of species and ecosystems

Living resources are renewable. As such, their yields may be sustained over long periods provided they are not utilized beyond their capacity to recover. The groups of species and ecosystems of immediate concern are: those on which people depend for subsistence, those that are commercially exploited, and those that are used for sport and recreation. These forms of utilization are not necessarily incompatible. Subsistence communities in particular can utilize resources from ecosystems to a significant degree and these can provide substitutes for more conventional resources. In Botswana, for example, a total of 3,4 million kg of springhare meat is taken each year by people living at the subsistence level. This is equivalent to that obtainable from 20 000 cattle.

Living resources, be they aquatic or land animals or wild plants, frequently are utilized to a degree that is not sustainable. For example, intensive industrialized monocultural practices in agriculture or pelagic fishing operations have the capacity to alter or damage ecosystems in a gross manner within a short period. The activities of subsistence communities may affect the systems at a slower rate and in a less direct fashion; nevertheless, this impact can be as serious. Both situations require management, albeit with a different emphasis.

Sustainable utilization of species requires knowledge of their abundance and demographies, together with measures which ensure that utilization does not exceed critical thresholds. In many instances the productive capacities of these resources are not known, and the first step towards sensible management is the gathering of information. Knowledge of the productive capacities of exploited species and ecosystems is important to avoid over-exploitation or to ensure recovery. The rate and nature of this recovery depend on the biology of the species, as well as on the quality of the ecosystem. Decisions often have to be made without detailed knowledge, and for this reason management objectives should be conservative to allow for error or uncertainty.

Access to the resource should not exceed the resource's capacity to sustain exploitation. Various methods which are available to deal with this include quotas and limited participation, and it is essential that such controls be introduced at the onset of exploitation. Unfortunately, this is seldom the case, and the severe problem of the reduction of existing participation must be faced. This inevitably requires short-term sacrifice of investment capital and labour opportunities and production, for future gains in the form of more stable utilization, which certainly requires fewer inputs. Control may also include restriction of access to the critical habitats of exploited species - those habitats crucial for feeding, breeding, nursery and resting functions. Suitable examples of critical habitats may be found in the marginal vegetation of shallow lakes, wetlands and floodplain rivers of tropical Africa.

It is also important to realize that focusing attention on the need to manage single target species only, without taking into account other species or the ecosystem, can have an adverse effect on yields. A mixed-species approach to management can often result in a greater total yield for the habitat, as the yields from each component are optimized.

In more extreme cases, a failure to take other species into account can result in a decline in the yield of one species, with a subsequent shift of attention to another, less desirable species. Continuation of this process can result in reduction of species required for the recovery of the original, more desirable species. Another possible alternative could be the replacement of the target species by a less desirable species, through a competitive advantage brought about by exploitation.

ACHIEVING THE OBJECTIVES

Only two per cent of the land surface of the planet and 0,001% of its waters are included in protected areas. Hence, the direct contribution of protected areas to maintaining essential ecological processes and to sustainable utilization (conservation's first objective) is not nearly as great as that of management of resources outside those areas. Domesticated varieties of plants and animals are best protected *ex situ* in gene banks, breeding farms and nurseries. Wild species are best protected *in situ* (e.g., nature reserves). Except for migratory and other wide-ranging species, protected areas in terrestrial ecosystems are likely to make a bigger contribution to the maintenance of biotic diversity than will management outside protected areas, but land and water uses in the vicinity of protected areas will need to be regulated carefully to reduce the "island effect" (see Chapters 7 and 8), as far as possible.

Management outside protected areas is of prime importance with regard to the other two objectives (ensuring human survival and well being, and keeping options open). Although some ecological processes can be associated with fairly well defined ecosystems (e.g., the provision of nutrients in coastal wetlands), many processes and their support systems are too large to be within protected areas. Furthermore, processes do not need to be given the same degree of protection that is required for the maintenance of biotic diversity. Many uses are acceptable, provided they do not undermine the support systems concerned. For example, properly managed logging may be reconciled with watershed protection, but such forms of use may be incompatible with maintenance of biotic diversity.

Although the direct role of protected areas is minor with respect to the maintenance of essential ecological processes or sustainable utilization of species and ecosystems, their indirect contribution is crucial. Protected areas provide essential research tools for advancing understanding of processes and of capacities of species and ecosystems to sustain particular levels and kinds of use. They also meet human recreational needs and serve as sites for conservation education. The importance of the latter needs emphasis. Without experience and an understanding of the significance of life-support systems and ecological processes, especially biotic diversity, it is unlikely that human societies will make the decisions necessary to ensure the continued functioning of the biosphere to sustain future generations.

The allocators of areas of water and land to protection should recognize that the indispensable functions of protected areas are: maintenance of biotic diversity, provision of research facilities, and promotion of public understanding and demand for conservation. The planners and allocators of land and water for all other uses should attempt to reconcile those uses with the achievement of the other two conservation objectives. This can be achieved principally by zoning (e.g., by reserving prime farm land for agriculture or excluding urban development from highly productive areas) and by scheduling (e.g., by prohibiting trawling off turtle nesting beaches during the nesting season). The sooner areas required for protection, zoning or scheduling are identified and land and water uses allocated accordingly (e.g. water use on a catchment basis), the easier it will be to avoid conflict among those uses and to achieve the objectives of conservation.

3. OBSTACLES TO THE CONSERVATION OF ECOSYSTEMS

G C Ray (convener)

K H Cooper, C B Cottrell, D R Given, J R Grindley, J C Scheepers, G Shaughnessy, K L Tinley

INTRODUCTION

Ecological processes are being disrupted on a global scale, biotic diversity is being lost at an accelerating pace, and many species and ecosystems are being overexploited. Yet, long-range global conservation programmes aimed at arresting desertification, destruction of tropical forest, loss of farmland, and overexploitation of marine resources, for example, are in no way sufficient. A second major obstacle to effective conservation lies in the mismatch that exists between the theory and facts of conservation science, on the one hand, and the practical management of ecosystems, on the other. Adequate knowledge is available, which favours the view that the ecosystem should be the fundamental unit for the conservation of renewable natural resources (see Chapter 4). However, management practice rarely makes the best use of such knowledge. This chapter addresses aspects of these problems, and suggests how they might be resolved.

THE LACK OF A STRATEGIC APPROACH

The benefits which societies stand to gain through the conservation of ecosystems will accrue only if clearly conceived strategies for global, regional or national action are implemented. The lack of such strategies means a continuation of haphazard approaches to nature conservation. The end result of this state of affairs cannot be predicted in detail, but undoubtedly there will be large-scale destruction of life-support systems, accelerated extinction of species, and a general deterioration of the quality of life for mankind (see Chapter 2).

Successful ecosystem conservation involves a strategy which encompasses the development and use of a number of concepts and tools, based on knowledge of how ecosystems function. However, the institution of conservation strategies is, in general, primarily determined by societal norms and personal preferences which are not necessarily co-equal with ecological considerations. Such value judgements vary greatly among cultures, whereas ecological features and functions have evolved over millenia. Thus, a major problem for conservation consists of successfully placing conservation actions high among the values of present-day cultures. Such re-adjustments to cultural values will require extensive programmes of public education. It is not the purpose of this chapter to examine this aspect further, but it is a subject requiring urgent attention.

The World Conservation Strategy (see Chapter 2) offers a blueprint which considerably expands "traditional" conservation practice. More particularly, it is concerned with the ultimate, often positive, relationships between conservation and development, and its objectives include the sustained use of natural resources as well as the protection of habitats and species. Thus, in order to develop sound ecosystem conservation strategies, development objectives require classification, so that development and conservation may enhance one another. Many, if not most, development and conservation schemes tend to address proximate, short-range problems only. For example, the overexploitation of depleted animal populations may be a simple proximate problem, but it can excite a great deal of public attention. The associated penultimate problem may be social or economic, such as a need for food or a market for skins. The ultimate problem, on the other hand, is almost always related to development policy and the long-range use of natural resources and, although such ultimate problems require most attention, they are the most neglected.

DETECTION OF THREATS TO ECOSYSTEMS

In order to select the priorities for conservation action, it is necessary to obtain a general picture of ecosystems and the factors threatening their maintenance on national, regional and global scales.

The term "threatened" is used here in a general way to include the four categories Extinct, Endangered, Vulnerable and Declining, and Rare. These terms cover ecosystems and habitats, as well as populations of plant and animal taxa, and are defined, according to the International Union for the Conservation of Nature and Natural Resources (IUCN), as follows:

> Extinct. No longer known to exist in the wild, after repeated searches in all former and other possible localities.
>
> Endangered. In immediate danger of extinction if the causes of endangered status continue to operate. Included are ecosystems and habitats where populations are so critically reduced that a breeding collapse due to a lack of genetic diversity becomes possible, whether or not they are threatened by human activity.
>
> Vulnerable and Declining. Used for ecosystem or habitat types which were recently more widespread, but are now not only in decline, but are likely to become endangered if the causal factors for their decline continue to operate.
>
> Rare. Ecosystems or habitat types which are limited in their distribution. They are not declining and are under no known immediate threat. Because of their rarity, such habitats should be checked regularly for a decline due to some unexpected pressure.

Certain ecosystems face greater risks than others. For example, although the marine coastal zone is home to 50 per cent of the earth's peoples, it is as threatened as tropical forests, but receives relatively little attention from conservation agencies. Coastal and inland wetlands of various kinds are also widely threatened, as are many species of potential commerical importance in many developing countries, but there are few inventories or records of their status. "Sensitive" ecosystems (see

Chapter 4), such as estuaries and certain peculiar ecosystems found in caves and hot springs, also require attention because of their uniquely adapted biotas.

The problems of detection of change in status of ecosystems, and methods of assessment of threat to them are very different for different ecosystems. Again, the marine environment serves as an example. In this case, it is extremely difficult to asses threats and changes, simply because they are less obvious than in the terrestrial environment. While certain ecological problems in estuaries may be obvious even to the layman, some of the more subtle changes taking place in the pelagic zone of the sea can be recognized only by experts.

Sophisticated human communities contrast greatly with those of developing countries in terms of the information available on the status of, and the public awareness of threats to, ecosystems. Often the greatest changes are taking place in countries where the significance of such changes is understood least. However, even so-called developed countries often fail to recognize the importance of threats to ecosystems, although the existence of certain threats may well have been noticed. For example, there may be more local concern about the failure of a rare migratory butterfly to appear in an English marsh than about a decision to clear a vast area of tropical forest in a developing country, yet the organization responsible for clearing the tropical forest may well be based in a highly-developed country. The contrast in understanding between the developing and developed nations is especially severe in the case of the need to conserve fresh-water ecosystems. While the ecological significance of aquatic systems is becoming recognized widely in developed countries, their utilization frequently is misguided elsewhere. Thus, an increased awareness of ecological principles is often in conflict with conservation, especially with regard to disease control, increased food production, and other aspects of development.

The nature of a threat, as well as its recognition, often involves complex interacting ecological and social factors. Each of these factors must be considered in the development of tactics for conservation action. It is not the purpose of this chapter to detail the methods involved (Chapter 10 contains suggested readings, which will serve as a guide).

IDENTIFICATION AND SELECTION OF ECOSYSTEMS FOR CONSERVATION

A fundamental requirement for the protection of ecosystem and biotic diversity lies in the identification and selection of representative, as well as unique, areas for special status as protected areas. However, at present there is only one satisfactory system for classifying ecosystems for conservation purposes. This is a terrestrial classification, and it must be emphasized that comparable systems are not available for fresh-water or marine ecosystems. Moreover, a spectrum of possible classifications exists, reflecting a wide variety of ecosystem boundary perspectives (see Chapter 4). Thus, there is an inherent incompatibility between possible classification schemes. This remains a major stumbling block to the successful design of a world-wide network of representative and unique ecosystem reserves.

The difficulties in identifying representative and unique areas, together with threatened systems within these areas, are heightened by biotic clines or changes along gradients, which are expressed in ecotones. Ecotones are often areas of considerable habitat and species enrichment which are, in themselves, of extreme importance for conservation, but which often are overlooked by classification systems that seek to identify core areas of representativeness. Ecosystems which are unique, such as caves, hot-water springs, mountain summits, oceanic trenches and sea-mounts, often are difficult to classify and often are lost in conventional classification schemes. Other examples in this category are the usually small disjunct core areas of migrant animals, biome or ecosystem outliers, such as remnants or refugia, and centres of speciation. These elements may be missed entirely if the survey scale used for classification is too coarse and if consideration is given only to the major and most widespread ecosystems. Despite these difficulties, the identification of representative and unique areas, based on ecosystem classification, should proceed as a matter of urgency. The use of over-lapping, even conflicting, schemes may result in redundancy, but this is preferrable to omission of some ecosystem types due to classification gaps.

Once the identification process is complete, the next step is the selection of areas for special protection status. This requires the development of a clearly defined set of agreed criteria. Without such criteria one cannot proceed any further and the omission of this step is as serious as the general lack of compatible classification schemes. As in the case of ecosystem classification and area identification, there are many criteria and associations of criteria which may be used in the selection of ecosystems that can serve as protected areas. However, the criteria should follow directly from the strategy mentioned above; that is, the "weighting" of criteria can only be achieved according to national, regional or other values. Thus, the selection of sites for the protection of species and habitats, or for the maintenance of ecological processes and resources, depends to a great extent on which classification is used and also on the objectives for which the sites are to be selected. For instance, if the objective is to select areas of high endemism, then a set of sites will emerge that differs from a set chosen to represent major biomes. In this context, past conservation efforts have placed far too much emphasis on the criterion of "naturalness". Indeed, if this criterion were extended to its logical conclusion, there perhaps would be only a few nature reserves in the world: one in Greenland, one in Antarctica and some in the deep sea. Therefore, the identification and selection processes should not exclude disturbed or man-modified sites, even those that are disturbed to a considerable extent. These processes should take into account the effects of human activities, as well as features of natural evolution. There is just as much need to study the recovery and restoration of biotic communities, as there is to study "natural" processes. The result of this logic is that, if suitable examples of natural systems are unavailable, all is not lost if damaged areas or those with restoration potential are selected. The other side of this coin concerns the fact that certain ecosystems and their components require natural perturbations, including catastrophic events such as fire and flood, for their maintenance (see Chapter 4). The important point here is that these ecosystems require protection from "stabilization" or other "preservationist" activities which may unwittingly destroy them.

In summary, the selection of representative samples and unique areas for conservation involves: first, their identification; secondly, the specification of selection criteria based upon conservation objectives and strategies; thirdly, the availability of suitable areas; fourthly, assessment of the quality of the areas identified for selection, whether intact or disturbed; and, most essential, the setting of priorities for strategic conservation action as discussed at the beginning of this chapter. Currently, most of the methods available for achieving these goals are much too generalized to ensure that representative samples and unique elements with the greatest potential for conservation will, in fact, be protected. Furthermore, most selection processes are by nature highly qualitative; there is a need for quantitative assessments of the values concerned.

Finally, care must be taken to avoid selecting too many sites, so that the responsible institutions are not required to manage more than they can handle efficiently and effectively. A particular problem in this context is that scientific criteria for nature conservation are still developing. Furthermore, such scientific criteria are not yet well integrated with management needs. This is at least partly the result of the long-range view of scientists versus the more immediate needs of management. The frequent result is that areas selected for conservation result from "what is left over", because scientific or ecological values remain unappreciated. Thus, no matter how good the classification, identification and selection processes, a truly representative network of ecosystems can hardly be implemented for purposes either of conservation or development, or of research and monitoring. This historical situation must be improved as far as possible.

MONITORING CHANGES IN ECOSYSTEMS

Although protected areas are an essential component of any conservation strategy, too much emphasis given to them may divert attention from unprotected ecosystems. At the same time, it may not be possible to protect certain ecosystems in designated areas only. Both marine and exploited ecosystems are most notable in this context; the former are generally too large for inclusion, while the latter may often be unsuitable candidates. Nevertheless, management and conservation based on environmental monitoring is essential for them all, and it must be emphasized that it is just as important to monitor ecological changes in designated areas (see Chapter 8), as it is in non-designated areas where threats and stresses are often greatest.

Monitoring is one of the most important aspects of ecosystem conservation and one of the most neglected. It is only by long-term monitoring, and the regular processing of the results of monitoring exercises, that theories and predictions concerning the proper functioning and conservation status of ecosystems can be evaluated. This is especially necessary, because so many of the current theoretical underpinnings of conservation science are based on information and concepts derived from many different fields of scientific endeavour. However, this poses a problem for conservation in so far as the general applicability of the findings of science to the field of conservation-management has not, as yet, been tested fully. In this context, museums throughout the world are charged with the responsibility for collecting, describing and recording the flora and fauna of their regions, but few, if any, of these institutions are required to record changes in ecosystems or to focus on "indicator" species. Of particular concern is the fact that alien plants and animals are nearly always neglected by scientific collectors, in favour of indigenous species. Ecologists tend to seek out "undisturbed" ecosystems for their studies, and neglect the ecological changes taking place in other systems.

Monitoring operations should be initiated as soon as a unique or representative ecosystem has been identified and specific localities or areas have been selected for conservation. This should be the rule irrespective of whether or not the areas concerned have already been designated or are about to be designated as reserves. This also applies even if an area may possibly fall under certain conservation legislation at some as yet unspecified time in the future. The immediate objective of monitoring should be arrived at as an examination of the characteristics of the ecosystem which determine its uniqueness or representativeness. The question which should be uppermost at this stage is: are these determinants being conserved adequately. The monitoring programme should detect any failure sufficiently early for effective remedial action to be taken (see Chapter 8).

PRACTICAL PROBLEMS

Even when information on a conservation site is satisfactory (which is rare), information dissemination is hampered by poor communication between decision-makers, scientists, managers and the public. As a result, numerous countries lack, or do not use properly, the information necessary for correct decisions and planning, and the consequent time-lag between framing and actually implementing recommendations frequently leads to unnecessary ecosystem damage or destruction. Procrastination by decision-makers exacerbates the situation and mechanisms are needed urgently, whereby critically threatened ecosystems can be safeguarded before detailed information is available on them.

Lack of co-operation and co-ordination among official conservation agencies (national, regional and local) is the rule, rather than the exception in most countries. A lack of co-operation between the public and private bodies also causes problems, in that time and effort are wasted on relatively petty arguments. Professional planners, such as architects, land-surveyors, engineers, and town and regional planners, whose actions frequently affect ecosystems, often neglect or reject interdisciplinary co-operation involving ecologists in development projects. Ideally, the technologies of engineering and planning should follow ecological considerations, not direct them. However, to bring this about, biologists in general, and ecologists in particular, must take a firmer and more positive approach to the promotion of their expertise and general public image. In practice, compromise solutions will often have to be arrived at after settling for various "trade-offs". Emotional criticism by segments of the general public, under the banner of "environmentalism", of the actions of planners and developers has contributed greatly to the retardation of effective conservation. This is by no means alleviated by the superior attitude often adopted by professional ecologists in their dealings with politicians, engineers, developers and others, and can only hinder the acceptance of the ecological point of view by these groups.

Since ecosystems do not observe political or official departmental boundaries, it is important that there should be close co-ordination between all governmental agencies responsible for the development and management of natural resources. It is also essential that the jurisdictions of the different agencies be defined clearly, so that they dovetail in such a way as to preclude any loopholes. Conservation opportunities often are missed, and problems frequently are left unresolved, when inter-departmental disputes over responsibility arise. A particularly vexing problem of institutional integration rests on the mismatch between government agencies, scientists and private conservation organizations. Indeed, some private conservation organizations go so far as to reject scientific knowledge as incompatible with their best interests, or as being out of harmony with their particular viewpoints. Furthermore, certain scientists seem to be either unaware of, or unconcerned with, conservation problems. It is crucial to conservation that appropriate scientific research and conservation aims be directed along similar lines, so that governments can respond simultaneously to both the facts of science and the requirements of conservation.

The lack of properly trained personnel in the field of conservation is yet another problem in ecosystem management in both developed and developing countries. Furthermore, the list of professional personnel needed by developing countries is long: ecologists, geologists, environmental planners, and this, together with a serious shortage of technicians, places a major constraint on the development of sound conservation programmes at this critical point in human history.

CONCLUSION

A lack of awareness of the benefits of scientifically-sound ecosystem management and its relevance to every-day concerns, prevents policy-makers from perceiving the urgent need to achieve conservation objectives. Ecosystems are being destroyed simply because people do not appreciate that it is in their interests not to destroy them. The benefits of untransformed ecosystems are regarded by most people as dispensable, in comparison with those benefits which may be gained from activities which lead to their destruction. In other words, there is a general inability to perceive the long-term consequences of actions intended to provide short-term benefits. The problem can be overcome, at least in part, through improved education, and this should be reflected in strategies which inextricably tie conservation and development together. Only in this way will the often observed adversary positions of conservation and development be transformed into mutual and long-term benefits, and only then will the two major obstacles of problem recognition and the mismatch between theory and practice, be properly addressed through the best use of all available ecological and socio-economic information.

4. ECOLOGICAL CHARACTERISTICS OF ECOSYSTEMS

D B Botkin (convener)

B R Davies, D Edwards, P G H Frost, G L Lucas, G Newman, A Rabinovitch-Vin, G C Ray, R L Specht, R van der Elst, B H Walker

INTRODUCTION

A large part of modern conservation effort focuses exclusively on single species. This action is misguided, since species can only be conserved successfully by recognizing that they form integral parts of ecoystems. Life is sustained by the flow of energy and the cycling of nutrients. These processes can only occur in systems that consist of interacting populations, together with a complex non-living medium that serves as a mechanism of storage and transport between individual organisms. One may preserve a genotype in a freezer or in a laboratory, and one may preserve individual organisms by nurturing them in a domesticated condition, in a zoo or farm or laboratory, but one cannot conserve a species in its natural state without conserving the ecosystem in which it lives. The ecosystem is the smallest unit that can have the characteristics of organic and inorganic interaction and recycling. Thus, the only relevant conservation strategy should be the conservation of ecosystems and their constituent communities of plants and animals.

The context should be even broader. Ecosystems are linked interdependently. Thus, to sustain one ecosystem one must sustain many. The only system we know of that can sustain life over very long periods is the earth's entire biosphere. Therefore, the goal of conservation must focus not on individual species, and ultimately not even on individual ecosystems, but on the conservation of the ecosystem mosaic which makes up the biosphere.

IDENTIFICATION OF ENDANGERED AND SENSITIVE ECOSYSTEMS

The practice of ecosystem conservation involves three sequential steps: identification of the overall problems and objectives of conservation; identification of the geographical areas in which problems exist; and, then, the design of a management programme which will achieve the objectives in the selected areas and systems (see Chapter 3).

In terms of threatened or sensitive ecosystems, four categories can be identified: ecosystems threatened by reduction in size or in number; intrinsically sensitive ecosystems; ecosystems threatened by disruption of essential processes; and, incomplete ecosystems. The somewhat indiscriminate use of terms such as vulnerable, threatened, fragile or sensitive, can lead to confusion. Here we will use only two terms to distinguish between two fundamentally different conservation problems. "Threatened" ecosystems are those which are indeed threatened by some form of development, leading to their partial or complete loss. In this case, protection is required regardless of the state of the ecosystem. "Sensitive" ecosystems are those with little resilience and which, when subjected to stress and change, are unable to recover, or which recover only very slowly and may even change further when the disturbance is removed.

1. Ecosystems threatened by reduction in size or number, and which are few in number, or small in extent

Certain ecosystem types are few in total number and some are small in size. Thus, there is at present a danger of their being lost. In North America, alpine tundra is an example of this kind of threatened ecosystem. In South Africa, the ephemeral pans of the highveld, the remaining natural forests, and estuaries and coastal wetlands all fall into this category.

2. Intrinsically sensitive ecosystems

Some ecosystems are extremely robust and relatively difficult to damage permanently, whereas others are sensitive to disturbance and have very long recovery times (e.g., mature rainforests and tundra). Still others depend upon periodic (but natural) perturbations for the maintenance of a "steady state" (e.g., barrier islands subject to overwash and certain coral reefs which may be subject to wave stress). Particularly sensitive ecosystems include those which lie on geologically unstable substrata (e.g., sand dunes and steep slopes subject to landslides) as well as those which are strongly dependent on external inputs (e.g., estuaries and mountain streams). In this context, it is important that ecosystems be classified or ranked according to their sensitivity to certain kinds of treatment by man, and it is crucial that we investigate the most useful indicators of sensitivity.

3. Ecosystems in which there is a disruption of essential processes

This category is exemplified in the northern hemisphere where many areas are subjected to the influences of "acid rain", produced by industry located sometimes hundreds or thousands of kilometres away. In Sweden, Norway and Canada this has altered the ecological processes in lakes, by changing the chemical composition of the water and thus reducing or eliminating the populations of many different species. A second example comes from Africa, where the loss of nutrients in most savannas through increased fire frequency and overgrazing has already reached serious proportions.

4. "Partial" ecosystems which are incomplete in terms of processes, such as may occur through the removal of key species, or by loss of area, or the introduction of barriers

CHARACTERISTICS OF ECOSYSTEMS

Ecosystem definition

An ecosystem is usually defined as an ecological community and its local abiotic environment. The ecological community is defined as a set of local interacting populations of organisms. However, the essence of each ecosystem lies in the ecological processes which take place within it. There must be a flow of energy and a cycling of vital chemical elements if life is to be sustained in any ecosystem: food converted into waste and *vice versa*. Hence, here we take the definition of an ecosystem to be a *community of* organisms interacting with the local abiotic environment and forming a system in which life-sustaining processes are maintained. The ecosystem involves the accumulation, circulation, and transformation of energy and matter through such biological processes as photosynthesis and decomposition. The processes are coupled by means of the non-living fluid media, in part involving precipitation, erosion, and deposition, and these provide the means of transfer and storage of energy and materials used by living organisms within the ecosystem, and in many cases by those of adjacent ecosystems (e.g., leaf-fall from a woodland into a stream).

Ecosystem boundaries are often identified by changes in vegetation, or physiographical, zoological, or geomorphological transitions, while the extent of the ecosystem depends on the focus of the observer. Some ecosystems, such as oceanic islands, may be isolated biologically from each other. Others, such as a fresh-water lake in a forested watershed, are strongly connected both biologically and physically, and changes in both lake and forest are often interconnected. Nature reserves with artificial boundaries may be whole or partial ecosystems, depending on the size of the area and the kind and degree of isolation provided by the boundary. Agricultural fields may also be thought of as ecosystems which are heavily managed both within and across the boundaries, by the farmer who substitutes crop maintenance for the ecological transfers that might otherwise have taken place naturally.

Ecosystem identification

The differeneces between current classification schemes for ecosystems in terrestrial, fresh-water, coastal zone, and marine environments constitute a major stumbling-block in the selection and design of a world-wide network of representative and unique ecosystem reserves (see Chapter 3).

Before representative ecosystems or their parts can be identified, it is necessary first to classify the major systems. This should be done in descending order of size. The largest ecological divisions are biomes that are identified by the coincidence of similar features, such as land-forms, water masses, soil types, and flora and fauna. The most rapid method of biome identification uses a mixture of indicator species, or dominant floral and faunal elements, conspicuous plant and animal associations, and physical features. It is fortunate that methods for classifying terrestrial ecosystems can be based on the use of distinct plant communities which represent integrated expressions of the ecosystems. However, the situation is much more difficult in the case of marine, coastal, and fresh-water ecosystems, where classification can only be accomplished by an analysis of several sets of information, such as substratum type, coastal land form, water chemistry, and biota.

When examined from the point of view of ecological processes, all ecosystems have variable and often imprecise boundaries, which spill over into other adjacent ecosystems. In such cases, it is important to recognize that boundaries are in part determined by the areas needed to sustain the processes of the system under examination. For example, the ecosystem of a water lily in a pool may be taken to be that pool, but in North American northern forested areas, moose (Alces alces) which feed on plants, including water lilies in fresh-water pools, also feed on terrestrial plants in the nearby forests. Thus, the ecosystem that sustains the life processes for moose is a large forested area with pools embedded in it. The moose obtain essential supplies of sodium from plants in the pools, and the bulk of their energy needs from forest plants. A manager who wishes to conserve moose must understand the structure and boundaries of the ecosystem required to meet that species' requirements and the boundaries he must set are different from those he would identify for a water lily.

Given that an ecosystem is defined by processes and has vague boundaries, how does the manager delineate the ecosystem he must manage and how does he determine the boundaries for practical purposes? Imagine a naturalist who is parachuted into an area, having been flown blindfolded over the landscape. How would he determine the ecosystem type that he had arrived in? He can make use of either biotic or abiotic features. For example, suppose that the first plant he sees is a succulent. He would then know that he is in a terrestrial biome of one of a few types. Looking closely at the plant, he discovers it is a euphorbia (Euphorbiaceae) and knows he is in an African biome. Looking further he sees an acacia tree and soon after Grant's gazelles (Gazella grantii), and recognizes he is in an eastern African ecosystem, a dry savanna. He may continue the process, identifying more and more species until these have provided sufficient information to identify the exact ecosystem; a good naturalist normally could identify the ecosystem rarely using more than 10 to 20 species.

On the other hand, the naturalist may take another approach and examine the abiotic components of the ecosystem. Looking at the soil, he would find no humus and little litter. With proper chemical and physical devices he might also have identified the ecosystem by determining the distribution of chemical elements and compounds, and the range of physical variables. Obviously, the most sensible approach is the use of both abiotic features, together with sets of species, not individual species, to identify the ecosystem.

Ecosystem dynamics

A fundamental principle of ecosystem conservation is that no biotic system is static or of fixed composition. All ecosystems are, to a greater or lesser extent, dynamic in time and space. This variability in composition and function is not only natural, but the persistence of many ecosystems often depends on these changes (see Chapter 5). Serious deleterious effects arise when the degree of change in the ecosystem is either increased or decreased too much. Both the amplitude and frequency of change may be increased to the point where they exceed the safe limits for the system, or decreased to the point where essential species, dependent on change, are eliminated. Such changes are of two main types: changes in the proportions of the system's components (e.g., species numbers, biomass of trees, etc.), and changes in the flow of energy and cycling of mineral nutrients through the system. We will consider these in turn.

Changes in an ecosystem's components

There are three main types of component changes: successional (including retrogressive succession), cyclic, and stochastic. Successional change implies that the system will pass in a directional fashion from one state to another, appearing to develop into something different from its original state. This presents a problem to preservationists, whose goal is to maintain the *status quo*. However, change in seral communities is inevitable, and any attempt to interfere with this process is bound to fail. Many biotic communities will change in various ways, despite artificial attempts to halt the process, and it is necessary that these communities be allowed to develop to mature (or more advanced) stages before being subjected to strong disturbance. For example, the natural development of lacustrine ecosystems is towards infilling, the production of marshland and subsequently the eventual disappearance of this marsh-land under terrestrial vegetation. The manager can, and should, control the rates of man-induced eutrophication (which if unchecked will accelerate infilling), but under no circumstances should he attempt to slow down the natural process of lake succession. If he does try, he will be wasting both time and resources. Prevention of the development of an early phase in this type of natural succession, may well lead to irrevocable, re-directed consequences for later stages in the same succession.

In some cases, the preservation of early seral stages is necessary in order to conserve habitats for dependent species, and although this may appear to be a contradiction - it is not. The concept simply requires that a nature reserve be large enough to maintain a shifting mosaic of the various seral stages. Thus, the ecosystem manager must be able to distinguish between inherently different, spatially separated sub-systems of an ecosystem, and those areas which are different temporal phases of the same ecosystem. In the former case, lakes and forests may form subunits of a larger system, while in the latter, a forest with patches recently destroyed by fire serves as a suitable example. In the first case, little can be done to change the areas occupied by either lakes or forest but in the second case a manager could influence the proportional representation of forest *per se* by either retarding succession or allowing it to proceed.

Cyclic change is also a phenomenon which, if interfered with, can have unexpected and undesirable consequences. For instance, it has been hypothesized that there is a 200-year cycle in the relationship between African elephant and the supporting woodland tree species. If this is true, then, interference, through elephant culling during the degeneration phase of the woodland, may lead to the development of instability within the ecosystem and subsequent extinction of one or both components.

Finally, there are stochastic changes which cause a system to fluctuate in a non-directional manner. The causes of such fluctuations are many and varied but comprise one of two main types: externally induced changes, such as changes induced by variations in rainfall; and, internally generated change, such as random changes in conception, birth, establishment, growth, dispersal, or death rates within individual populations.

Energy flow and nutrient cycling within an ecosystem

The ways in which these processes take place strongly influence ecosystem productivity and sensitivity. For example, the rates of cycling of chemical elements may be accelerated by trophic-level effects: carnivores feeding on herbivores may change the rate of accumulation of critical elements in either dead or non-productive, living, vegetation.

Systems that are nutrient- or energy-limited, or both, will require much longer recovery times than more productive ecosystems subject to the same degree of perturbation. In nutrient-poor systems, much of the nutrient pool is often tied up in living biomass, and that which is released is recycled rapidly *via* the substratum back into vegetation and animals (e.g., rainforests in the Amazon basin). Thus, destruction of biomass in these systems leads to rapid loss of nutrients.

Ecosystem stability and resilience

From the above, the question arises: what are the permissible limits of "natural" change within which the ecosystem remains "safe" (i.e., it will not change irrevocably, or to such a degree that major efforts are needed to restore it)? To define these limits and to understand what keeps an ecosystem within such safe limits requires a careful and detailed study of each particular system. There are no short-cuts. Nevertheless, sound ecosystem management requires identification of those aspects of the system's dynamics which influence its sensitivity to interference. To begin, we need to clarify the terms "stability" and "resilience".

If an ecosystem can always recover from change (short of extinction) in its components, it is globally stable. This is rare, however, and more often than not the system will have certain bounds which if exceeded, change its dynamics and cause permanent change to its status. These bounds represent the safe limits of change for the system, and within these bounds the system is said to be stable. If the limits are broad, allowing considerable change followed by recovery, then the system is said to be resilient. The narrower the limits, the more sensitive the system is to disturbance.

In the context of traditional conservation, the term "stable" has been taken to mean unchanging. For example, prior to the middle of the nineteenth century, Mount Monadnock, in New Hampshire, USA, was forested to the summit. This forest would have undergone many changes over time; recovering from wind storms and natural, relatively infrequent fires. In the middle of the nineteenth century, however, land-clearing practices initiated fires so intense that the thin mantle of organic soil on the summit was destroyed completely, leaving bare rock. Consequently, the summit has remained bare of forests for more than 100 years and, except for some lichens and mosses, has supported no vegetation. In other words, the range of variation in biomass over time has narrowed greatly, and the ecosystem no longer bears any resemblance to the original. Moreover, measurements indicate that the forest border is moving downhill, increasing the barren area.

This case illustrates the fact that certain ecosystems, which have relatively greater variation in biomass over time, are more desirable than others with fairly constant biomass. In addition, it illustrates that certain types of ecosystem disturbance may either push the ecosystem from one region of stability to another, or even completely convert it to another form. This can be seen in South Africa where, since the advent of European settlers, many grasslands have been overgrazed grossly and have converted to less productive Karoo shrublands.

Systems which have evolved under variable climates and which have been subjected to a high degree of periodic stress and disturbance over long periods of time (e.g., drought, fire, overgrazing), are not only adapted to such variability, but become progressively more vulnerable to these stresses if they are postponed by man's activities. Hence, the tendency in management to prevent fluctuation in numbers of organisms (by culling on the one hand and restocking or feeding on the other) and to reduce variability in their spatial distribution (e.g., by introducing artificially maintained water-holes) may be dangerous.

Ecosystem structure

Though species are inter-related through complex food webs, they tend to be arranged in different trophic groups in an ecosystem. The first trophic group, the autotrophic organisms or primary producers, manufacture their own food. The second trophic level is made up of herbivores (primary consumers) which feed on living autotrophic tissues. Carnivores which in turn eat the herbivores form the third trophic level. Detritivores utilize the dead tissues of all organisms. The trophic-level scheme is a useful generalization and provides the basis for ordering species into functional groups, in spite of the fact that many organisms utilize more than one trophic level.

Species can also be classified according to the rates at which chemical nutrients and energy pass through individuals. For example, some slow-growing lake fish may feed on microscopic plankton which have very rapid growth rates. The plankton, in this case, require energy and nutrients at far faster rates (fast processors) than the fish which feed on them (slow processors).

There is a definite relationship between body-size and life-history strategy within the animal kingdom. This relationship includes similarities in reproductive rates, longevity, metabolic rates, and food-quality requirements. For instance, among large mammals, body-size tends to be correlated with few offspring, a large investment in a small number of offspring per annum, long periods of gestation and parental responsibility, great longevity, and low metabolic rate per unit body mass. Species at this extreme are referred to as K-selected. Small animals, on the other hand, tend towards the other extreme and are known as r-selected species, with large numbers of offspring, little parental investment, short gestation periods, short life spans, and high metabolic rates per unit body mass (see Chapter 7).

A final and important category embraces all the prokaryotic and eukaryotic organisms. The prokaryots, such as bacteria, lack distinct cell nuclei, whereas eukaryots include all organisms which possess cell nuclei, such as higher plants and animals. In the past, conservation has focused entirely on eukaryotic species. These organisms (e.g., eagles, cranes, whales, elephants, and redwood trees) tend to impress people by their size and undomesticated status. Viewed, however, from an ecosystem perspective, the maintenance of these organisms depends entirely on essential chemical transformations and nutrient cycling. It is a curious fact that some of the crucial chemical transformations that occur in the biosphere can only be carried out by prokaryots. Thus, the biological fixation of nitrogen, essential to all life, is mainly achieved by certain prokaryots. Similarly, the transformation of sulphur from large organic compounds back into inorganic forms is only carried out by prokaryots. Some prokaryots require peculiar habitats (e.g., oxygenless muds in salt marshes, the bottoms of fresh-water ponds, or water-saturated soils in terrestrial ecosystems), and as such the ecosystem manager must recognize and maintain conditions which allow these organisms to carry out their ecological roles. If these habitats cannot be maintained naturally, the manager must find a way to replace such activities artificially.

While most eukaryotic organisms do not carry out essential chemical transformations so vital to the functioning of ecosystems, they do affect the rates at which these processes take place. For example, ruminants provide an optimal environment in their intestinal tracts for the bacterial fixation of nitrogen. By the same token, many invertebrates gather fine particles during their feeding processes (the "collectors"), and make these substrata available for subsequent prokaryot action (e.g., pseudofaeces production of mussels), while other species break up large particles (the "shredders"), thereby increasing the surface area to volume ratio, and enhancing subsequent prokaryot decomposition.

Key or non-replaceable species

Some species are critical determinants of ecosystem functioning, while others play a more dependant role; that is, they are influenced more by the structure and dynamics of ecosystems than they themselves influence that structure. The former, called "key" species, are often excellent indicators of ecosystem structure and functioning, and these species should be identified by research and subsequently used in ecosystem management (see chapter 8). For example, the obvious research target in the Southern Ocean is krill (Euphausia superba) which, although a small shoaling, planktonic, shrimplike animal, eaten by fish, whales, seals, and penguins, accounts for a huge biomass.

A key species does not necessarily have to be abundant in order to influence vital ecosystem processes. The removal of the sea otter (Euhydra lutris), a predator of sea urchins, can result in an overabundance of the prey, leading to an alteration of the kelp forest and the concomitant loss of the kelp-associated fish community. An even more striking example may be seen where a single annual selective feeding episode of a population of a particular granivorous bird species may strongly influence the subsequent composition of plants in the field in which the birds feed.

THE MANAGER'S TASK

The manager charged with the primary task of conserving ecosystems must ensure that the flow of energy and cycling of nutrients is sustained within acceptable bounds and at the required rates, ratios and concentrations. In this context, there are several classes of managerial action. The manager may act within an ecosystem, at its boundaries, or across its boundaries. For example, in the Kruger National Park the roan antelope (Hippotragus equinus) population apparently comprises between 200 and 300 individuals, which may be too low to maintain sufficient genetic diversity for its indefinite survival (see Chapter 6), and the manager might act within the system to increase the population. Since roan antelope appear to prefer the ecotone between grasslands and woodlands, the manager could cut trees and burn grass to increase the area of edge-habitat. If this action, affecting many species as it must, is regarded as too drastic, the manager might act across the boundaries of the system by occasionally (every decade or less) introducing a small number of roan antelopes into the Kruger Park from another area.

Obviously, the manager of a nature reserve should choose those actions which involve the minimum disruption of an ecosystem, but he must recognize that this means minimizing any alteration of the normal temporal and spatial patterns of the system. In this context, the manager must keep in mind that a decision to take no action is just as important as a decision to take certain actions. For example, if fire is a normal feature of an ecosystem, then the proper management policy would be to promote fire in those reserves in which the natural frequency of fire is reduced.

One of the most difficult problems facing the manager is the recognition of complete or partial ecosystems. The manager must know whether or not an area to be managed contains all the necessary energy transfers and nutrient cycling processes necessary to maintain a functioning ecosystem. He must also know whether or not it is large enough and contains sufficient diversity of characteristics to enable the necessary and desired species to complete their life processes. If these features are not present, the system is only a partial ecosystem. In such cases, the less complete the system, the more intense the necessary management.

A simple example of an incomplete system is provided by the so-called "bottle effect" which occurs in studies of photosynthesis of phytoplankton. Here, bottles of lake-water from different lakes, which are incubated over long periods, tend to develop biotic communities which resemble each other more than they resemble the original lake communities.

Conversely, the larger the bottles, the less the communities in the bottles resemble each other and the more they remain like those of the original sources.

Occasionally, ecosystems which are, apparently, self-sufficient (e.g., a lake) are, in fact, part of a tightly coupled association of several ecosystems (the watershed, the stream, and the lake). In this case, there is no hope of successfully managing any single unit without understanding its relationship to the whole set of ecosystems, and managing the whole. For example, the levels of nutrients flowing into small dams should be regulated in order to avoid excessive fertilization which leads to eutrophication and aquatic weed problems.

Marine ecosystems are notoriously difficult to identify and classify as discrete entities. Coastal upwelling zones, however, appear to be manageable as ecological units, and the management of the fisheries within them should not be based on single species isolated from their environment, as has been tried in the past. The failure of many of the world's major fisheries is testimony to the inappropriate nature of this type of approach.

In the case of incomplete ecosystems, one of the most important managerial tasks is the identification of missing ecological processes, together with the determination of compensatory managerial actions. There are various methods for achieving this objective, mainly because there are so many ways in which an ecosystem may be incomplete. For example, if the ecosystem lacks a habitat in which crucial chemical transformations take place, then the manager may have to remove undegraded material and add fertilizers. He might, on the other hand, manipulate the available area to create the habitat required.

Many African nature reserves contain incomplete ecosystems in so far as they lack permanent water sources. In many cases, this deficiency has been offset by the introduction of wind-powered pumps drawing water from deep wells. The manager must not be satisfied, however, to merely add water; he must ensure that the water supply is within the bounds of the normal range for that ecosystem. At Tsavo National Park in Kenya, for example, efforts were made to increase the water supply simultaneously with attempts to reduce poaching. This improved the survival rate of elephants and increased their numbers beyond that which could be supported during drought years. Thus, although managerial action was taken, it was not of the type required for sound management of an incomplete ecosystem. A proper framework would have included factors which tend to increase elephant population growth and those necessary for reduction of population growth.

Artificial actions to mimic natural perturbations of ecosystems pose many problems, requiring careful investigation before action is taken, and great care in implementation. For example, a number of coastal lakes in South Africa are connected to estuaries whose mouths to the sea are subject to natural opening and blocking at irregular intervals. Some of these ecosystems are densely inhabited by people who make heavy use of the living resources, particularly fish, in the systems. The fish populations depend on natural periods of floods, and the periods at which estuary mouths open and close. In the case of flooding, the question arises: to what extent should lake water levels be allowed to rise before estuary mouths are opened artificially? The potential damage to property by flooding has to be weighed against the potential effects that delay in opening might have on the passage of fish, together with the effects of sea-water input on the flora and the invertebrate fauna. Out-of-season estuary manipulation by artificial means, can have considerable effects on future fish stocks. The length of time which flushing is allowed to occur is also important: too little outflow leads to cumulative build-up of sediment in the estuary, with subsequent detrimental effects, whereas prolonged outflow periods may lead to excessive loss of nutrients from the ecosystem.

Managers are often confronted by problems which need immediate action, but for which they lack sufficient ecological information. When immediate action is required, the manager should seek the advice of those ecologists best acquainted with the ecosystem and, maintaining an ecosystem perspective, consider the "best educated guesses" of those ecologists in determining how to proceed. There is no other option in many instances. In general, however, the situation is not so desperate as to be hopeless. Much of the research and monitoring required for proper ecosystem management can be achieved in a relatively short time with the aid of modern techniques, and as long as sufficient manpower is available.

5. DETERMINANTS OF CHANGE IN ECOSYSTEMS

W R Siegfried (convener)

R Allen, A P Bowmaker, C K Brain, G Fryer, J R Grindley, M Hall, L Hutchings, K R Miller, R N Owen-Smith, G Shaughnessy, K L Tinley

INTRODUCTION

All ecosystems are continually changing in response to influences from both outside and within. Thus, any attempt to preserve any ecosystem as a static entity is unrealistic and unwise. Ideally, a proper understanding of the determinants of change in ecosystems should be the starting point of any conservation programme, and it is the aim of this chapter to outline the scope of some of the principal factors responsible for such changes. Factors affecting change vary considerably in the time scale of their operation. Certain changes may occur slowly, over thousands or millions of years, while shorter-term changes may be superimposed on them.

CHANGES IN CLIMATE

Variation in climate causes short- or long-term, regular or irregular changes in all ecosystems, while human activities may influence changes in climate. For instance, it has been suggested that increasing carbon dioxide concentration in the atmosphere, resulting from the combustion of fossil fuels and the disturbance of carbon stores, could reduce heat-loss in the form of long-wave radiation from the earth, and that this heat-loss reduction might result in a general increase in ambient temperature through the "greenhouse effect." However, an alternative hypothesis claims that incoming radiation is reduced by scatter, due to increasing loads of dust and smoke particles in the upper atmosphere and that, anyway, the vast thermal inertia of the oceans of the world will considerably dampen any effects of heating due to increased carbon dioxide in the atmosphere. The argument still rages. In the meantime, it is clear that man's clearing of forests is changing the albedo of the earth, and changes in cloud formation and rainfall are held to be the result.

Long-term variation in solar radiation reaching the earth is believed to be responsible for periodic changes in ambient temperatures in terrestrial and marine environments. Studies of continental European geological deposits have shown that there have been at least 17 alternating glacial and interglacial episodes during the last 1,7 million years. This European stratigraphy corresponds with cycles in the deep-sea sediment record, and it now seems that such gross long-term temperature fluctuations have been globally synchronous. These changes have had significant impacts on regional biotas, resulting, *inter alia*, in vegetation zone shifts (e.g., relict patches of once continuous forests).

The effects of global temperature changes may be different in different areas because of geographical shifting of atmospheric pressure belts and other factors. There is no direct relationship between cold conditions and increase in rainfall and decreases in temperatures have, in fact, caused increased aridity in certain areas of the world. Present conditions are abnormally warm, if considered on the time scale of the Pleistocene. Viewed in the short term, however, there is some evidence of world-wide cooling since about 1940, but this is now complicated by arguments concerning the "greenhouse effect".

Variations in rainfall, wind and other meteorological phenomena may occur on time scales of decades or less. Some of these short-term variations appear to have regular patterns, but such patterns are apparently not sufficiently well established for predictive purposes. However, fluctuations in the weather may initiate short-term trends in vegetation features, including the grass-woody plant balance in savanna regions, and wetland vegetation type and distribution. Further, catastrophic events, such as floods, droughts, hurricanes, frosts, and unusually cold periods, may have fairly long-term effects on ecosystems even though they may be of short duration and occur only rarely, say once in a century. Certain plants and animals may be decimated during such events and their populations may take some time to return to their former abundance. For example, it has been shown that frequent hurricane "blow-outs" in moist deciduous forests of the New England region of North America prevent forest succession from ever reaching a mature stage of climax trees.

Climatic change has had major effects on aquatic ecosystems by altering water levels. Lake level changes, which occur as a result of changes in river and aquifer input, have drastically altered lacustrine environments in the past, causing lake expansion, or separation into isolated basins, and promotion of biotic speciation. In the oceans, the expansion of the polar ice-caps during cold periods has led to major sea level reductions. Conversely, warmer conditions have raised sea levels and have resulted in the formation of what are now raised beaches. Such changes have reshaped coastal areas by producing alternating periods of flood, or exposure of the continental shelf.

Although the oceans are linked as a single ecosystem, with measurable interchange between all parts, some pelagic areas can be distinguished on the basis of the rate of nutrient supply to the upper, sunlit water layers. For instance, areas containing upwelling water tend to have relatively high rates of primary production and maintain a relatively high biomass of herbivores and carnivores. By using counter-currents, many species in these areas maintain themselves in zones of abundant food. It is obvious that any changes in current patterns, which may be induced by climate changes and corresponding shifts in wind belts, may have profound consequences on the biota within such ecosystems.

CHANGES IN GEOMORPHOLOGY

Weathered material, including soil, is subject to erosion, transportation, and deposition. Erosion may occur by chemical means, such as when soil components are leached out in solution, or by mechanical means, when agents such as wind, water, and ice, operate in conjunction with gravity. Erosion is a natural process, but the rate at which it occurs may change. Thus, if the land surface is protected from wind and flowing water by a dense plant cover, erosion will be slow. If the plant cover is destroyed (e.g., by overgrazing), the rate of erosion may increase. There is also a correlation between the angle of slope of a hillside and the rate of erosion. If tectonic uplift of land occurs, the angle of slope of the rivers increases, as does their eroding potential. Similarly, when a road cutting is made through a hillside, effectively steepening the slope above the cutting, erosion may accelerate.

New land-forms are created as a result of erosion, and comprise two basic kinds: erosional land-forms that remain at the site from which material is being removed; and depositional land-forms, created at sites where the eroded material is eventually deposited. Thus, at river-bends, banks are carved out on one side, whereas river-bars are formed on the other. The erosion of cut banks is a continual process of substratum alteration in riparian ecosystems. On the other hand, plant succession is stimulated on river-bars. The rates of erosion and deposition may vary depending on outflow and sediment load in the case of rivers, or wave action and sediment load on coast-lines. These are purely mechanical actions, and both tidal range and coastal currents have complex interactions within the processes of erosion and deposition. If coastal currents are weak, the orientation of the coast may be greatly modified, as in the Mississippi or Amazon deltas where shifting sand-bars are common features. Sediment load also affects turbidity of the water and may limit primary production. Outflow of fresh water entrains nutrient-rich subsurface sea-water into the upper layers, and may set off a cycle of production which can vary in response to the outflow. For example, transport of fresh water by both the St Lawrence River and the Nile River, and catches of certain fish in the Gulf of St Lawrence and the south-eastern Mediterranean, have been found to be linked in a cause-and-effect relationship. Thus, river regulation by dams may have profound effects on the biota of ecosystems far from the source of regulation, and this is certainly true in the case of the River Nile. In the marine environment, long-shore currents, coupled with wind action, can result in a continual process of erosion and deposition at any one site along a shoreline. If the period of geomorphological change is prolonged, this can result in the burial and eventual elimination of the reef biota along the shoreline.

The deposition of sediment, which occurs naturally in lakes, is an integral part of their evolution. Even in lakes with a small inflow, and, therefore, small input of inorganic material, some autochthonous production of organic sediments takes place. In deep lakes, in which relatively little biological production occurs, this deposition is slow, but in shallow, productive lakes it may be rapid, especially where nutrient input is increased by human activity outside a conserved area.

The water levels of a number of lake ecosystems (e.g., the African great lakes) have fluctuated, sometimes greatly, over very long periods. At present these lakes display short-term fluctuations in water level, associated with fluctuations in rainfall, concomitant with changes in the intensity of sun-spot activity. However, sun-spot activity and rainfall do not have a clear-cut cause-and-effect relationship. Irrespective of cause, water level fluctuations will affect the relatively diverse biota of littoral regions, even in deep lakes. The effects of such fluctuations can be dramatic in larger shallow lakes. Lake Chad, for instance, varies enormously in area over relatively short periods, and several other lakes, including Rukwa and Chilwa, periodically dry out. However, the biota in these systems are adapted to such events. Fluctuations in water level can also have a marked influence on the water salinity, which in turn affects the biota.

Increases in water level can be enhanced by events in the watershed. For example, the reduction of forest, as a result of felling, or climatic change, leads to increased water run-off as well as changes in the chemical composition of that runoff. Short-term, unpredictable fluctuations in the water levels of man-made lakes often result in great reductions in the biotic diversity of littoral regions, although such fluctuations may even be advisable in certain circumstances. For instance, artificially-induced fluctuations can help control the growth of aquatic plants which harbour the vector snails of bilharzia (schistosomiasis) in certain African dams. They can also be used to reduce mosquito populations. Finally, it must be remembered that although such water bodies may be unattractive both biologically and aesthetically as sites for nature reserves in terms of reduction in diversity and unpredictable water levels, they may still be valuable for human recreation, including water-sport, thereby perhaps relieving "people pressure" at other sites.

CHANGES IN BIOTIC DETERMINANTS

All ecosystems are to a greater or lesser degree in a state of flux, caused in part by changing interactions between their plants, between their animals, or between their plants and animals. For example, in savanna the selective dispersal of plant seeds by certain birds and mammals has resulted in the replacement of relatively open vegetation by thicket. This change, in turn, has affected the structure and functioning of foodwebs, and, ultimately, all other relationships within the ecosystem. Ideally, an understanding of the biotic determinants operating in ecosystems should be a prerequisite for any management strategy or tactic. In reality, however, many of these ecological processes are subtle and complex and, hence, are difficult to recognize. The prediction of their effects is even more difficult! Nevertheless, often included among important biotic determinants are those organisms which have considerable impact (e.g., man, large ungulates, and disease vectors), and those with large spatial requirements (e.g., whales and wildebeest). Of course, these two categories are not mutually exclusive.

Those organisms which most influence ecosystem dynamics in terms of habitat modification, numbers and biomass of plants and animals, energy flow or nutrient cycling, are termed the "key" species or "prime-mover components". The major large herbivores, such as elephant and buffalo, are prime-mover components of savanna ecosystems, insofar as in their absence much of the biomass produced by plants passes directly to decomposer organisms or accumulates as litter, and thus promotes fires or senescence in grassland. Very small organisms can be just as important as prime-mover components, as exemplified in savanna ecosystems by mound-building, herbivorous termites, and certain epizootic diseases. The rinderpest (a virus) outbreak in Africa at about the turn of the century caused large-scale die-off in wild and domesticated ungulate populations, and resulted in extensive ecosystem changes.

In any dynamic ecosystem, the prime-mover components of a particular period can be replaced consecutively by others. For example, an injection of nutrients into the euphotic zone of the sea is often followed by the multiplication of pioneering planktonic organisms, to the point that nutrient levels are reduced, and penetration of sunlight through the water is decreased. In this new habitat, phytoplanktonic species adapted for growth under conditions of reduced nutrient concentrations and sunlight soon attain dominance, followed by a third or fourth change in the composition of the biota. Moreover, the response of herbivores to increased food levels may result in size-selective feeding, changing the population structure of phytoplanktonic organisms. Similarly, carnivores may alter the size spectrum of the herbivores. As animal populations increase with time, regenerated nutrients may allow a secondary phytoplankton maximum to develop, and depending upon the sequence of the nutrient supply to the euphotic zone (once a year in typically temperate seas (e.g., the North Sea) to many times a year in coastal upwelling zones (e.g., the Benguela Current area)), the cycle of primary to secondary production to fish will repeat itself and oscillate with time.

Many animals considerably influence their environment (e.g., corals build huge reefs, and ants and termites transport large amounts of inorganic and organic material). Man, as an animal, is no exception, and his influence differs only in degree. Many changes wrought by humans are persistent and of great antiquity. In Africa and North America, for example, the extinctions of many large terrestrial animals at the end of the Pleistocene have been attributed to human hunters, climate change, or (what is more likely) both. On the other hand, man-induced change has sometimes resulted in increased biotic diversity within particular regions. A good example comes from long-fallow swidden systems, practiced for millenia in many sub-tropical and tropical areas. These practices involve the clearance of patches of woodland and forest, thus promoting increased "edge effect" with a consequent increase in local species diversity.

Man's use of fire has extensively transformed ecosystems, as exemplified by the expansion of the African savanna, the reduction of temperate woodland in Europe, and the expansion of the North American prairie. However, as man developed agriculture and animal husbandry, human populations burgeoned, and increasingly large areas of land were transformed further to create and maintain arable fields, pastures, and plantations. Subsequently, the introduction of large-scale plantation agriculture in the eighteenth century greatly expanded man's simplification of ecosystems.

This sequence of development has reached the point where there is scarcely an ecosystem not affected by man. The most significant, recent, and widespread human effects include: replacement of entire ecosystems by settlements, harbours and other human constructions, by mines and quarries, and by croplands, pastures and plantations; the effects of dams (blocking animal migrations, alteration of flood sequences in floodplains, flooding of spawning and other critical habitats, alteration of chemical or thermal conditions and, hence, alteration of the biota); drainage, canalization, and flood control; pollution of air, soil, and water by chemicals (from industrial and agricultural sources and from mines, oil wells, and motorized transport); over-extraction of water (for domestic, agricultural, and industrial purposes); injudicious exploitation of resources such as plants, gravel, and stones; dredging and dumping; overgrazing and overbrowsing; and, erosion and siltation.

THE MANAGER'S RESPONSE TO CHANGE

How should a manager respond to change in an ecosystem? In the first instance, his response should be guided by specific objectives attending the type of designation accorded to the ecosystem. Secondly, although this is not always possible, the specific cause of the change should be identified and, thirdly, a prediction should be made as to the likely consequence(s) of the change. If the change is generated within the ecosystem, then the basic choice of response is between doing nothing and thereby allowing changes to progress in a successional or cyclic direction, or combating such changes by manipulating the system so as to favour the successional or temporary phases which are regarded as desirable. Great care should be taken in choosing what is or is not desirable. If a change is induced extrinsically (e.g., due to the elimination of predators, or due to invasion by alien species which affect a key ecosystem process), then similar choices arise, and the manager may either accept cascading changes among other species in the community as inevitable, or adopt actions designed to combat, suppress, or deflect the consequences of the anticipated change in ecosystem functioning.

6. GENETIC ASPECTS OF ECOSYSTEM CONSERVATION

M E Soulé (convener)

C B Cottrell, J C Greig, A V Hall, R G Noble, P Shaughnessy, J M Thoday

INTRODUCTION

Diagrammatic representations of ecosystems commonly show the names of the species comprising the biotas. Enclosed in little boxes, the species are interconnected by arrows, representing interactions of various sorts that occur between them. While such a schema emphasizes the interdependence and interactions of the component species, it does not bring out the important fact that each box represents a heterogeneous array of individuals, no two of which are genetically alike. This genetic diversity, which is the basis of much of the morphological and behavioural variation in a local population, is sometimes referred to as the "gene pool."

For several decades, conservationists have paid lip service to genetic conservation and to the idea that the health of the gene pool of the species is both a goal and a necessary condition of success in the management of ecosystems. Yet, it has been only in the last year or two that specific recommendations and guidelines have been suggested by conservation biologists to ensure the maintenance of "healthy" gene pools. The degree of "health" of a gene pool is sometimes referred to as "fitness." However, fitness has many definitions, and the word is used in several different ways. In this chapter we are concerned with two kinds of fitness. Fitness in the short term, proximal fitness, and fitness in the long term, or ultimate fitness. Fitness in the short term means the maintenance of the structure and functioning of a population, which permits it to survive and successfully reproduce under particular conditions. In this sense, fitness is often broken into components, such as fecundity (e.g., litter size) and viability (e.g., the longevity of newly-born individuals). A loss of fitness in this sense will lead to a decrease in abundance, and ultimately to local extinction, of a species.

Fitness in the long term has to do with natural selection and evolution. For a species to persist, generation after generation, it is not enough that it maintains a status quo. Environments are changing continually, and individuals, in order to survive, must adapt to these changes; this adaptation has a genetic or evolutionary component.

Thus, fitness in the long term means the capacity of the population to change genetically in an adaptive way. This, in turn, requires that the gene pool should contain the raw material that permits natural selection to operate. In addition, the population must be large enough so that the effects of chance (genetic drift) will not override the effects of natural selection. Thus, long-term fitness presupposes both genetic variation and a moderate-to-large population size.

Resistance to pesticides in insect populations provides many examples of long-term fitness and adaptation. In general, the application of a pesticide to a previously unexposed population results in massive mortality. The reason for the die-off is that only very few individuals will, by chance, have a gene that permits them to detoxify or somehow avoid the effects of the pesticide. The smaller the population size, of course, the lower the chance that any individual will have such a rare gene. However, insect populations are often very large (hundreds of thousands or millions of individuals), and it is likely that they will contain some resistant individuals which will pass on the genetic basis for this resistance to their offspring. Thus, the next generation will contain a higher proportion of individuals with the built-in resistance. Similarly, most species and most populations have the capacity to adapt to predictable catastrophes such as drought and disease. For most species of higher plants and animals, therefore, long-term survival of populations presupposes the capacity for evolutionary (genetic) "tracking" of environmental trends.

Are all species equal? Perhaps they are at an ethical level, but when approaching this question from a biological point of view it is probably true to say that some species are functionally more significant than others in an ecosystem. One might even be able to rank species according to the impact their extinction would have on an ecosystem. The most important species, those with the greatest impact, are called "key" species, and these species should be considered as the targets for management based on genetic principles. Examples include representatives of top-order carnivores and other large animals with low reproductive capacities, such as aquatic filter feeders, especially large ones. Even apparently insignificant forms (e.g., parasitoid insects), which have important mutualistic relationships with others, often have key functions. Among plants, key species are exemplified by certain trees which, although they may occur at relatively low densities, provide shelter and food, such as nectar, pollen or fruit, for animals. These resources may be vital to certain birds, mammals, and insects which in turn, play important roles in linking other species in a community. Managers should guard against the loss of fitness of key species.

Quite often the "key" status of a species will be unrecognized until it is absent or until conditions change. In other words, a species may not appear to be particularly significant in a particular habitat or ecosystem, but in another habitat its presence or absence can have a profound effect. For example, the infestation of Australian pasture-lands by the American cactus (*Opuntia* sp.) was countered successfully by the introduction of a moth (*Cactoblastus cactorum*). Before its use as a biological control agent, this insect would hardly have been considered a key species. Thus, certain insects may contribute significantly to the regulation of populations of certain plant species, but this regulatory role may only be obvious in the absence of those insects.

Finally, the purpose of this chapter is to describe what constitutes a genetic danger or a threat to the fitness of populations, both in the short and long term, and to recommend actions which managers can take to mitigate ecologically deleterious effects. In this context, it should be noted that the phrase "conservation of genetic variation" is sometimes used to mean conservation of species and is thus a synonym for nature conservation in the old sense. In this chapter, however, the emphasis is on the genetic variation within populations or species and how this objective can be achieved.

THE NATURE OF GENETIC VARIATION

It is useful to think of genetic variation as existing on three levels: within individuals, between individuals in a population, and between populations. With regard to the first level, the individuals of most species of flowering plants and animals contain two representatives of each of their genes, one copy from the male parent and one from the female. These copies are called alleles, and if they are identical in an individual, the individual is said to be homozygous (or a homozygote) for this gene or locus. However, if these two forms of the gene are different (i.e., different alleles from the male and female parents respectively), the individual is heterozygous (a heterozygote). Each individual is believed to have from several thousand to a hundred thousand genes and a large proportion of these, as much as 15% or more, may be heterozygous.

What is the role of the differences between alleles at a locus? For some genes allelic differences have very obvious effects (e.g., the genes that control flower colour in plants). For the large majority of genes, however, the allelic differences are more subtle. The characteristics with which both geneticists and conservationists are usually concerned, are affected by a large number of such genes. Traits such as competitive ability, height and body conformation, are controlled by a great many genes, each of which has a small effect. This is why variation in height or skin colour, for example, appears to be gradual or continuous, forming a spectrum of variation - short to tall, dark to light. In many characters, such variation is difficult to detect or measure and can only be revealed by specific tests. Electrophoresis of proteins, including enzymes, is an example of the kind of variation that can only be studied by biochemical screening techniques.

This leads to the second level of variation, variation between individuals or within populations. Except for inbreeding plants and a minority of animal species which are genetically uniform (homozygous) or parthenogenetic, most local populations are made up of non-identical individuals, due in large part to heterozygosity for different alleles of the thousands of genetic loci. Within a species, some populations are more variable (heterozygous) than others. Small or ecologically marginal populations are typically less heterozygous than large or "central" populations. Among species or other taxa, are some which are typically very heterozygous, while others tend to be less variable. For example, invertebrates are, as a rule, more heterozygous than vertebrates, while within vertebrates, fish are more heterozygous than birds and mammals. There are, however, many exceptions to these generalizations.

Discussion so far has been limited to the variation within interbreeding groups of animals. Such groups are known as populations or demes, and the total of all the genetic material in these groups is the gene pool. Most so-called species of plants and animals are actually the sum total of large numbers of gene pools or populations, and these demes are to some degree isolated both from each other in space, and sometimes in time. If these populations in different parts of the range of a species are noticeably different in one or more traits, they are sometimes referred to as subspecies or races. This third level of variation is referred to as "geographical variation".

In most cases of geographical variation, the differences between populations are adaptive. For example, the very long ears characteristic of races of certain foxes and other mammals living in deserts facilitate radiation of excessive heat-loads accumulated by the animals during the day. Conversely, the relatively short ears of animals living in cooler climates assist in the conservation of body heat. The term "ecotype" is used sometimes for such locally adapted populations. If populations of a subspecies are separated from each other in time and space, they may become different in a number of respects, some of which may make interbreeding between them impossible. They may then be recognized as separate species.

GENETIC VARIATION AND SHORT-TERM FITNESS

Wildlife conservation programmes can be divided somewhat arbitrarily into two kinds: "short-term" holding operations, including the propagation of species in captivity; and "long-term" operations, normally associated with nature reserves. For reasons discussed in the following section, the numbers of individuals maintained in short-term operations are smaller than the numbers that should be maintained in long-term operations. Of course, the smaller the number of individuals, the greater will be the dangers of losing genetic variation, inbreeding and the consequent loss of fitness.

What is inbreeding? Inbreeding occurs when genetically closely related individuals mate and reproduce. Extremes of inbreeding involve matings between cousins, between brothers and sisters, and between parents and offspring, or self-fertilization in some hermaphroditic plants and animals. In less obvious forms, some measure of inbreeding must result from any restriction of population size; the smaller the population, the greater the chance that two individuals that meet and mate will be fairly close relatives. Most animal species have mechanisms to limit or prevent breeding between close relatives. Separate sexes (i.e., males and females) is one such mechanism. Recent studies of birds and mammals suggest that individuals, when given a choice, prefer to mate with unfamiliar or unrelated individuals. Many species of plants have mechanisms to promote cross-pollination. These include incompatibility arrangements which prevent individuals from pollinating and fertilizing themselves. Such arrangements are called outbreeding mechanisms, and their ubiquity and diversity indicate that outbreeding has advantages. Inbreeding is more common among plants than among animals, and in the latter, it seems to be restricted to species for which finding a mate is a difficult process (e.g., certain tape-worms and other flatworms).

Inbreeding among normally outbreeding organisms nearly always leads to deterioration and loss of fitness. The reason is that inbred individuals are homozygous for more genes than non-inbred individuals, and, further, a certain proportion of the newly homozygous genes causes problems. Individuals in outbreeding species carry a "gentic load" comprised of a number of deleterious, recessive genes or alleles. Under normal circumstances very few individuals are homozygous for the most deleterious ones. If, however, an individual which has one such "bad" allele mates with a close relative, that relative is likely to have received the same allele from the common ancestor (say a grandfather).

The offspring of such a mating can be very inferior, depending on how "bad" the allele is. In short, inbreeding increases the frequency of unfit homozygotes for deleterious, recessive genes. In contrast, the superiority of relatively heterozygous individuals has been demonstrated in many natural populations.

The loss of fitness that accompanies inbreeding is referred to as "inbreeding depression." One consequence of inbreeding depression is that inbred lines generally show a decrease in vigour and fecundity, and many are very difficult to maintain at all. This is common laboratory and farm experience. In fact, about nine out of ten attempts to create an inbred line fail because of extinction of the line. In addition, the experience of breeders with many species of domesticated plants and animals has demonstrated that for every 10% increase in the amount of homozygosity due to inbreeding, there is a very significant decrease in fecundity, vigour, longevity, and other components of fitness. In fact, the decrease in fitness, as estimated by these components, may be as high as 25% for each 10% increment in the amount of inbreeding. Incidentally, a 10% increase in homozygosity is equivalent to the amount of inbreeding that occurs in one generation when five individuals are breeding at random. These generalizations, however, do not apply to species or populations which habitually inbreed in nature. Species of plants that are predominantly inbreeding have fewer deleterious genes. Of course, plants that avoid breeding altogether, and reproduce vegetatively instead, do not suffer from inbreeding depression unless they are forced to breed sexually.

Inbreeding is often a consequence of confinement. A reduction in the area of wild habitat and the limited extent of many nature reserves can result in a restriction in population size and, hence, some degree of inbreeding for many of the species; the amount of inbreeding being greater with decline in population size. Nevertheless, the effects of inbreeding may not be immediately obvious. Small populations can persist for many generations, and indeed, many populations persist while at the same time showing strong effects of inbreeding. However, inbreeding remains a threat and may lead ultimately to extinction *via* a gradual reduction in viability, fecundity and vigour.

What is the smallest number of individuals needed to give a population of organisms a reasonable chance for survival in the short run? The answer depends on what is meant by "short run." In most cases, a manager will want to consider the time scale of his management objectives. Whereas a manager of a nature reserve may wish to maintain as much genetic variation as possible in key species, a more limited objective of a manager of a commercial fish hatchery or of a game farm may be the retention of the vigour and fecundity of his breeding stock for a finite period, say 10 or 30 generations. The latter short-term objective is also typical of the husbandry of domesticated animals and of captive breeding of animals in zoos.

In such short-term projects, there is evidence for genetic systems tolerating breeding populations comprising as few as 50 individuals. In cattle and poultry, fitness of the group drops if it contains fewer breeding adults, and generally in domesticated animals an inbreeding rate higher than one per cent per generation will result in a noticeable loss of fecundity (such as litter size or egg production), viability of young, and longevity. This one per cent rate of inbreeding translates into an effective population size of about 50 breeding adults, but even at a one per cent inbreeding rate the population can be expected to show signs of inbreeding after 20 or 30 generations. Actually, this "rule of 50" may not be sufficiently conservative, because it is based on inbreeding effects in domestic stock, and the longer a population has been in domestication the fewer deleterious genes it seems to have. In other words, domestic stocks are to some degree purged of their deleterious genes, and there is evidence that inbreeding depression of their wild relatives may be even greater.

In animals such as elephants, which breed slowly, many years may pass before significant levels of inbreeding are reached. Thus, a randomly breeding herd of elephants kept at 50 individuals may require some 200 years before inbreeding reaches a level of 10%. Nevertheless, this should not justify keeping small numbers of elephants; the genetic damage done to the stock may take a relatively long time (but not in generations) to manifest itself, but it is just as serious. A long generation time is no justification for ignoring genetic effects.

NATURAL SELECTION AND LONG-TERM CONSERVATION

Genetic variation is necessary if a population is to be able to adapt to changing environmental conditions. A species which comprises several populations, with genetic variation both within and between them, will be better able to withstand catastrophic changes in the short term, as well as more gradual changes in the long term. Genetic variation is a necessary condition of survival in many, if not all, pioneering plants. For example, resistance to "rust" fungus diseases in wheat depends on genetic variation within a population. In general, the alleles that provide resistance to rust occur at low frequencies in natural populations. These alleles can easily be lost by chance (i.e., by genetic drift or inbreeding) when a population is reduced to small numbers.

It obviously is necessary to maintain more than 50 individuals, assuming that the population is to retain its long-term potential for adaptation and survival. How many more, however, is subject to considerable debate. Recent advice from some zoologists gives an effective size of 500 as a lower limit but, for various reasons too complex to discuss here, botanists usually recommend 1 000 to 4 000 individuals. (Botanists, however, are concerned with a one-time collection of seeds and the maintenance of very rare alleles within these collections.) In any case, one guiding principle is to maintain sufficient numbers of individuals so that the loss of variation from genetic drift (and possibly from selection) is balanced by input from mutation. What little evidence there is suggests that the threshold is around 500 individuals. This recommendation does not, of course, apply to organisms which reproduce vegetatively or by apomixis.

A census number of 500 breeding adults is not necessarily equivalent to an effective population stock of 500. If the ratio of males to females is not 1:1, the effective size is less than the actual number. If only

10 males breed with 90 females the effective population size is 36, not 100 (the formula (1) for this calculation is given at the end of this section). An appropriate management tactic in such a case is to balance the sex ratio. In polygamous species with harems, for example, dominant males should be rotated as frequently as possible, social behaviour permitting. Another factor that may reduce the effective population size is fluctuation in numbers. For example, an apparently safe 1 000 individuals may crash to 50 individuals, say, once in every 10 years. This lowers the effective population size to about 345 (see formula (2) at the end of this section). In ecosystems subject to periodic drought and other stresses, such swings in population size are not uncommon, and holding the population concerned at fewer than 1 000 individuals in the "good" years would be undesirable.

A third factor is the distribution of offspring among families. It is assumed that this is a random variable. In humans, for instance, most women produce a single infant but some have twins, fewer have triplets, etc. One way to increase the effective population size is to manage the group so that all families have equal numbers of offspring. If family size can be held uniform, effective population size is twice the number of breeding adults. This is perhaps the most important management tool, although its utility depends on the ability of managers to exercise close control over breeding individuals and their offspring.

Calculation of effective population size

Unless the sexes are equal (N_e), the effective population size is less than the actual number of breeding adults (N). Consider a herd of zebras comprising one male and nine females. All the offspring in such a group will be either half-siblings or full siblings. In a population comprising five males and five females, the progeny will, on average, be much less closely related. Clearly the chance of an allele becoming lost is greater in the former population; that is, the amount of genetic drift in the herd with the skewed sex ratio is higher than in the herd in which the sexes are equal. To be precise, when considering the sex ratio, the formula for N_e is

$$N_e = \frac{4N_mN_f}{N_m + N_f} \qquad (1)$$

where N_m and N_f are respectively the number of breeding males and females. In the zebra example, N_e for the skewed herd is 3,6. In other words, the sampling error in a population of 3,6 individuals with an equal number of males and females is equal to the sampling error in a population of 10 individuals with a 9:1 sex ratio. Thus, N_e is the size of an ideal population subject to the same degree of genetic drift as a particular real population. In this definition, "ideal" means a randomly breeding population with a 1:1 sex ratio, and in which the number of progeny per family are distributed randomly (Poisson).

When populations decline or "crash," the survivors are the progenitors of all future generations, and any deviation in the genetic make-up of these progenitors from the gene pool of the original population will be reflected in future generations. More particularly, if the progenitors contain only a sample of the kinds of genes which existed in the original population, future generations will have a corresponding deficit in genetic diversity. In more quantitative terms, the effective size of a population when the number per generation varies over time is the harmonic mean of the effective number of each generation, or

$$\frac{1}{N_e} = \frac{1}{t}\left(\frac{1}{N_1} + \frac{1}{N_2} + \ldots + \frac{1}{N_t}\right) \qquad (2)$$

DO THESE PRINCIPLES APPLY TO ALL GROUPS OF ORGANISMS?

The proposed minimum effective population sizes (50 and 500 individuals for short- and long-term conservation, respectively) do not apply to all groups of organisms. The breeding system is particularly relevant, especially when dealing with plants. As mentioned, many plants are predominantly inbreeding and will not suffer from inbreeding depression, or will be depressed by a relatively smaller amount than animals. Also, when dealing with plants, one must not forget the hidden, dormant plantlets of some species, lying as embryos in seeds. These may be numerous or depleted, according to ecological conditions and the reproductive strategy of the plant. Most importantly, there is every need to avoid uncritical application of the idealized predictions and recommendations of genetics without first getting to know basic details about the biology of the species in question. Conservation programmes involving genetic criteria should be developed in consultation with population geneticists familiar with conservation issues.

APPLICATION OF GENETIC PRINCIPLES FOR MANAGEMENT

It is clear that genetic principles must be taken into consideration by nature conservation authorities. Ecosystem managers, including fisheries biologists, limnologists and foresters, are the trustees of the world's genetic resources and the "arbiters" of evolution. Nevertheless, the preceding sections of this chapter could, wrongly interpreted, lead a conscientious manager to despair. This is because the area under his care may be small, with a significant fraction of the constituent species which do not satisfy the recommended numerical requirements, and they may thus be candidates for extinction within a few generations. These difficulties are real and should not be dismissed. In spite of this, and in spite of the apparently "hopeless" position of some populations, especially in small reserves, there are nearly always actions for mitigating the more serious effects. Even a small increase in the effective population size of a group is advisable. If nothing else, such actions will buy time, but even an increase, say, from three to six adults in a reserve could double the time that the population persists. The following sections describe some mitigating actions and examples of their implementation by managers.

Translocations

When the effective population size of a species is too low to satisfy the genetic requirements for successful conservation, there are several courses of action. The exchange of individuals among populations, even if only a single individual per generation, is usually very effective in enhancing effective population size. Thus, when the population of a species drops below a critical level, fresh genetic stock should be brought in to counteract inbreeding and the inevitable loss in genetic variation. It should be ascertained beforehand, however, whether the organisms to be translocated are chromosomally and ecologically compatible with the recipients. In normal circumstances, translocations should be made from the nearest natural population, assuming that the genetic adaptations of the donor and the recipient populations will be similar and that they would almost certainly be compatible. Many populations which were described in the past as races or subspecies are now turning out to be "good" species, as a result of modern examination of their chromosomes. It goes without saying that mixing of such gene pools would produce harmful effects. This is why cytogenetic studies must precede translocations, if there is any doubt at all about the genetic identity of the populations in question.

It is, perhaps, necessary to point out again that taxonomic arrangements at the subspecies level are often arbitrary. Some subspecies are not worthy of separation and others may subsequently turn out to be full species. It must be borne in mind that if geographically remote populations must be mixed, then, there is always a possibility that ecological and genetic incompatibility will result. Genetic compatibility per se is, however, no guarantee that the source and recipient populations have similar ecological adaptations. Ecotypes of plants and animals might be able to interbreed without loss of fitness, at least in a benign environment, but it is possible that the local adaptations of each of the source populations may not "mix" well, particularly when the environment changes.

Translocations are expensive. In some nature reserves 10-15% of the budget may be allocated for translocations, siphoning off money that might be spent better elsewhere. Before translocations are implemented, cost-benefit analyses, involving ecological, genetic, and other factors, should be made. One factor mitigating the high cost of translocations is the consensus among population geneticists that translocations need not be large or frequent. One successful transfer per generation suffices to completely mix two populations, regardless of their sizes.

If a habitat is not sufficient to accommodate an increase in a population to a desirable level, there may still be good reasons for going ahead with an introduction of additional individuals. Too small an area should not be considered an obstacle, since the advantages of restoring an ecosystem to an approximation of its original ecological condition justifies the transfer. There is also the very important benefit to the species as a whole, in that its total membership is increased even if the genetic health of the newly established population has to be maintained artificially by regular transfer of individuals. Obviously, the smaller the population, the more essential are periodic transfers from other groups. The success of such introductions probably is enhanced if new populations are established in a part of the species' former range. Two excellent examples spring to mind: mountain zebra (Equus zebra) recently established at Beaufort West in South Africa, and the establishment of the Arabian oryx (Oryx leucoryx) in Oman, Israel and Jordan after its extinction in the Middle East.

Botanical gardens are used to build up populations of depleted plant species, genetic stock being used to replenish wild populations or being stored in seed banks for the future. Care must, however, be taken to avoid genetic "contamination" from closely related species occurring in unnatural, confined situations, and artificial selection during the plant's tenure in the botanical garden must be guarded against. Similarly, groups of breeding animals are kept under closely managed conditions in zoological gardens. These populations can serve several purposes, including future re-introductions and genetic exchanges with the original populations at periodic intervals.

An imaginary example of good and bad management

The benefits of sound genetic management can be illustrated by a hypothetical case involving two nature reserves of equal size, each containing a population of 60 rhinoceroses at a 1:1 sex ratio. If genetic principles are ignored and no transfers of animals are made, genetic variation will decrease gradually in the populations. Moreover, if hunting is allowed, to keep each or both of the populations at about 60 animals, with hunters tending to shoot the "best" males for trophies, a selective reduction will occur in the incidence of those genes in the populations which promote "superior" males. Further, the sex ratio will alter in favour of females and a higher level of inbreeding will result as fewer males reproduce. Assume that the sex ratio of breeding adults falls to 20 males and 40 females. Further, assume that during droughts, when there is no supplementation of food or water, each of the two populations is allowed to drop to four males and eight females once in every five years. The result is that the effective population size in each reserve is about 26 animals. In contrast, in a well-managed scheme in which genetic considerations are borne in mind, regular transfers of animals are carried out between the two populations. Hunting may be permitted, but the males are chosen at random and not for "good" appearance or large size, and the females also are shot to restore the sex ratio to 1:1, while maintaining the population at 60 animals. Under this system, the effective population size will be the sum (120) of the two populations, and loss of genetic variation will be minimized. In an even more optimistic scheme, it might be possible to manage breeding in the herd by culling offspring in order to approximate an equal reproductive output per individual; the result would be an effective total population size approaching 240 (2 x 120) animals.

In summary, in the poor-management set-up, the herds can be expected to become less fit every generation as a result of inbreeding depression, although it may be several generations before this is noticed. In the case of proper management, however, genetic fitness of the herds should remain at an original level for the forseeable future.

Deleterious effects of artificial selection

Inadvertent artificial selection, through the removal of the largest, the most beautiful, or in some other sense the most desirable members of the populations, will leave relatively smaller, less showy, or more slowly growing individuals to reproduce. This results in a decrease in genetic fitness. In some tropical areas, fish belonging to the genus Tilapia are reared artificially in ponds and are harvested with nets. Often the largest fish are retained for eating, and the small ones are returned to the pond. Many of the small fish are juveniles, but some are adults which have relatively slow growth rates which, in part, are determined genetically. Thus, relatively fast growth rates of the fish remaining in the pond are selected against, and the fish will become progressively smaller generation after generation. Similar effects have been noted in lake fisheries as a result of "over-fishing."

In the south-western region of South Africa, wild flowers are collected on privately and state-owned land for sale in local and overseas markets. Most of these flowers are from plants belonging to the families Proteaceae and Ericaceae. The collectors choose the largest and most attractive flowers, leaving small flowers or those showing defects. This form of artificial selection favours the reproduction of plants with small or abnormal flowers, and a gradual change in the incidence of these flowers in the populations can be expected.

Under this subhead, a final caveat for managers of nature reserves is that they should avoid killing all the members of family groups in culling operations, since entire sets of co-adapted genes can be lost in this way.

EXCEPTIONS TO THE RULES: REAL AND APPARENT

Although there are several well-known and often-quoted examples of populations of certain species which have declined to near extinction and then subsequently recovered, it is essential to consider two points in such cases. First, the population crash will certainly have caused absolute losses of genetic variation. Bottle-necks in population size should be avoided for this reason alone. Secondly, a single crash, or bottle-neck, can be relatively less harmful, as long as the population returns quickly to adequate numbers. Statistically, even a single pair of individuals can contain 75% of the total genetic variation in the source population, and populations of certain organisms can pass through small bottle-necks and return quickly to relatively large effective size without suffering any subsequent genetic handicaps. If the population, however, remains small for several generations, it is very likely to undergo significant inbreeding and loss of fitness.

The golden hamster (Mesocricetus auratus) is often cited as an example of a population suffering no inbreeding depression, in spite of "inbreeding." In this case, the founder stock was indeed a pair of individuals, but the high reproductive rate of the individuals may have been a factor in the successful recuperation of the population. The European bison (Bos bonasus) was destroyed in the wild during World War 1; only about 17 animals survived. However, more than 800 individuals now exist, bred from stock in zoos, and although inbred, the European bison has been re-established successfully in nature reserves. On the other hand, the inbreeding bottle-neck in Przewalski's horse (the Mongolian wild horse Equus przewalskii), now bred up to 200 from a minimum effective population size of eight animals, has resulted in reduced fecundity and longevity of the existing individuals, and it would be very difficult to reverse the damage at this point. Thus, while occasionally a population will undergo severe inbreeding without becoming extinct, such populations, even if they are established successfully, generally suffer from a variety of genetic handicaps. Even the most successful inbred lines of maize, for example, are, on average, 30% less productive than outbred lines.

CONCLUSION

The modern scientific management of plants and animals requires: (1) familiarity with some simple genetic processes; (2) agreement as to the conservation objectives for each species; and, (3) the application of some simple rules or guidelines.

The relevant genetic processes are inbreeding, genetic drift, artificial selection and artificial hybridization. Inbreeding is the mating of close relatives; its major effect is the loss of fitness due to homozygosity of deleterious genes. Genetic drift is the random loss of genetic variation; it is inversely proportional to population size. Artificial selection is the effect of human intervention on survival and breeding success; it can cause non-adaptive evolutionary changes. Artificial hybridization (introgression) is the unnatural crossing of stocks; it can be beneficial or harmful, depending on the genetic differences between the stocks and other circumstances.

A set of well defined objectives is the second requirement of sound scientific management. Early on, it must be decided whether the project is short term or long term. Prudent managers will consider how the temporal objectives affect their projects with respect to the above four genetic processes, particularly with regard to: (1) the number of individuals to be maintained in the populations; (2) the manner in which individuals are culled; and, (3) the manner in which translocations are made.

The rules regarding minimum population sizes are simple: a minimum effective population size of 50 for short-term programmes; a minimum effective population size of 500 for long-term programmes. These rules are, of course, ideals. When they are beyond reach due to limitations of space, funds, or skilled personnel, it must be remembered that a major objective of conservation is to keep open the options of future generations. This can best be done by making every reasonable effort to maximize population size, even when the results might seem trivial when compared to the guidelines for minimum population sizes just mentioned. More concretely, a breeding stock of six individuals is much better than a stock of three, especially if the matings and family sizes can be influenced by the manager.

7. IMPLICATIONS OF ISLAND BIOGEOGRAPHY FOR ECOSYSTEM CONSERVATION

J M Diamond (convener)

J Breytenbach, G Child, K H Cooper, P G H Frost, D R Given, A E F Heydorn, I A W Macdonald, A J Ribbink, G A Robinson, J C Scheepers

INTRODUCTION

The science of island biogeography concerns itself with the distributions of plants and animals on oceanic islands and on island-like mainland ecosystems, such as mountain tops, lakes and forest patches. What, if anything, have practical managers of nature reserves to learn from the findings of fieldwork and theory in island biogeography?

The relevance of island biogeography to conservation stems partly from the fact that many reserves have become, or are becoming, islands in a sea of man-modified ecosystems. What is more, the questions asked by island biogeographers have also been asked by reserve managers who are concerned with practical problems, such as: what populations in a reserve are in risk of extinction; how many species, or how much of an ecosystem, can a reserve hold; and, what effects will the extinction of one species bring?

There is a large literature dealing with such questions. In effect, nature, through island and island-like ecosystems, has created thousands of reserves as natural experiments. Research on these natural islands offers a rich array of case studies with many lessons for the reserve manager. These studies should indicate the length of time that a particular population may be expected to survive within a reserve, as well as the number of species of a particular group which may be likely to survive within the reserve. They also assist the reserve planner to solve problems, such as: how large should the reserve be in order to achieve a particular conservation objective; what should its shape be; would one large reserve be better or worse than several small ones; how should reserves be located relative to one another; and, should reserves be selected in areas of homogeneous or heterogeneous ecosystem types?

DEFINING ISLANDS AND THEIR BORDERS: SHARP AND FUZZY ISLANDS

The biosphere is composed of a mosaic of ecosystems. The nature of these patches and their degree of distinctiveness from adjacent patches varies. Some, like real islands, differ markedly from surrounding ecosystems; the boundaries between patches are clearly defined, and they share few, if any, component species. Examples include islands of land surrounded by water, lakes and other water-bodies surrounded by land, forest patches in grassland, granite inselbergs in desert, mountain tops isolated from one another, undersea mounts, and oceanic trenches. Conversely, there are ecosystem mosaics in which the boundaries of the patches are defined less clearly, and some of the faunal and floral elements are shared between adjacent patches. These patches, therefore, would serve as islands to some species but not to others.

THE NUMBER OF SPECIES DEPENDS ON ISLAND AREA

Consider an island, with an undisturbed physical environment, and count the total number of species in either the animal or plant group in which you are interested. This could mean, for example, all higher plants, or members of the plant family Proteaceae, or butterflies, or land-birds, or cichlid fishes. Then consider how the number of species in your group varies among different "islands" in the same geographical area and climate zone.

The number of species depends on environmental factors, such as habitat diversity, and on geometric factors, especially the size, location and shape of the "island". Taking area first, the number of species increases with area of island. A rough general rule is that a 10-fold increase in area means a 2-fold increase in species number; a 100-fold increase in area, a 4-fold increase; and a 1 000-fold increase in area, an 8-fold increase. The factor of two for increase in species number with an order of magnitude increase in area is a mean value; the usual range in this factor (among different organisms and islands) is from about 1,4 to 3,0. In cases of linear habitats, such as rivers and coast-lines where it is hard to define the area of the system, the number of species is related to their length. For example, the number of fresh-water, molluscan (snails and bivalves) species in a river increases with the length of that river and its tributaries.

Since the number of species increases with increasing area, it follows that ecosystem fragmentation will lead to fewer species being present. Similarly, the designation of a particular area as a reserve will inevitably lead to the exclusion of some species characteristic of the region as a whole. This result is termed the "sampling effect", due to the analogy of taking samples from an heterogeneous population; the heterogeneity in any one sample seldom ever equals the heterogeneity of the population as a whole.

Quantitatively, the rough general rule given in the previous paragraph has the following meaning: if 10% of the original area of an ecosystem survives (whether in reserves or non-designated areas), 50% of the species of that ecosystem will ultimately survive. If 1% of the area survives, then 25% of the species will ultimately survive. The rate at which the 50 or 75% of the species ultimately disappears is discussed later.

THE NUMBER OF SPECIES DEPENDS ON ISLAND DISTANCE

Area is not the only geometric factor affecting the number of species in an ecosystem or habitat. Another important factor concerns the distance or extent of isolation. The greater the distance between one environmental patch and another similar patch, the fewer the species those patches will contain. For example, if one compares the number of land-bird species on different tropical islands of the south-west Pacific Ocean, in relation to the source (New Guinea), the number on an island of a given area decreases by a factor of two for each 2 500 km from that source. Similarly, the number of rocky-shore cichlid fish species on islands in Lake Malawi decreases with distance from other rocky shores.

Thus, the effect of distance simply illustrates the ability of species to disperse across intervening zones between islands. Obviously, the greater the ability to disperse the less the effect of distance on the number of species. For example, the distance of an island from any mainland will have little or no effect on the number of sea-bird species (which alight and feed freely on the ocean), but will cause some reduction in the number of species which are dependent on wind as a dispersal agent (e.g., ferns, grasses and orchids). Similarly, one could expect a larger reduction in the number of species of bats and land-birds, and a still larger reduction in the number of species of lizards (which could only disperse by rafting over water on floating vegetation), and a reduction, which almost amounts to a barrier, in the distribution of large land-mammals.

THE NUMBER OF SPECIES DEPENDS ON ISLAND SHAPE

The number of species within an island ecosystem may vary with the shape of the island, although the evidence for this statement is limited. However, if one compares long, narrow systems (with large surfaces, relative to the volume contained), with circular land masses which are ecologically similar and of the same area, then the latter usually contain more species which are characteristic of the ecosystem type found in both areas, but at the same time, they tend to have fewer species which are more commonly found along the edges of such systems. For example, the land masses adjacent to long, narrow peninsulas of the type found in Florida, the Baja, California, the Ucatan peninsulas of Mexico and the Vogelkop of New Guinea, contain many more species characteristic of those land masses than the named peninsulas which extend from them. Exceptions to this apparent trend occur in the case of long, narrow systems which have ancient connections to the "parent" land mass, such as in the case of the Cape Peninsula of South Africa. In this, and other isolated exaples, extraordinarily rich communities of plant (e.g., fynbos) and animal species may be found. Such occurrences are directly related to the long evolutionary history of both peninsula and adjacent land mass, together with high habitat diversity.

THE BALANCE OF COLONIZATION AND EXTINCTION

Why do large islands tend to have more species than small islands? Why do remote islands have fewer species than less isolated islands? Why do peninsulas apparently have fewer species than central mainland areas? The answers to these questions relate to "species turnover". To illustrate this point, we may use the example of a thorough census of species on an island. If this census is repeated in subsequent months or years, it will not necessarily produce precisely the same list of species, simply because both species extinction and colonization are dynamic processes which take place continually.

In fact, species turnover rates vary among plant and animal groups. For instance, the turnover of land-bird populations is sufficiently rapid that changes can be detected from year to year in the breeding species of mainland census plots, or of oceanic islands near mainlands. On the other hand, turnover in lizard populations on islands may be so slow that censuses many decades apart may show no differences. For plant species with long-lived seeds, the risk of total extinction may be negligible as long as the physical environment itself is not destroyed; dormant seeds may remain whole in the soil long after the last mature plant has died. Thus, rates of species turnover depend on the nature of the ecosystem and the size of the census plot relative to the dispersal properties and biology of the organisms concerned.

Colonization and extinction rates depend on island area and distance. Relatively isolated islands receive fewer colonists. Thus, at any given instant, isolated islands harbour fewer species than islands near a source of colonists. By the same token, peninsulas may have fewer species than equivalent central habitats, because they receive colonists from only one side, whereas central habitats are open on all sides. Conversely, animals moving more or less at random within home ranges that are substantially larger than the peninsula will tend to be "funnelled" off it, as was evident with large mammals and some birds during the formation of Lake Kariba in Zimbabwe.

WHAT HAPPENS TO THE NUMBER OF SPECIES WHEN ISLANDS FORM?

Species numbers decline as ecosystem fragmentation increases. This raises the question: how rapid are these types of decline? The smaller the area, the more rapidly species will be lost. This is exemplified by the forest reserve of 17 km^2 at Barro Colorado Island, in Panama. Seventy years ago this system was converted from a hill top into a real island when construction of the Panama Canal flooded surrounding valleys. Subsequently, Barro Colorado Island has already lost at least 10% of its species of forest birds. Recent studies of birds in Brazilian forests, which were formerly part of a continuous expanse and which have now become isolated tracts due to the development of coffee plantations, also show similar trends in reduction of species numbers.

While species number reduction appears to be a common feature of island creation, some species still manage to survive "insularization", while others do not. Why should this be so? First, there may be certain species which are present in a protected area only as non-breeding transients. They will disappear, unless the breeding population outside the protected area remains viable and continues to be a source of supply. Secondly, certain species may exist as marginal breeding populations sustained by dispersive individuals which originate from breeding populations lying outside the island. This has been termed the "rescue effect". Thirdly, certain species may be dependent on certain resources located outside the protected area, and unless the future existence of these resources is assured, as well as continued access to them, the loss of the dependent species will follow. Finally, certain populations may become locally extinct, due to chance fluctuations in their small populations, chance environmental catastrophes or because of inbreeding (see Chapter 6).

Of course, habitat fragmentation automatically leads to the development of barriers to dispersal and, hence, colonization rates will decline as areas of similar habitat become more isolated from one another. The resultant decrease in the number of species may reduce the resilience of the new community, resulting in further accelerated changes.

DIFFERENTIAL DISPERSAL ABILITY AND ITS EFFECTS

Dispersal differs greatly among species, and evolves in relation to the ecological requirements of each species. Flying animals tend to disperse farther and in larger numbers than non-flying animals. However, there are large behavioural differences even among flying animals. Many bird species of tropical rain forests will not fly across water barriers, of even a few kilometres, or clearings no wider than a road. Wind induces certain species of butterflies to crawl into vegetation, and others to climb onto exposed perches. The latter are more widely dispersed by wind than the former. Large mammals tend to disperse farther than smaller ones, but in the modern world with its many artificial barriers (e.g., fences) small mammals may now be more effective dispersers.

In aquatic environments, pelagic larvae may float for weeks or months before settling and can be carried thousands of kilometres in ocean currents. In this context, marine reserves should be sited so that they may be colonized by organisms carried by currents and, in turn, act as source areas for the subsequent colonization of other areas. At the opposite extreme, cichlid fishes of east African lakes are mouth brooders; the young seeking shelter in the mouth of a parent. Thus, these fish are often extremely sedentary and, indeed, the whole geographical range of such species may be very limited indeed, and confined, for example, to the shallow waters surrounding one island in a lake.

Plant species also differ greatly in seed dispersal adaptations. Some seeds are carried far by the wind, (e.g., those of certain ferns and grasses with circumpolar distributions, such as Grammitis poeppigiana). Others are carried by the sea, floating and surviving months of immersion in salt water (e.g., the tropical beach plant Ipomea pes-caprae). Still others are carried by birds. At the other extreme, many plant species are so sedentary that their seeds may be dispersed only a few metres, leading to the development of very localized endemic populations.

There is an inverse relationship between the ability of a species to disperse and its risk of extinction in isolated populations. Provided that gene flow within a large population (500+ individuals) is unimpeded, the probability of extinction of that population is remote. If the population is divided so that gene flow is retarded or ceases, then the likelihood of extinction of each population increases (the possibility of speciation is not considered here), and this probability increases further as the population continues to fragment. The degree to which gene flow is retarded between the various populations of a species depends upon the manner in which the organism is dispersed and the nature of the barriers between populations. Clearly, as the distance between populations increases, so their exchange of genes decreases, until a distance is reached which makes such exchanges impossible. Similarly, physical barriers may totally prevent the members of separate populations of the same species from coming together.

DIFFERENTIAL EXTINCTION RISK

The risk of extinction varies greatly among species, depending on their effective population size (see Chapter 6), metabolic requirements, population fluctuations, area requirements, dispersal ability, and the vulnerability of their habitats. The risk of extinction is also directly related to population size. The smaller the population the more likely the risk of extinction. In real terms it is the effective population size, not the actual population size, that is important. Effective population size is the actual number of breeding individuals, averaged over population fluctuations, and taking into account factors such as polygamous mating systems and unequal individual contributions to reproduction (see Chapter 6). A second indication of vulnerability to extinction is the degree to which the population fluctuates with time. Thus, comparing two species with the same population size, averaged over time, the species whose population fluctuates more widely is more prone to extinction. For example, on small European islands large enough to hold only a few pairs of ravens and warblers, the ravens breed annually without interruption for decades, while the warbler populations disappear and reappear every few years, because they have a higher intrinsic rate of fluctuation.

Species having small geographical ranges also tend to be vulnerable to extinction, due to environmental catastrophes affecting their whole ranges. For example, certain plant species in the fynbos of South Africa's Cape region are confined to single valleys; certain species of cichlid fishes in Lake Malawi, to the shallow water around single islands; many species, to single oceanic islands. A fire that burns the vegetation of an entire valley, a slight rise in lake level that submerges the whole island, or the introduction of grazing animals to an oceanic island, may exterminate any of these species types, even though they may have originally numbered hundreds or thousands of individuals, and may also have formed stable populations.

Some taxa of animals exist at lower densities than others. Mammals, with their relatively high metabolic requirements, generally exist at lower densities than reptiles and amphibians, and larger mammals often exist at lower densities than small mammals. The trophic level at which an organism exists is also relevant; carnivores generally occur at lower densities than herbivores. Cold-blooded animals may tend to be less extinction-prone than warm-blooded animals, because they have lower metabolic requirements and can survive longer without food. In general, insects, lizards, and many plants, which tend to have higher population densities than most birds or mammals, will tend to have lower extinction rates in a reserve of a given area, and may survive in small reserves too small for many birds and mammals. These considerations lead to predictions concerning the characteristics of the more vulnerable species within a system. Generally, large species that exist near the tops of food chains, or that rely on scarce resources, will be the most vulnerable to extinction. More specifically, they include large mammalian carnivores, large frugivorous birds and large predatory fish.

Relict populations of plant species consisting of only a few mature individuals may maintain a precarious existence for a long time and then recover if conditions improve. For example, on Kermadec Island between New Zealand and Tonga, four plant species that were reduced to exceedingly low population levels by goats, introduced in the first part of the nineteenth century, have made a spectacular recovery. This recovery has occurred in only a few seasons, after removal of most of the goats in the 1970's.

Among plants, the effective population includes not only the plants themselves but also viable seeds and spores in the ground, so that for certain species, the potential population may be large even when no mature plants are visible. Certain plant species will be resistant to extinction, because their seeds remain viable for a long time. For instance, in the Recherche Archipelago of south-western Australia, certain herbaceous plants collected in 1802 disappeared subsequently, but germinated after a fire in 1976. Certain plants have germinated from seeds many centuries old. However, it is certainly not true that all plants are relatively resistant to extinction because of long-lived seeds and, in fact, many species, such as those belonging to the genus Crinum (Amaryllidaceae), have short-lived seeds.

Finally, dispersal ability tends to offset effects of small population size. A locally extinct population may be re-established by immigrants from another population, before that population also becomes extinct. If dispersal between reserves or islands does not occur, each population may successively cease to exist, until the species is extinct. Thus, all other things being equal, sedentary species are more prone to extinction than vagile species. There are, however, some notable exceptions to this generalization. For instance, if only one-tenth of a desert region is contained in reserves, then the resident species in the reserves will be less prone to extinction than presumably some nomadic species which naturally roam over the whole region.

LIFE HISTORY EFFECTS

Species differ not only in dispersal ability but also in other ecological attributes, such as longevity, competitive ability, number of offspring per brood, frequency of broods, parental care of young (in animals), occupation of climax or successional habitats, and occupation of permanent or transient habitats. Certain sets of life-history traits tend to be associated with each other. At the risk of grossly oversimplifying a complex real situation, we describe two extremes in life-history strategy which represent opposite ends of a continuum. These customarily are termed the r-strategy and the K-strategy. The r-strategy derives its name from the fact that r is the standard symbol used for describing growth rate in demographic equations. The r-strategy characterizes species of successional, transient, or frequently disturbed habitats. Individuals of such species tend to have short life-times compared with taxonomically related species of mature ecosystems, because the entire system may be destroyed or become unsuitable within an individual's life-time. Such systems include small fresh-water pools that dry up and early successional forest, and their species tend to have a high dispersal ability, in order to be able to find the scattered and shifting patches of suitable habitat. They have also evolved high reproductive rates, with frequent breeding, many young per brood, early breeding and little parental care for the young. Large numbers of young disperse, but most are doomed to die as a result of inability to find suitable habitat. However, a few individuals normally find areas of suitable habitat unoccupied by conspecifics. Competitive ability is low in these species, and rather than put energy into biological attributes which could enhance such competitiveness, their adaptive abilities consist of rapid reproduction, growth, and dispersal. In this way these species are able to survive in systems which are highly unstable in space and time. Examples of *r*-selected species include invertebrates of temporary rain pools, "weeds", and plants and animals of second-growth habitats.

The opposite extreme is the *K*-strategy, where *K* symbolizes the population carrying capacity in demographic equations. The *K*-strategy characterizes species of species-rich, stable ecosystems, such as tropical rainforest and Mediterranean oak woodland. Individuals of such species tend to have long life-times, while their dispersal ability tends to be low, and habitat patches rarely contain depleted populations of species. Thus, there are few opportunities for colonization. Reproductive rates are similarly low. However, a premium is placed on competitive ability, to be able to persist in saturated habitats. Therefore, the first age at which reproduction takes place is relatively late, broods are infrequent, few young are produced per brood, and (in the case of animals) the young are often given prolonged care by parents. In effect, a few "expensive" young are launched into life with the best preparation, rather than many "cheap" young being "scattered to the winds". Examples of *K*-selected species include many plants and animals of rainforest, and mouth-brooding cichlid fishes, large whales, large terrestrial herbivores, and large birds.

A wide variety of breeding systems occurs among flowering plants, including both sexual and vegetative strategies. Within these categories many variations occur, such as dioecism, monoecism and apomixis (where there is production of viable seed without the necessary intake of genetic material from another individual). In some instances, individual plants make use of a range of reproductive strategies or can switch from one system to another, especially at times of stress. For example, certain species found on the margins of lakes and streams sometimes reproduce only vegetatively when water levels are high, but lowering of water levels and drying out of soil around the plants induces flowering and subsequent seed production. Moreover, the occurrence of polyploidy and similar variations is common in plants, but these genetic variations are rarely found in animals.

An important result of this variety of breeding systems is that many plants have a range of reproductive options available, depending on the particular prevailing environmental conditions. Plant species can sometimes survive at low population levels which would lead to extinction in many animals. Extreme examples are found on some oceanic islands where certain plant species may survive for many decades, even though their populations number 10 or fewer individuals. On Stewart Island, south of New Zealand, the plant *Gunnera hamiltonii* forms a single discontinuous mat of several hundred square metres at only one site. Female plants of this dioecious species have never been seen at this site. Hence, it is possible that the "population" consists of a single plant maintained by vegetative means. The chances for survival of plant species which reproduce in this way, and which are *K*-selected, are much greater than for *r*-selected species.

TROPHIC CASCADES

Species do not exist in isolation. They exist within systems and are linked by the flow of energy, the cycling of nutrients, as well as competitive, predatory, and mutualistic interactions (see Chapter 4). Thus, the loss (or overabundance) of a particular species may have repercussions throughout a system, triggering a wave of decline or extinctions among associated species. For example, the extinction of a top carnivore which affects, but normally does not limit, its prey population, can lead to an increase in the prey to levels at which other associated species become affected adversely. In the province of Natal in South Africa, increasing fragmentation of evergreen forest and human pressures have led to the disappearance of top carnivores, such as crowned eagles (*Stephanoetos coronatus*) and leopards (*Panthera pardus*), from many of the forest remnants. Partly because of this, populations of vervet monkeys (*Cercopithecus aethiops*) have increased. These omnivorous animals are major predators of eggs and nestlings of certain birds (particularly sunbirds of the genus *Nectarinia*), with the result that the breeding success of these species is lowered drastically. A further example from Natal concerns an oceanic shark (*Cacharhinus obscuris*) that comes inshore to give birth to young. Normally, many of the young are eaten by a number of chiefly inshore sharks (e.g., *C. leucas* and *C. milbertii*). However, there are indications that a reduction in the populations of these inshore species by gill-netting has enhanced the survival of young sharks, resulting in larger numbers of *C. obscuris*. This increase has paralleled a decline in the number of fish caught by anglers and commercial fisherman, which suggests that the local populations of these fish are being reduced in part through the predatory actions of the extra-large population of young sharks.

In the moist tropics, the predominant organizational patterns of biotic communities appear to comprise many similarly structured food webs that differ primarily in taxonomic composition, and in which the participants are co-adjusted to each other's presence and actions. These subsystems are linked by faunal pollinators and seed dispersers whose activities significantly influence the success of the plant species which support these separate food webs. These link-species are termed "mobile links," and their persistence in turn often depends on another group known as "keystone mutualists" which are those species which provide essential support for complexes of mobile link species. Changes that adversely affect the survival of keystone mutualists or mobile link species can reverberate through many different subsystems, with the potential for progressive disintegration.

In the Cape fynbos biome, the rat *Praomys verreauxii* which feeds on the seeds of certain proteas also acts as a pollinator of geophilous (ground-clinging) protea species. The food plants of this rat may be eliminated or reduced by out-of-season fires (although certain geophilous species can evade the effects of fire or can resprout after fire). In a small reserve, a widespread fire in the wrong season, or a fire too long delayed, will reduce the abundance of the protea food plants, leading to food shortages for the rodents and, hence, probably to reduced pollination and seed set of the rarer geophilous proteas. The potential for such "cascading" extinctions is widespread, and the inevitable consequence will be a reduction in the diversity of species and the interactions in which they take part.

HABITAT DIVERSITY

A wide diversity of habitat type within an ecosystem will affect species diversity in two distinct ways. First, particular habitats often have specialized species which are confined to them. Hence, the greater the diversity of habitats within a nature reserve, the more "specialist" species the reserve will contain. Secondly, a reserve that embraces forest, savanna and grassland ecosystems and their respective habitats is more likely to harbour a larger species number than a reserve of the same total area but containing only one of these ecosystem types.

A more subtle effect of habitat diversity involves species which occupy multiple habitats, either simultaneously or sequentially. If a species requires several different habitats for completion of its life-cycle, one might easily be misled into believing that conservation of one habitat will therefore ensure survival of a population of the species, while not realizing that at some other time the species will require an entirely different habitat. Thus, maintenance of habitat diversity in a reserve is essential for the maintenance of populations of such species. This important point is reinforced by the following examples.

Birds of paradise are the most distinctive and spectacular bird species of New Guinea, and some are endangered. Certain species have a characteristic population structure, in which individual birds shift their altitudinal distribution with age. Thus, higher elevations are occupied by adult breeding males and females, lower elevations by females and immatures but no adult males, and the lowest and highest elevations by immatures but no adults. If one conserved only those altitudinal zones in which breeding adult males and females were observed to be common, and if a reserve did not contain the highest and lowest elevations, essential for immatures, only a short time would elapse before the bird of paradise populations disappeared.

Many frugivorous birds are nomads and wander seasonally in search of fruiting trees. In such cases, habitats in which a particular species is abundant for 11 months of the year may be insufficient to preserve a self-sustaining population of the species, because the fruit trees on which the species depends in the twelfth month may be located in another area. The distances which some frugivores traverse in their annual cycle are surprisingly large. Certain New Guinea montane parrots spend the austral summer in the highlands and the winter in the lowlands, and commute over 100 km daily from their nocturnal roosts in search of fruit trees in some seasons. Frugivores exemplify numerous species which exploit unpredictably fluctuating resources. Resource production often is triggered by stochastic events, such as rainfall in arid regions, and reserves should be large enough to ensure that such events can occur within them with sufficient frequency to promote the survival of nomadic species.

Many large mammals in fluctuating, semi-arid environments (e.g., Kruger and Serengeti National Parks) seasonally migrate in response to rainfall cycles and changes in vegetation. Thus, habitat diversity manifested by a temporally changing mosaic of vegetation is essential for self-sustaining populations of the ungulates and associated predators, for which these parks are famous. The construction of a game-proof fence around Kruger National Park, which intersected the west-east migration pathways of the ungulate populations, apparently contributed to a drastic decline in the wildebeest population in the western sector of the park. Seasonal migration on a larger scale is conspicuous among birds, certain species undertaking regular transequatorial movements. While it is impossible to encompass all the spatial requirements of these long-distance migrants within the reserve system of a single country, consideration should be given to securing representative areas at both ends of the migration routes and, where these are necessary, areas which serve as intermediate stop-over points along routes.

It is often tempting to try to maximize the number of species contained in a reserve by initially locating the reserve in an area of high habitat diversity. However, a disadvantage of a high diversity of species in areas of limited extent revolves around the fact that many of the species concerned are represented by small populations. This is exemplified by the Hluhluwe-Umfolozi Reserve in South Africa. In this reserve, covering approximately 900 km^2, habitat diversity is extremely high and 58% of all the land and fresh-water bird species of Natal (a region of 87 000 km^2) were found there during the decade 1970-1979. However, only 50 of the 327 bird species in the reserve consisted of effective resident breeding populations, exceeding 500 individuals. Since small populations are prone to extinction, this means that a vast majority of the reserve's bird populations are unlikely to be self-sustaining. In addition, 35 bird species formerly recorded in the reserve were not found there during 1970-1979, and are presumed to have become locally extinct. Most of these species are habitat specialists that probably became extinct as a result of habitat changes within the reserve, coupled with their already small population size.

EVALUATION OF COMPROMISES

It is hard to formulate universal principles for design and management of reserves. Depending on one's goals, a design principle that is optimal in one situation might be counter-productive in another situation. The following examples bring out the considerations that may favour one option against another in a particular situation.

Given the same total area, should a reserve be simple or complex, in terms of habitat diversity? The answer depends on one's goals. The more simple the system, the greater the potential to harbour large, populations of species characteristic of that system, and which are less prone to extinction. The disadvantage lies in the fact that the relatively simple reserves sacrifice species which have wide requirements. They also sacrifice those species which use the reserves aperiodically. The more complex reserves have the advantage of containing more species which are habitat specialists, as well as species with multiple habitat requirements, but they risk losing species with small populations if many of the habitats are contained only as small areas.

In locating and designing marine reserves, one should similarly balance the advantages of a large permanent reserve against a series of smaller reserves designated at different locations in different years. The large reserve provides maximum species diversity, long-continued successional build-up, colonization, and "seeding" of outlying areas.

Given the same total area that can be allocated to a reserve, it is often difficult to decide between one large reserve or several small reserves of the same aggregate area. The several small reserves may offer the advantages that each contains different localized species, different habitats, or different representatives of a set of competing species. The small reserves also provide some safety against disease outbreaks, in that an outbreak that ravaged an animal population in one reserve would be unlikely to affect populations of the same species in the separate small reserves. Risks of small reserves include problems with species that live at low densities, and require large areas (e.g., wild dog (Lycaon pictus) and certain eagles). These may disappear in all the small reserves, and they can only persist unassisted in large reserves. Species included in this category are top predators, whose losses are likely to promote trophic cascade effects.

Similar compromises attend the question of whether or not to connect separate reserves by corridors of similar habitat. A corridor has the advantage of effectively transforming several small reserves into a large reserve, by expediting gene flow and minimizing extinction risk. However, corridors do have the disadvantage of facilitating the transmission of diseases as well as undesirable colonizing alien species, and possibly of constituting narrow peninsulas of low species diversity and limited habitat diversity.

What is the optimal shape of a reserve? In terrestrial situations, if a reserve is being set aside from a continuous expanse and if dispersal is more or less random with respect to direction, then the optimal shape will often be circular. The worst shape will be long and narrow. Circular reserves afford the best chance for the reversal of local extinctions, mainly by facilitating rapid dispersal from other parts of the reserve. Secondly, a reserve generally contains habitat types which are different from those outside its borders, and in the case of circular reserves, which have the smallest perimeter relative to area, those species which are characteristic of the area and which are likely to avoid habitat interfaces at the perimeter will remain within the reserve. Long and narrow reserves risk being split into effectively two reserves by local habitat degradation. The reasoning is similar, but the conclusions different, when biotic dispersal is non-random with respect to direction. This will generally be the case in river reserves, where dispersal is along the river, and in marine reserves where dispersal is strongly influenced by ocean currents. In such cases the reserve shape should conform to the direction of biotic dispersal, so as to maximize the interconnections of different parts of the reserve.

POSTCRIPT AND GUIDELINES

The main discussion themes of this chapter do not imply that only large reserves (thousands of square kilometres) are of any use, and that one should give up if one cannot get a reserve of this size. The necessary area of a reserve depends partly on the goals of that reserve, and partly on the effort and expense that can be devoted to overcoming the disadvantages resulting from a small area. We now summarize specific considerations and a decision-making strategy for defining reserve area. The topic is discussed more fully in Chapter 8.

1. Define one's goals

If the aim of a reserve is to conserve ecosystem or habitat type, then the manager must identify the key species of the habitat or ecosystem, such as top predators, important food plants, species important in plant dispersal and pollination, and other species whose loss would transform the whole habitat or ecosystem through a trophic cascade. Different goals require different strategies.

2. Calculate the area required to maintain key species at effective population sizes

This requires estimations of population density of key species. An effective population size of several hundreds is necessary and is dictated partly by the ecological considerations discussed in this chapter (to minimize risk of extinction due to population fluctuations), and partly by the genetic considerations discussed in Chapter 6. For species whose populations exhibit large fluctuations in time, the desired effective population size should exceed several hundreds. As an alternative to this procedure one can examine species lists which are available for isolated patches of habitat similar to those in the reserve. In this way one may determine empirically the size required by key species. Naturally, the resulting area estimate will vary greatly with the species. For example, certain eagles are likely to require thousands of square kilometres to maintain effective populations of several hundreds; small invertebrates and plants may achieve this population in a fraction of a square kilometre. The actual available area for calculating effective population size may be greater than the reserve area itself, if the ecosystem outside the reserve is similar to that inside it. An example is the case of a forest reserve which is surrounded by forest managed for selective logging, rather than, say, grassland.

3. Does the area really correspond to a self-contained ecosystem?

There are at least two types of reasons why an area presently containing an effective population of several hundred individuals of a particular species may nevertheless lose that species quickly, even in the absence of an unusual catastrophe. First, one must ascertain that the area contains the necessary resources for an effective population of several hundreds on a year-round basis, not only at an instant. The difference is significant for species undertaking seasonal or irregular movements. Secondly, the area must be sufficient not only for the species of immediate interest, but also for other species on which that species depends. Thus, a particular plant species cannot be effectively conserved in a reserve which is too small to secure the future of its chief pollinator or seed disperser.

4. Is the proposed area "catastrophe-proof"?

We refer here to the risk of an extinction that is not related to population size *per se*, but instead to area itself. A local population may be extirpated by a catastrophe, such as a fire, drought, landslide, or change in lake level. Such catastrophes destroy all individuals within the affected area, regardless of whether the individuals number ten, hundreds, or tens of thousands. Each type of catastrophe has a characteristic range of impact area (e.g., a landslide may easily devastate tens of hectares, almost never tens of square kilometres). Thus, the proposed reserve should contain effective populations of several hundred individuals and must also be much larger than the typical impact area of relevant catastrophes. This consideration is likely to be crucial in reserve design in the case of certain plants and invertebrates. For such species, one hectare may contain thousands of individuals and appear safe on a population-size criterion. The real risk of extinction, however, comes in the form of fire, landslide and a variety of other local disasters.

5. What if the available area is insufficient to meet one's initial goals? Present an explicit argument for enlarging the area

Part of the reason why official decision-makers have often allocated areas too small to serve as effective reserves is that ecologists were unspecific and unpersuasive in arguing for larger areas. A specific argument could take the following form. Based on knowledge of population densities in the system or systems under consideration for incorporation in a reserve, and of how population size affects risk of extinction, the following outcome can be predicted: if the area of this reserve remains at only *x* square kilometres, there is a greater than 90% chance that species *a*, *b*, *c*, and *d* will go extinct within 5 years; a 50% chance that species *e*, *f*, *g*, and *h* will go extinct within 10 years; and only for species *i*, *j*, *k*, and *l* will the chances of long-term survival be high. Increasing the area to *y* square kilometres would give 75% of these species a high chance for long-term survival.

6. Manage the available area so as to enhance survival prospects for the species of interest

There are numerous steps that a reserve manager can take so as to favour particular species or habitats. These include: creating the desired habitat or mixture of habitats by preventing fires, instituting fire rotation, or other means; maintaining permanent or rotated water sources in an arid environment; periodically introducing additional individuals of a particular species of interest; introducing, or regularly adding, prey species, pollinators, or other species enhancing the species of interest; elimination of competing species; and culling the species of interest so as to optimize the sex ratio or age structure.

The greater the effort and expense devoted to management, the smaller the area in which a given species can be accommodated. An effective population of several hundred lions may require thousands of square kilometres under natural conditions; perhaps only hundreds of square kilometres if suitable prey are released periodically for food. Procedures of this type are now being carried out in the case of the last Indian lions in the Gir forest. As far as zoos are concerned, one square kilometre may be all that is necessary.

Three caveats should be added when considering management of undersized reserves. First, management is expensive, and the expense may be required indefinitely. Culling and transfers of large mammals account for a substantial fraction of the budget of South African reserves. Ongoing management expenses should be compared with the one-time costs of more land acquisition that would render these management costs unnecessary. Secondly, we simply do not know enough about most species to manage them properly. Finally, management of a small number of species may be a tenable strategy in a reserve aimed at protecting a few particular species, but it is a hopeless strategy in a reserve aimed at protecting ecosystems with many key species and thousands of constituent species.

7. Accept realistic goals

If the area available for a reserve is limited and is insufficient to meet one's initial goals, given the constraints on knowledge and the financial budget available for management, the remaining option is to work in reverse. That is, one should investigate the most important goals that could be attained realistically, given the available area and budget.

CONCLUSION

The science of island biogeography is concerned with the distribution of species on real islands, and on virtual islands such as incomplete indigenous ecosystems surrounded by alien ecosystems. This science is relevant to conservation, because nature reserves are islands in a man-modified landscape, and because island biogeographers have been asking many of the questions asked by reserve managers.

The number of species on an island is related to island area, isolation, and shape. These relationships can be interpreted in terms of the balance between colonization and extinction rates of species on an island. For several different reasons, a system that becomes an "island" loses species, but species differ greatly in their susceptibility to such extinctions, as well as in their ability to recolonize an island following extinction. Extinction of one species can lead to extinctions of other species, through trophic cascades. Compromises must often be made in the design of nature reserves, and the conflicts between the choices involving single large versus many small reserves, relative homogeneity of habitat type within a reserve versus heterogeneity, and, to connect reserves with corridors, or to leave them isolated from one another, are extremely important considerations.

8. MAINTAINING ECOSYSTEMS IN DESIGNATED AREAS

K R Miller (convener)

J Breytenbach, G Child, P G H Frost, J C Greig, I A W Macdonald, G A Robinson

INTRODUCTION

Certain protected terrestrial, wetland, coastal and marine areas contain entire ecosystems and others contain features and processes which are vital to the maintenance of ecosystems. Through careful management, in a wild or semi-wild state, these areas can contribute to the major goal of conservation, while also providing other benefits to man. Ideally, such protected areas are designated as national parks, wildlife sanctuaries, or other types of reserves. In this chapter, for convenience, designated areas are called reserves.

Human societies tend to establish several types of reserves, in response to their ethics for conservation and their requirements for goods and services from natural resources. Thus, most reserves are selected to meet a series of goals, including the conservation of nature *per se*. Decisions were made at a time when ecological theory was being pioneered and few, if any, scientific principles were available to aid in proper planning for conservation. Hence, most reserves contain biophysical resources which may or may not include important ecosystem processes and elements. Many reserves are too small to cover the ideal or theoretically minimum area, and they conform to the shape of local political subdivisions, land-survey mechanisms, or topographical features. Moreover, management activities in reserves tend to concentrate on several divergent objectives, and they generally feature either preservation or manipulation, both based upon little clear analysis. Frequently, research is scarce or absent, and management is generally intuitive rather than being based on systematic observation and analysis of key environmental factors. Furthermore, physical development more often than not takes place in and around reserves, with little scientific relationship to the functioning of the ecosystems embraced by the reserves.

As unallocated natural resources diminish, as a result of expanding agriculture, grazing, fishing, timber harvesting, industrial/urban development and increases in human population, increasing demands are placed on reserves for a variety of human requirements. At the same time, the need for ever more careful treatment of biophysically important areas increases, and the roles that reserves are playing in ecosystem maintenance must be ensured. In order to achieve this, the management of reserves is in need of greatly amplified support from science. Concomitantly, managers of reserves urgently need to incorporate scientific principles into decision-making and management procedures. This chapter sets out guidelines by which managers can apply modern methods in making their work more effective. More particularly, the chapter stresses principles which are crucial for the maintenance of ecosystems in nature reserves.

LOCATION, SIZE AND LAYOUT OF RESERVES

Decisions for the selection of reserves cover a range of choices in a hierarchy from the general to the specific. At the highest level, areas must be identified that represent the major ecosystems in the nation, or any other regional level at which governmental administration is carried out. Specifically, areas are chosen which have the biophysical capacity to maintain one or more ecosystems.

Ideally, a network of reserves is established and managed to maintain representative samples of various major ecosystems, in perpetuity. Classification schemes based upon biogeography, geomorphology, and other characteristics can serve as a framework for identifying a nation's major ecosystems. Criteria and guidelines are designed to search for, and select, those areas which are representative of each major ecosystem type.

In practice, existing reserves are examined to determine their viability as representative areas. Using a classification framework, each existing reserve is evaluated as to its representativeness of a major ecosystem type. Often, some existing reserves will contain partial systems and habitats and, if adjacent wildlands remain, boundary amplification may provide options for obtaining the necessary additional elements needed to meet the objective of maintenance of ecosystems. However, these reserves may continue to play important roles in other aspects of conservation.

New areas are identified to represent major ecosystem types not already found in established reserves. Given a general description of the kind of area needed to cover the unrepresented major ecosystem type, field surveys can search for potential candidate areas. Such alternatives are then examined using a procedure similar to that applied to the established reserves, to judge suitability and choice. Table 1 suggests one method for planning a system or network of reserves where the maintenance of ecosystems is a major objective. While this and similar methods have been tested for terrestrial ecosystems in South America, the selection of fresh-water, marine and coastal reserves may require different methods.

Multiple-reserve systems may be required to ensure the maintenance of ecosystems. While it is occasionally possible to set up large, simple reserves which incorporate the ingredients necessary for ecosystem maintenance, most situations suggest the need for a multi-reserve system for each macro-ecosystem type. Many ecological processes and features, such as streams and watersheds, cover extensive areas impossible, in practical terms, to incorporate in single reserves. However, a series of multi-use reserves can, for example, protect a water-catchment, complement a reserve located downstream, and cater for local migratory or mobile species.

TABLE 1
STEPS FOR PLANNING SYSTEMS OF NATIONAL ECOSYSTEM RESERVES

STEP 1	Design a conceptual framework for the reserve system Following a review of the national development plan, and laws and policies related to wildland management, the objectives of conservation are reiterated, and they should include a statement that the major objective is the maintenance of ecosystem processes and functions. The existing categories of management are analysed. Biological and geomorphological classification systems are selected for the determination of major ecosystems. Criteria for the category of national reserves are prepared.
STEP 2	Study the existing national reserves A pro forma data sheet is designed for use in the field examinations of each existing reserve. A workshop is held to orientate the interdisciplinary planning team, and the logistics and field programme are prepared. The team travels to the field and analyses each existing reserve.
STEP 3	Classify and qualify each national reserve Each reserve is classified in terms of the category for which it is actually being managed. Each area is rated according to the criteria established for national reserves.
STEP 4	Summarize the information and propose a draft reserve system Integrate the information and identify the reserves which best qualify for one or more criteria. Select those reserves which most qualify to form part of the reserve system.
STEP 5	Search for new areas for inclusion in the reserve system The biological units (ecosystems, habitats) which are not represented by accepted existing reserves are identified. Conceptual descriptions are prepared for each unrepresented ecosystem and the specifications are elaborated on field-data sheets. New areas are then sought in the field which meet the requirements. The new areas are classified and qualified, and the most suitable areas are chosen for the system.
STEP 6	Suggest adjustments or the re-assignment of existing reserves which do not meet the stated requirements The field-data sheets on the reserves which are disqualified are re-examined to determine appropriate designations for these reserves, either through ready adjustments in management or their transfer to another category or organization.

STEP 7 Propose the system of national ecosystem reserves

The system of national reserves, now adjusted to ensure representativeness and the maintenance of major ecosystems, is now proposed. The proposal is compared with the national development plan, sector plans, and other proposals for wildland use, to ensure the system's long-term future.

Long-term maintenance of ecosystems in reserves depends in part on relationships between the reserves and their surroundings. The selection process for reserves must be cognizant of the interrelations between reserves and their surroundings. For example, reserves should remain free of negative influences, such as air- and water-borne contaminants, and they should contribute to the welfare of the surrounding human community without causing a deterioration in ecosystem processes.

In effect, areas for reserves should be selected so as to favour options for the buffering of external effects. Ideally, reserves should be surrounded by areas in which other forms of conservation management (e.g., multiple-use forests) contribute to a gradual transition from natural areas to agriculturally and other transformed land.

Size of reserves

After deciding on where to site a reserve, and before deciding on the exact boundaries of the reserve, it is necessary to determine the optimal size of the reserve. If the primary aim of the reserve is to maintain one or more ecosystems, then it should be large enough to hold self-sustaining populations of the rarest key species. Key species are those whose disappearance would produce cascading local extinctions of other species or severe changes in habitat structure. Likely candidates for key species are: top carnivores, such as lions and eagles; large frugivores, such as certain pigeons, toucans, hornbills, monkeys, and fruit bats; and large herbivores, such as elephants. It should be noted that while these examples of key species are described here as taxonomic groups, they are included because of their important functional attributes (e.g., plant pollinators, seed-dispersers, predators, etc.). Biogeographical (see Chapter 7) and genetic (see Chapter 6) considerations suggest that the minimum size for a self-sustaining population of a species is an effective breeding population of several hundred individuals.

The reserve should be large enough to permit local seasonal and nomadic movements of most species and all key species. Naturally, the winter and summer ranges of bird species that are trans-equatorial migrants cannot be encompassed in a single reserve. The local movements of relevance here include these two examples: the altitudinal movements of many montane species, and migrations of herbivores, correlated with rainfall patterns (as shown by certain ungulates in Kruger and Serengeti National

Parks). A reserve that provides a species with the needed resources for 11 months of the year but not for the twelfth month, would save none, rather than eleven-twelfths, of the population.

If possible, the reserve should be large enough to encompass its watersheds. This means control of watersheds, so that vegetation and soil run-off on slopes can be regulated. The most famous reserve for waterbirds in Europe, Spain's Coto Donana, has an excellent geometry except in one respect: it receives its water from surrounding agricultural land, whence pesticide run-off is now threatening the reserve's waterbirds.

If the reserve aims to maintain particular species, then it should contain those associated components which are essential for the species' long-term survival (see Chapter 4).

If the available area for the reserve is insufficient for achieving the initial objectives, then the following options should be considered: join two smaller areas by a corridor, to create a reserve of the desired size; determine whether the buffer zone surrounding the reserve in effect contributes to requirements for the area; perform periodic transfers of individual plants and animals to maintain effective population size and genetic variability of a species for which the reserve would otherwise be too small; and, redefine the objectives of the reserve.

Shape and layout of reserves

This subject is discussed in Chapter 7, but two aspects are worth noting here: the shape of a reserve should as far as possible conform to the boundaries of ecosystems; and, in considering shape, cognizance should also be taken of the time factor (the fourth dimension), for ecosystem boundaries are sometimes dynamic, moving over considerable distances (e.g., oceanic fronts). Conservation of the entire geographical area may call for unacceptably large allocations of land or sea. In such cases, restrictions relating to smaller regions in different seasons could be a substitute capable of satisfying the major conservation objective(s). For example, seabirds breeding on islands off southern Africa's west coast are dependent on marine food resources which are also exploited intensively by man. The fish species concerned exhibit seasonal patterns of distribution, influenced by environmental factors. Cessation of commercial harvesting is unlikely, but a compromise measure could be made to encourage perpetuation of a healthy adult fish population, concurrently permitting fishing for juveniles. This could be accomplished by closing different areas to fishing in different seasons, concomitant with the seasonal distribution of adult fish.

PLANNING THE MANAGEMENT OF RESERVES

Management planning

Management plans are prepared by managers (ideally as members of interdisciplinary advisory teams) to guide the operation of reserves. These plans bring together and analyse scientifically biological, sociological, economic, and engineering information, and state explicitly the prescription for management research, monitoring, development, and other activities to achieve the objectives contained in a policy statement for the designated area. Generally, management organizations have pro forma procedures for the presentation of plans. Managers of reserves who seek to maintain ecosystems are required to select, design, and operate such areas for a variety of purposes. In order to ensure that adequate and timely consideration be given to the maintenance of ecosystems, managers are required to take cognizance of the following principles and guidelines.

Zoning of permissible activities in reserves

In order to manage relatively large and complex ecosystems in reserves, it is useful to subdivide the area into units that can be managed in practical terms. Typically, management zones include: scientific zones where maintenance of ecosystems is dominant and uses such as recreation are prohibited; primitive zones where ecosystem maintenance is a major concern but where dispersed non-motorized recreation is allowed; extensive-use zones where small-group recreation and education are developed in a natural setting; and intensive-use zones where visitor reception, rest camps, and other high-density uses are managed. Research and monitoring take place throughout the reserve, with facilities generally located in the extensive-use zone. The determination of zones appropriate for a particular reserve which seeks to maintain ecosystems requires the identification of key ecological processes, sensitive and fragile ecosystems, and biotic and geomorphological trends. This requires scientific research and monitoring activity.

RESEARCH IN RESERVES

Research has often been viewed as something discrete from, and incidental to, management for the maintenance of ecological systems within reserves. However, this attitude is changing rapidly and the role of research as an integral part of management is now widely recognized.

Research can never occur too early in management. Ideally, research should form part of the selection process for reserves and subsequently, it should assist management in the lay-out and zoning of reserves. Many of the management problems currently faced in reserves could have been avoided if research had been allowed to contribute more prominently in the past. It is stressed that research in reserves should be carried out in such a way that its aims and benefits are clearly apparent to all involved in management. This may include politicians and administrators with no ecological appreciation, as well as actual management personnel.

Research should be directed at identifying and obtaining an understanding of key processes and their functioning in conserved ecosystems. Unless the key ecological processes underpinning the ecosystems within reserves are identified and understood, there is no method of detecting and, consequently, attempting to rectify any malfunctioning of those processes which might (and often do) occur as a result of the containment of incomplete ecosystems within the boundaries of reserves. In the absence of a thorough understanding of these processes, management is reduced to *ad hoc* reactions to observed changes. Very often these reactions are directed at symptoms rather than causes (e.g., removal of woody plants which are spreading as a result of alterations in soil-moisture regimes).

Research should investigate new management actions. Research should focus on the practical approaches that are available to managers for manipulating ecosystems, including the cost and effectiveness of alternative management techniques.

Research should identify processes for monitoring. Monitoring can never be carried out for all the components and processes of conserved ecosystems. Research should define those minimum geographical areas, ecological processes, and indicator species which need to be monitored to ensure an adequate coverage of the conserved ecosystems. Monitoring, however, should not become a research responsibility. Rather, monitoring should identify new questions requiring research which, in turn, should provide new insights into and possibly improved approaches to monitoring.

MONITORING IN RESERVES

Monitoring is the process through which managers acquire information on the state of the system. The following principles require consideration in the design and execution of any monitoring programme.

The objectives of a monitoring programme should be defined clearly. This principle is fundamental to good management. Decisions regarding the selection of species, areas, and processes for monitoring, and the subsequent interpretation and dissemination of the results, are critically dependent on the setting of clear objectives. Two aspects on which monitoring programmes most frequently focus are trends displayed by key species, and ecological processes which serve as indicators of system functioning, which may reflect the effects of management actions or user pressures on parts of the system.

Monitoring programmes should focus on key processes or species. Most monitoring programmes focus on the demographic status of populations of particular species, or on the state of the soil or vegetation. Few currently focus on ecological processes. However, the functioning of an ecosystem is most sensitive to changes in the rates of ecological processes, and less sensitive to changes in their products. Since there is often a delay between the initiation of change in an ecological process and the demonstration of its effects, management action that responds only to changes in the status of particular species could be unavoidably delayed. Under certain circumstances, this delay can lead to an amplification of undesirable effects, creating instabilities in the system. Therefore monitoring programmes which focus on the rates of ecological processes, such as birth and death, immigration and emigration, consumption, etc., will be suited better to providing timely indications of the impending behaviour of that particular part of the system.

Key species which should be monitored include predators at the top of food chains in both terrestrial and aquatic systems, and species whose populations have a dominant effect on habitats or appear to be close to threshold levels. However, this list is neither complete nor comprehensive, and each ecosystem will have its own most sensitive indicators; research is needed to identify what they are in each case.

The genetics of rare species need to be monitored. There is a need to identify and monitor those species whose populations may be susceptible to inbreeding depression (see Chapter 6). Usually these will be species with small effective populations, such as large carnivores. Staff in reserves may be able to monitor increases in the frequency of recessive forms, such as may be manifested by changes in the colours of flowers or the pelages of certain animals. However, most indicators of inbreeding depression, such as changes in breeding rate or decline in longevity, may require more detailed study. Evidence of decline in heterozygosity will need to be provided by experts who should be available at universities or research institutes. When monitoring identifies a specific genetic problem, then decisions need to be made as to whether or not the translocation of suitable individuals from other populations is feasible (see Chapter 6).

The requirements for accuracy, precision, repeatibility and comparability need to be clearly established. It is essential that sound statistical advice be obtained at the outset of the monitoring programme. It must be possible for managers to distinguish real changes from variations due to sampling errors, if the results are to be considered at all reliable.

Monitoring should be carried out with sufficient frequency so as to detect change in time for appropriate management actions to be implemented. Generally, when monitoring key species, the frequency of sampling will be determined by the frequency of perturbations and the average generation time ("turnover" time) of the species and its capacity for rapid population change. Thus, insects should be sampled at a greater frequency than large herbivores. The increased sampling effort will enable the manager to monitor changes more closely, and it will also ensure that appropriate management actions can be planned and implemented quickly.

Data analysis and interpretation must follow closely after data collection. In as much as monitoring is designed to provide information on which managers can act, it is essential that this information becomes available quickly. Too often the data are stored, and the opportunity to detect, interpret, and respond to changes is lost.

Monitoring is an integral part of management. Research within a reserve is responsible, in part, for identifying the monitoring needs. Monitoring must feed back information to both the research and technical staff responsible for implementing management actions. The process of feedback should include a review by research staff and managers of the need for further monitoring. In this way the monitoring programmes remain relevant.

Consideration should be given to the use of remote sensing wherever possible. Monitoring usually involves the use of considerable man-power. Remote sensing, including aerial photography and radio-tracking of animals, may reduce the time and effort of field workers in data collection but, because the data inputs can be considerable, attention needs to be given to an enhanced capacity for data analysis and interpretation. Remote sensing may also enable reserve managers to monitor the state of, and changes in, surrounding areas. In this respect satellite imagery is potentially very useful. However, it needs to be emphasized that not all monitoring programmes need to be skilled technical exercises. Often, a competent field naturalist may be more perceptive subtle changes that feature in the dynamics of many systems, than more elaborate mechanical techniques which lack the ability to discriminate.

MANAGEMENT ACTION FOR THE MAINTENANCE OF ECOSYSTEMS IN RESERVES

Active management (interventions) aimed at the maintenance of ecosystems within reserves should be based on the best possible understanding of the ecological processes underpinning these ecosystems. Only when one or more of these processes is found to be malfunctioning, often as a result of the incomplete nature of the conserved ecosystem, should active management be instituted. This knowledge must be gained through research and monitoring. The decision as to whether or not active management is necessary should be guided by the following principles. The first principles relate to malfunctions in the dynamics of ecological processes.

Process rates artificially modified

When the rate of a particular process occurring in a conserved ecosystem is found to be outside the range of rates which have evolved with the ecosystem, active management is necessary. An example is accelerated erosion of sedimentation rates, which leads to long-term reductions in species diversity of conserved ecosystems. In almost all known cases, this type of process malfunction manifests itself as a reduction in landscape heterogeneity. The management action must attempt to normalize the process rate by manipulation of the causal factors; management should not only attack the symptoms. For example, in the case of accelerated erosion, the drainage characteristics of the catchment should be improved, rather than the installation of artificial anti-erosion structures. However, in practice it may not always be possible for the manager to attack causes immediately and he then should direct his efforts towards cushioning adverse effects.

Characteristics of original disturbance regime altered

Ecosystems are subject to "abnormal" disturbances of variable severity (e.g., fires, floods, hurricanes) at various times. If these disturbances are reduced artificially in intensity or frequency, the ecosystem to be conserved may be deprived of vital long-term environmental change. For example, if a river is dammed for irrigation or flood control purposes, periodic floods may be prevented altogether, and a terrestrial reserve down stream would no longer receive deposits of silt; an estuarine reserve would not be subjected to the periodic scouring it previously received. Similarly, periodic fires may be prevented artificially to suit human needs, yet a particular ecosystem may contain plant species that are dependent on fire to remove senescent vegetation and to stimulate germination. In cases where the reserve is smaller than the average size of the area affected by a disturbing factor (e.g., fire or flood), the disturbance should still be simulated at the correct time in the year and, if possible, on a reduced scale. There are obviously situations where the biota of a very small reserve could be destroyed totally if a fire were permitted to spread unchecked, and in such cases, a patchwork burn effect should be aimed at.

Overpopulation of species formerly regulated by dispersal

Where the nature of the boundaries of reserves or the nature of the modified ecosystems surrounding the reserves is such that movement out of the reserves is reduced, then active management of populations of plants and animals may become necessary for species whose former abundance was regulated through dispersal. Most of the population reduction campaigns currently being conducted on large ungulate populations in southern African reserves fall into this category. Wherever possible, these population-reduction operations should be managed so as to mimic the selective effects of natural dispersal.

The "trophic cascade" effect

An incomplete complement of the species responsible for making up a conserved ecosystem can often give rise to process malfunctions which, unless rectified by management, result in further losses of species in the reserve. These sequential extinctions are termed "trophic cascades" (see Chapter 7). The appropriate management action to arrest and reverse a trophic cascade depends on the details of any particular case. Wherever possible, losses should be remedied by the re-introduction of the missing species. As a second-best tactic, an ecologically analogous species from a similar area and habitat can be introduced (e.g., when an original pollinator has become extinct). As a last resort, the process (e.g., pollination or defoliation) could be done artificially (e.g., hand pollination or mowing), but in certain cases artificial methods, in addition to being very expensive, are unlikely to be practicable in the long term. For instance, the local extinction of hippopotamuses from tropical flood-plain ecosystems would not only affect many other species, but it could influence the effect of functioning of the hydrological processes involved in the maintenance of the ecosystem, as well as energy inputs.

Mobile faunal elements moving out of a reserve

Where the size of a reserve is less than the size of the area over which individuals of mobile species move during their lives, then active management may become necessary. Management is always necessary when commercial exploitation of certain species occurs outside reserves (e.g., fish moving out of a marine reserve).

Populations below minimum genetic threshold levels

When species populations within a reserve reach levels approaching the minima for genetic viability, then active management may be necessary. First, it should be established that natural gene flow between the population in the reserve and populations elsewhere is not occurring. Only when this is determined should active genetic management be embarked on. If possible, the population of the species in the reserve should be encouraged to increase beyond the critical threshold level. If this is not possible, individuals from other reserves should be translocated. It is essential that genetic monitoring of these populations be carried out prior to and during these translocation operations (see Chapter 6).

Alien species invading reserves

When the rate of colonization of a reserve by species not indigenous to the conserved ecosystem reaches unacceptable proportions, active management procedures have to be undertaken. However, it is generally best to eradicate aliens as soon as possible after their first appearance in a reserve. If large areas are infested, and rates of infestation are too large to contain, it is advisable to designate smaller, uninfested core areas from which aliens are eradicated at all costs. Currently, this is of special importance in the Cape fynbos, and many aquatic ecosystems in southern Africa.

User impact and its control

Traditionally, reserves have been assumed to be resilient to use by visitors due principally to their large size. Yet, expanding demands for recreation and tourism have begun to show impacts upon vegetation, soils and animal behaviour. Furthermore, protected areas are being subjected to evolving uses including scientific research, collection of genetic materials and environmental monitoring. Management will need to regulate human activities of all kinds to minimize negative impacts upon natural ecosystems.

"Core" areas of particularly vulnerable or sensitive ecosystems should be sacrosanct. Protected areas should be zoned to reflect the various objectives of management. At best one major portion of each reserve should be maintained in an undisturbed state, as free of human impact as possible. Such "core" zones will generally include representative samples of ecosystems, critical habitats and unique sites. Management activities should be restricted to the minimum necessary for protection and maintenance. Exceptions may arise where habitat manipulation is required as part of an overall plan for biological conservation.

The impact of vehicular traffic on ecosystems should be reduced to a minimum. The need for the control of vehicular traffic in reserves is obvious. Quite apart from noise and chemical pollution from exhaust emissions (the former will disturb certain sensitive animals, the latter will have a deleterious effect on sensitive plants such as lichens), ordinary motor vehicles can promote the formation of pot-holes in gravel roads, with a possibility of causing gully erosion, or can raise clouds of dust which deleteriously affect roadside vegetation. Some forms of transport may have to be banned outright. Examples include the use of dune buggies or trail bikes on sensitive coastal or inland dune formations, the use of "sno-cats" (snow mobiles) on fragile alpine or tundra plant communities, even if apparently protected by snow, or the use of four-wheel-drive vehicles on sensitive desert or semi-desert communities of plants such as lichens. Water-skiing and power-boating on rivers and lakes can cause severe disturbance to breeding birds, and the disturbance caused by motor-boats can be extended to the erosion effects created by wash on the banks. Hovercraft, occasionally used by managers in wetland areas, may have to be banned at least during the breeding season of aquatic birds, because of direct destruction of nests, eggs, and nestlings by down draught. A problem of a different sort arises with the use of horses, commonly seen as an ecologically satisfying alternative to the internal combustion engine. Horses' hooves do create disturbed areas, and their droppings are likely to contain seeds of alien plants which may become established as weeds along trails.

The impact of humans on the ecosystem should be reduced to a minimum. The presence of large numbers of human visitors in a reserve is a managerial problem of some considerable importance, particularly as it is often the duty of the manager of such an area to encourage visitors. As with vehicular traffic, the manager may reduce absolute numbers, channel and regulate human activities to minimize damage, or both. Complete freedom may only be tolerated if, in the opinion of the manager, the area is large, the number of visitors low, and the vegetation and its associated fauna are resistant to disturbances.

Visitors may, for example, be obliged to keep to clearly defined trails which the manager must site in areas which will not be disturbed unduly. Nevertheless, erosion resulting from such trails, is of notoriously common occurrence and emergency measures may have to be taken at short notice; off-trail rambling may be restricted or forbidden. It should be unnecessary to stress that flower-picking, collection of firewood and disturbance of nesting birds or ostensibly tame creatures should be forbidden, as should the removal of souvenirs such as sea-shells, driftwood, animal bones, and so on. An educational centre to explain such things as the ecological importance of dead wood, or the effects of flower-picking on both seed production and biological interactions between flowers and animals, should be a prerequisite of the overall programme of visitor control. Regulations are also required to prevent visitors from importing live plant and animal material into reserves. It is a common misconception amongst laymen, for example, that reserves are suitable repositories for unwanted pets of wild animal species.

In summary, use of reserves for recreation and other purposes may be incompatible with the objectives of biological conservation. While some types of impacts are obvious, many are subtle and are manifested indirectly within the ecosystem. As custodian for natural protected areas, the manager is responsible for the regulation of all human uses within reserves and for achieving biological conservation. This will require a strong, clear and consistent managerial regime which ensures the citizenry of its rights to benefit from nature protection while maintaining the natural reserve base in perpetuity.

Physical development in reserves

Ecological principles should be borne in mind when deciding on physical structures to be sited within reserves. First, it is stongly advocated that physical structures be located peripherally when at all possible. Secondly, the idea of creating an environmental gradient from development to wilderness should be adhered to. The aim should always be to reduce the impact of an activity and its related facilities on the environment. Both facilities and activities will have an adverse effect on maintaining the ecosystem in pristine state. Visitor accommodation, restaurants, shops, maintenance workshops and stores for equipment, etc., should be kept on the boundaries of reserves or if possible in adjacent buffer areas. If development for visitors is to take place within reserves, it should be limited to granting visitors facilities of a largely non-consumptive nature, and would be in the form of roads, bridges, trails, ski-lifts, educational centres, etc.

In each case of development, information on the following aspects should be collected and mapped, and made available to the manager before the choice of the location of facilities is taken:

- geology and geomorphology
- climate
- hydrology
- soils
- plant and animal (particularly invertebrates) communities
- sensory impact analysis (i.e., visual and auditory impacts).

These maps should indicate the suitability of an area for roads, bridges, trails, housing, recreation, etc., and the actual siting of the development will be influenced by more detailed analysis of the information available.

Development in dynamic ecosystems, such as dunes, estuaries, lakes, and coastal areas, must be avoided or sited in such a way that the dynamics of the systems are taken into account. Structures near lakes, rivers and estuaries must either be floating or high above the long-term cyclic flood levels. Structures such as jetties or breakwaters, projecting into a lake or the ocean, must be built taking into account the currents and the effects which these structures will have on the deposition of sand and the resultant change to the coast. Bridges may change entire systems downriver. This is especially true in estuarine situations.

The materials to be used in constructing facilities should be considered with regard to the effects they might have (e.g., reduction of dust in the choice of material for roads).

Roads in particular can have significant effects. They serve as corridors for the dispersal of some species; for instance, the spread of introduced weeds through Australia has been mainly by motor vehicles and along roads. Roads also provide significant barriers to dispersal of sedentary organisms; certain small mammals of the north-temperate zone are reluctant to cross roads, to a degree that genetically distinct mouse populations may develop on opposite sides of a highway. The situation is more serious in the tropics, where numerous bird species of the forest interior are reluctant to cross even a one-metre-wide opening in the understorey. In certain nutrient-poor ecosystems, such as fynbos, roads act as nutrient corridors and plant communities are effectively changed along drainage lines. In other areas, roads act as corridors for the spread of disease organisms, and as wind channels causing peripheral forest to die back.

In any development, effluent disposal will have to be given considerable attention. Soils must be examined critically to ascertain their absorptive capacity. The enrichment of the soils and adjacent water-bodies must be carefully monitored.

NOMENCLATURE FOR DESIGNATED AREAS

Typically, reserves are held under public stewardship to provide long-term care for natural resources which are of particular ecological, economic, scientific, recreational, and educational value. In an attempt to simplify complex nomenclature attending the many types of reserves in the world, IUCN (1978)[1] proposed a basic set of categories:

I Scientific Reserves/Strict Nature Reserves
II National Parks/Provincial Parks
III Natural Monuments/Natural Landmarks
IV Nature Conservation Reserves/Managed Nature Reserves/Wildlife Sanctuaries
V Protected Landscapes
VI Resource Reserves
VII Anthropological Reserves/Natural Biotic Areas
VIII Multiple-Use Management Areas/Managed Resource Areas
IX Biosphere Reserves
X World Heritage Sites (natural)

Each category focuses on a specified set of objectives for management, which in turn determine the activities of management. Thus, although the name of any particular reserve is of less significance than the aims of management, ideally all national parks, for example, should be managed for a common set of aims.

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[1] IUCN 1978. Categories, objectives and criteria for protected areas. Morges, Switzerland.

While all ten categories involve, to a greater or lesser degree, the protection of natural ecosystems, the first four categories, and of course biosphere reserves, make major commitments to the maintenance of ecosystems, biological diversity, and genetic resources. All other objectives should be implemented in ways which are compatible with these aims.

CONCLUSIONS

Protected areas, including national parks, nature reserves and other wildland categories, have traditionally been established for recreation and tourism, protection of scenery and landscape, and the preservation of individual species. These endeavours and purposes remain valid and important to society. Present research indicates, however, that the conservation of ecosystems can only be attained if criteria for the selection and management of protected areas are derived from science and applied in practical ways by managers.

Reserves should contain areas of land and water which are representative of major biogeographical units. They should be large enough to embrace key ecological processes as well as to meet the requirements of major groups of species. Given that ecosystems are dynamic, it is necessary to provide for diversity in protected areas, and to promote it when a tendency towards homogeneity appears which may affect the long-term viability of an area.

Thus, conservation management is an active endeavour by man to plan and implement programmes for the maintenance of biological diversity. It should embrace, often simultaneously, the design and selection of reserves, protection of certain areas from external influences, manipulation of selected sites or species, construction of facilities, monitoring of trends, research to support managerial decisions, and working with the general public to promote adequate understanding and appreciation of the biosphere upon which human life depends. Far from the historical passive role of protection and control, management emerges as a professional endeavour demanding integrative skills from the sciences and the field.

9. PRINCIPAL CONCLUSIONS

At present, nature reserves constitute about two per cent of the earth's land surface and some 0,001% of the area that is covered by water. Nature reserves account for up to 11% of the land surface of certain countries. However, in most countries, including a number of those in which the most diverse concentrations of habitats and species are found, far smaller proportions of the surface area either are currently, or are likely in the future to be, set aside as nature reserves.

Many thousands of rare and threatened species are not found in nature reserves but survive, often precariously, in habitats of limited extent within ecosystems that have been altered to a greater or lesser extent as a result of human activities. By far the greatest threat to their survival in either the short- or the long-term is the reduction, invasion or degradation of their limited habitats. There are several obvious concentrations of these rare and threatened species within areas which should be part of the core of a new, and urgently needed, international system of nature reserves. It is unlikely, however, that enough nature reserves could ever be set aside to provide for the large number of scattered and isolated species which will presumably still only occur outside of whatever reserves may be created in the future. International surveys of biotic communities, or of ecosystems, would probably also reveal concentrations of rare and threatened types in areas ideally suited to being set aside for conservation, and many scattered and isolated types for which it would be extremely difficult to create nature reserves.

At a national level, many countries, will find themselves in a position of being unable either to create enough nature reserves to provide protection for many species or to make reserves big enough and diverse enough to give the species found in them a reasonable chance of survival through even a few decades. Countries with large or rapidly growing human populations, those faced with poverty and those under pressure to use their natural resources to the maximum and to alter landscapes drastically to provide for pressing human needs are especially likely to find themselves in this position. In these countries particularly, as in South Africa, a re-appraisal is needed of the possible ways in which skillful planning and management can be used to provide for the preservation of indigenous species within altered and even highly exploited ecosystems.

The major parts of the earth's surface should, and will, be used to supply food and other basic resources for the expanding human population. Transformation and significant modification of the earth's surface are, therefore, inevitable. However, conservation-management, based on ecological principles, would ensure that such transformations and modifications do not result in "biological deserts" which are incapable, in the long-term, of sustaining the life-support processes on which man's survival depends.

It is likely that many, if not most, nature reserves as we know them have no long-term future (here "long-term" is taken to mean a relatively short period of time, spanning only three to four human generations), unless they are integrated into a series of development programmes designed to promote the survival of man himself.

The International Union for the Conservation of Nature and Natural Resources (IUCN) has identified three principal goals for the conservation movement:

- ensuring that the biosphere continues to renew itself;
- ensuring human survival and well being; and,
- keeping ecological options open for the future.

These goals can be reached only by way of adopting a sensible approach to the utilization of natural resources. In short, this means adopting the concept of the ecosystem as the basis of management and planning decisions. Clearly, species stand no chance of long-term survival unless the ecosystems, of which they are an integral part, are intelligently conserved. By managing ecosystems, including man-transformed ecosystems, correctly, essential life-support processes will be conserved as well as a selection of the species which naturally make up the biota of those ecosystems.

Many of the earth's ecosystems, both within and outside protected areas, show signs of gross mismanagement and degradation. The collapse of fish populations and declining productivity in subsistence farming, for example, give testimony to the consequences of excessive extraction and incorrect use of natural resources, often motivated by short-term gain. Unless this trend is arrested and reversed, many ecosystems are likely to become less resilient, less viable, and unable to contribute to the world's life-support systems. A new set of guidelines is urgently required for the optimal use of all ecosystems. Ecological principles should be of paramount importance, if the guidelines are to promise any success. The immediate universal acceptance of this ecological dictate is unlikely, but unless human societies make a firm commitment to treat ecological causes, and not only socio-economic symptoms, the quality of life for all mankind will decline rapidly in the foreseeable future.

10. SUGGESTED READINGS

To keep the number of entries to a minimum, this list of references is confined to books. These books will guide the reader to additional principal sources of information. We suggest that the reader should start with *Conservation Biology: An Evolutionary-Ecological Perspective*, edited by Soulé and Wilcox, which is an admirable synthesis of the dynamic, modern approach to nature conservation.

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11. GLOSSARY OF SPECIAL TERMS

ABIOTIC: not biotic; not involving or produced by living organisms (see ORGANISM).

ADAPTATION: any characteristic of a living organism (see ORGANISM) that contributes to its fitness (see FITNESS); the evolutionary process of acquiring adaptations.

ALBEDO: the fraction of incident light or electromagnetic radiation that is reflected by a surface or body, such as the earth or a cloud.

ALGA: any of a group (algae) of chiefly aquatic nonvascular plants, such as seaweeds, with chlorophyll (see CHLOROPHYLL) often masked by brown or red pigments.

ALIEN: belonging to another place; a foreign organism.

ALLELE: one of several alternative forms of the same gene (see GENE); thus A B O blood types are formed in human beings by three alleles A, B and O, any two of which are present in an individual.

ALLOPATRIC: having separate or mutually exclusive areas of geographical distribution (opposite SYMPATRIC).

AMBIENT: surrounding on all sides; i.e., the environment (see ENVIRONMENT).

APOMIXIS: reproduction not dependent on fertilization (see FERTILIZATION), but involving specialized generative tissues, such as parthenogenesis (the development of an ovum without fertilization by a male reproductive cell) (see CELL).

AUTOCHTHONOUS: from within; independent of external sources; self-produced, pertaining to the ecosystem (see ECOSYSTEM).

AUTOTROPH: (autotrophic), self nourishing. Producing food independently. Applied to photosynthetic (see PHOTOSYNTHESIS) or chemosynthetic plants and bacteria (see BACTERIUM).

BACTERIUM (plural: BACTERIA): any of a group (Schizomycetes) of microscopic organisms having round, spiral or rodlike single-celled (see CELL), multicelled or noncellular bodies which lack chlorophyll (see CHLOROPHYLL). Bacteria live in soil, water, organic matter and in the bodies of plants and animals. Bacteria are parasitic (see PARASITE), saprophytic (see SAPROPHYTE) or autotrophic (see AUTOTROPH) in nutrition.

BIOGEOGRAPHY: that branch of biology that deals with the geographical distribution of plants and animals.

BIOLOGY: that branch of knowledge that deals with living organisms (see ORGANISM) and vital processes; the science of life.

BIOMASS: quantitative term used to express the total weight (mass) of living organisms (see ORGANISM) per unit area (standing crop biomass) or the total weight (mass) of living organisms of a specified kind (usually expressed as dry weight (g) per unit area (m^2)).

BIOME: a major biotic community; i.e., one existing in a wide area defined by certain general environmental (see ENVIRONMENT) features and often defined on the basis of the physiognomic form of its principal vegetation formation. Effectively the biological component of a large geographical region (e.g., Arctic Tundra).

BIOSPHERE: the sum total of the environments capable of supporting life, extending from deep oceanic trenches to the atmosphere, about 12 km above sea level.

BIOTA: the plants (see FLORA) and animals (see FAUNA) and other living organisms (see ORGANISM), such as bacteria (see BACTERIUM), of an area.

BIOTIC: of or relating to life; caused or produced by living organisms (see ORGANISM).

BIOTOPE: particular area substantially uniform in environmental (see ENVIRONMENT) conditions and living organisms (see ORGANISM) for which it is the habitat (see HABITAT).

BIOTYPE: a population of the same genotype (see GENOTYPE).

CARNIVORE: a flesh-eating animal; an insectivorous plant.

CELL: a (usually) microscopic mass of protoplasm (see CYTOPLASM) enclosed by a semi-permeable membrane also including one or more nuclei (see NUCLEUS) and nonliving products; the smallest structural unit of living matter capable of functioning independently.

CHLOROPHYLL: the green photosynthetic (see PHOTOSYNTHESIS) colouring matter of plants. Chlorophyll-containing tissues of plants synthesize chemical compounds to form carbohydrates, with the aid of radiant energy from the sun and simple compounds such as carbon dioxide, water and essential elements.

CHROMOSOME: the protein structure within the nucleus of a cell (see CELL) that contains genes (see GENE) encompassing the genetic material (see DNA) of a living organism (see ORGANISM).

CICHLID: any of the family Cichlidae, a group of mostly tropical spiny-finned fresh-water fish particularly common in African fresh-water systems.

CLIMAX: a relatively stable stage or community (see COMMUNITY) of living organisms (see ORGANISM) (especially plants); usually the final stage in ecological (see ECOLOGY) succession (see SERAL).

CLINE: a population aggregate within a species (see SPECIES) showing gradation in its characters from one end of its geographical range to the other.

COMMUNITY: (see BIOTIC) interacting populations (see POPULATIONS) of various kinds of species (see SPECIES) in a common location.

CONSPECIFIC: of the same species (see SPECIES).

CYTOGENETICS: that branch of biology (see BIOLOGY) that deals with heredity (see HEREDITY) and variation, by the study of both genetics (see GENETICS) and cells (see CELLS).

CYTOPLASM: substance of the cell (see CELL) body, exclusive of the nucleus (see NUCLEUS).

DEMOGRAPHY: the statistical study of populations (see POPULATION), especially with reference to size and density, distribution, growth and mortality.

DESERTIFICATION: the act or process of desert formation.

DIOECIOUS (DIOECISM): having male reproductive organs in one individual and female in another; separate sexes.

DISPERSAL: the process of the spreading of living organisms (see ORGANISM) from one place to another.

DISPERSION: the result of dispersal; the spatial distribution of living organisms (see ORGANISM).

DIVERSITY: an index for measuring the information content of many different biological (see BIOLOGY) systems ranging from cells (see CELL) to complex communities (see COMMUNITY) of organisms (see ORGANISM). For example, a forest with 100 trees belonging to 10 different species (see SPECIES) each of which has 10 individuals, has the maximum diversity for a system of that many species and individuals; the minimum diversity would occur when there were 91 individuals of one species and only one of each of the other nine. Species diversity is often confused and incorrectly equated with "species richness" which is the number of species (irrespective of the number of individuals of each of those species) in an area.

DNA: de-oxyribonucleic acid, the inherited (see HEREDITY, GENETICS) material of almost all living things, usually housed on the chromosomes (see CHROMOSOMES) within the nucleus (see NUCLEUS) of a cell (see CELL).

DYKE: a usually tabular body of igneous (see MAGMA) rock injected while molten into a fissure.

DYNAMIC: marked by continuous change, usually by productive activity.

ECOLOGY: a branch of science concerned with the interrelationships of living organisms (see ORGANISM) with each other and their environment (see ENVIRONMENT).

ECOSYSTEM: the totality of factors of all kinds (see BIOTIC and ABIOTIC) that make up a particular environment; the complex of a biotic community (see COMMUNITY) and its abiotic, physical environment, functioning as an ecological (see ECOLOGY) unit in nature.

ECOTONE: a transition (area) between two adjacent ecological (see ECOLOGY) communities (see COMMUNITY).

EDAPHIC: relating to the soil; resulting from or influenced by the soil rather than the climate.

EFFLUENT: something that flows out; usually waste material discharged into the environment (see ENVIRONMENT), and acting as a pollutant.

ELECTROPHORESIS: the differential movement of suspended particles in a fluid under the action of an electromotive force applied to electrodes in contact with the suspension. Biologically useful in the separation and identification of proteins (see PROTEIN) and their constituent amino acids.

EMPIRICAL: based on observation or experience alone, but capable of being verified or disproved by further observation or experiment.

ENDEMIC: native, restricted or peculiar to a locality or region.

ENVIRONMENT: all of the physical, chemical and biological factors impinging on a living organism (see ORGANISM).

ENZYME: a protein (see PROTEIN) molecule that catalyses (speeds the rate of) (bio)chemical reactions.

EPILIMNION: the upper, warm waters of a standing water body above the thermocline (see THERMOCLINE).

EPIZOOTIC: a term for a disease affecting many animals (of one species) at the same time, corresponding to an epidemic of man.

EUKARYOTIC: of or relating to cells (see CELL) having the nucleus (see NUCLEUS) separated from the cytoplasm (see CYTOPLASM) by a nuclear membrane, and the genetic (see GENE; GENETIC) material borne on a number of chromosomes (see CHROMOSOME). Eukaryotic cells are the units of structure in all organisms (see ORGANISM) except bacteria (see BACTERIUM) and blue-green algae (see ALGA). (see PROKARYOTIC).

EUPHOTIC ZONE: the upper layers of a body of water into which sufficient sunlight penetrates to permit growth of green plants; well illuminated.

EUTROPHICATION: the act or process making a body of water rich in dissolved nutrients (particularly nitrogen and phosphorus), and usually deficient in oxygen, as a result of high plant productivity and decay, providing adequate food.

EVOLUTION: the theory which states that the different kinds of living organisms (see ORGANISM) have been produced by descent with modification from previously existing forms (see NATURAL SELECTION).

EXTINCTION: the evolutionary termination of a species (see SPECIES) caused by failure to reproduce and death, the natural failure to adapt to environmental change.

FAMILY: a taxonomic (see TAXON) unit; a group of related genera (see GENUS).

FAUNA: the total animal life of an area; usually the total number of animal species (see SPECIES) in a specified period, geological stratum, geographical region, ecosystem, habitat or community (see ECOSYSTEM, HABITAT, COMMUNITY).

FERTILIZATION: the union of male and female gametes (see GAMETE) to produce a new individual.

FITNESS: a measure of evolutionary success that applies to genes (see GENE), traits (see TRAIT), individuals or populations (see POPULATION). More precisely, fitness is a number that when multiplied by the proportion of members in one generation gives the proportion of representatives in the next generation.

FLORA: the total plant life of an area; usually the total number of plant species (see SPECIES) in a specified period, geological stratum, geographical region, ecosystem, habitat or community (see ECOSYSTEM, HABITAT, COMMUNITY).

FOOD WEB (CHAIN): arrangements of the living organisms (see ORGANISM) of ecological (see ECOLOGY) communities (see COMMUNITY) according to the order of predatory (see PREDATOR) activity in which each group of organisms uses the next (usually lower) members as a food source; e.g., carnivores (see CARNIVORE) eat herbivores (see HERBIVORE) which eat plants.

FRUGIVORE: a fruit-eating animal.

FUNGUS: any of a group (Fungi) of lower, often parasitic plants lacking chlorophyll (see CHLOROPHYLL), and including moulds, mildews, rusts and mushrooms.

FYNBOS: a broad category of vegetation formations in the mediterranean climate zone of South Africa; these comprise sclerophyllous (hard-leaved plants) shrublands of the mountains of the Cape Folded Belt, their foothills and the coastal lowlands.

GAMETE: cells (see CELL) which join (conjugate) to form new individuals; sexual cells.

GENE: a section of a chromosome (see CHROMOSOME) containing enough DNA (see DNA) to control the formation of one protein; a gene controls the transmission of a hereditary (see HEREDITY) character.

GENE POOL: the total of the alleles (see ALLELE) in a population (see POPULATION) of organisms (see ORGANISM).

GENETIC DRIFT: changes in the genetic (see GENE) composition of a population (see POPULATION) of an organism (see ORGANISM) due to chance preservation or extinction of particular genes (see GENE); especially pronounced in small populations (see POPULATION).

GENETICS: that part of biology (see BIOLOGY) which deals with variation and heredity (see HEREDITY).

GENOTYPE: the genetic composition of an individual organism (see PHENOTYPE).

GENUS (plural GENERA): a taxonomic (see TAXON) category between species and family (see FAMILY); a grouping of closely related species (see SPECIES).

GEOLOGY: that branch of knowledge that deals with the history of the earth and its life as recorded in rocks.

GEOMORPHOLOGY: that branch of knowledge that deals with the land and submarine relief features of the earth's surface.

GUILD: a group of two or more species (see SPECIES) which jointly use some aspect of their environment (see ENVIRONMENT) in the same area.

HABITAT: the place or type of site where a plant or animal naturally and normally lives and grows; its "home".

HERBIVORE: an animal that eats plants or parts of them.

HEREDITY: the organic relationship between successive generations of a population (see POPULATION) or species (see SPECIES).

HERMAPHRODITE: (see MONOECIOUS).

HETEROZYGOUS: the state in which the paired alleles (see ALLELE) at the same locus (see LOCUS) on homologous (common evolutionary ancestry) chromosomes (see CHROMOSOME) are different.

HOLOCENE: geological period consisting of recent times since the end of the last ice-age (about 10 000 years ago).

HOMOZYGOUS: the state in which the paired alleles (see ALLELE) at the same locus (see LOCUS) on homologous (common evolutionary ancestry) chromosomes (see CHROMOSOME) are the same.

HYDROLOGY: that branch of knowledge that deals with the properties, distribution and circulation of water on the surface of the land, in the soil and underlying rocks, and in the atmosphere.

HYPOLIMNION: that part of a lake below a certain level (see THERMOCLINE) that is made up of stagnant water of relatively cool, uniform temperature, and which is prevented from mixing with surface waters as long as the thermocline is present.

HYPOTHESIS: a tentative explanation of some phenomenon, which can be used as the basis of an experimental test.

INDIGENOUS: having originated in and being produced, growing, or living naturally in a particular region or environment (see ENVIRONMENT); native.

INTERTIDAL: that zone of the seashore that is alternately flooded and exposed by the rise and fall of the tides.

INVERTEBRATE: any of a major group of animals (accounting for 96% of the animal kingdom) lacking a spinal column.

LACUSTRINE: of, or relating to, lakes.

LARVA: (plural: LARVAE) a term for the early immature form of an animal that at birth or hatching is fundamentally unlike its parents, and must alter in size and form by passing through several stages before assuming adult characteristics.

LEACHING: the process by which percolating liquid, such as water, separates, or dissolves out, soluble components.

LICHEN: any of a numerous complex group of plants made up of an alga (see ALGA) and a fungus (see FUNGUS) growing in a presumed symbiotic (see SYMBIOSIS; MUTUALISM) association usually on a solid surface, such as a rock.

LIMNOLOGY: that branch of knowledge which deals with the physics, chemistry, biology and ecology of inland waters (rivers, vleis, lakes, man-made lakes, swamps and so on).

LITTORAL: of or relating to a coastal region (of the sea or a lake); on or near a shore.

LOCUS: the position of a gene (see GENE) on a chromosome (see CHROMOSOME).

MACROMOLECULE: a molecule is the smallest unit of a compound substance composed of two or more atoms; a macromolecule is a large molecule.

MACROPHYTE: a member of the macroscopic (large enough to be seen by the naked eye) plant life, especially of a body of water, usually applied to the submerged or semi-submerged vascular plants.

MAGMA: molten rock material within the earth from which igneous rock results by cooling (e.g., to produce a DYKE).

MANAGEMENT: the efforts of humans to select, plan, organize and implement programmes designed to achieve specified goals; activities can range from protective measures to ensure that nature remains uninterrupted by human influence, on into ever-more manipulative (active) tasks required to maintain diversity, install facilities, control populations or eradicate aliens (see ALIEN).

MARINE: of, or relating to, the sea.

MILLENIUM: (plural: MILLENIA) a period of 1 000 years.

MONOECIOUS (MONOECISM): having male and female reproductive organs in the same individual. No separate sexes (= HERMAPHRODITE).

MONOTYPIC: a taxon (see TAXON) that has only one unit in the immediately subordinate category, e.g., a genus (see GENUS) comprising only one species (see SPECIES) or a species not divisible into subspecies.

MONTANE: of, or relating to, mountains.

MORPHOLOGY: literally, the science of form or shape; commonly extended to cover all external and internal characters of an individual plant or animal, or as a collective term for the "morphological" characters of a taxon (see TAXON).

MUTUALISM: a relationship between two unrelated (different species) organisms (see ORGANISM) in which both of them benefit (see SYMBIOSIS).

NATURAL SELECTION: the differential reproduction of individuals; the tendency for some individuals (plants or animals) to produce more successful offspring than others. Natural selection is generally acknowledged to be the primary force responsible for evolution (see EVOLUTION).

NICHE: the sum total of all physical and biological requirements for a species (see SPECIES), different species occupying different niches; the ecological role of an organism (see ORGANISM) in a community (see COMMUNITY), especially in regard to food consumption. Literally, the "profession" of a species.

NUCLEUS: a complex mass essential to the life of most cells (see CELL), containing chromosomes (see CHROMOSOME) and DNA (see DNA), and essentially controlling all functions.

OMNIVORE: an animal that eats both plant and animal matter.

ORGANISM: only living thing, animal or plant, that is capable of carrying out life processes.

PARAMETER: the actual value of a certain characteristic.

PARASITE: an organism (see ORGANISM) living in, or on, another unrelated organism (the HOST) from which it obtains benefits and usually injures, sometimes fatally.

PARASITOID: an insect (usually a wasp) which develops inside the body of (usually) another insect, eventually killing it.

PARTHENOGENESIS: parthenogenetic, the development of the ovum (female germ cell) without fertilization by the male reproductive cell (see CELL) (see APOMIXIS).

PELAGIC: of, or relating to, the open sea or a lake.

PHENOTYPE: the totality (but usually physical appearance) of an organism (see ORGANISM); the product of the interaction between the genotype (see GENOTYPE) and the environment (see ENVIRONMENT).

PHOTOGRAMMETRY: the science of making reliable measurements by the use of photographs, especially aerial photographs, as in surveying.

PHOTOSYNTHESIS: the process by which simple carbohydrates (sugars, starches) are formed from carbon dioxide, water and essential nutrients in special plant cells (see CELL), using sunlight as the energy source (see CHLOROPHYLL).

PHYSIOGRAPHY: a description of physical geography.

PHYTOGEOGRAPHY: that branch of biology that deals with the geographical distribution of plants.

PLANKTON: the passively floating or weakly swimming usually microscopic animal (zooplankton) and plant (phytoplankton) life of a body of water such as a lake or the ocean.

PLEISTOCENE: geological period (epoch) covering the last one million years or so.

PLUVIAL: a prolonged period of wet climate, such as occurred repeatedly in the early Pleistocene (see PLEISTOCENE).

POISSON DISTRIBUTION: a probability function (mathematical) used to model the number of outcomes in time and space; the expected distribution of isolated events in a continuum of any kind.

POLLINATION: the process involving the transfer of pollen from a stamen (male organ) to an ovule (female cell (see CELL)), promoting the production of fertile seeds in plants.

POLLINATOR: the agent (usually animal) responsible for pollinating flowers (see POLLINATION).

POLYGAMOUS: a relationship in which a male is mated to more than one female (polygyny) or vice versa (polyandry), either simultaneously or in sucession.

POLYPLOIDY: the state of possessing more than two complete sets of chromosomes (see CHROMOSOME) per cell (see CELL).

POPULATION: a somewhat arbitrary grouping of individuals of a species (see SPECIES), that is circumscribed according to a set of specific criteria; usually taken as all the individuals of a species in a given time and place.

PREDATOR: an organism which preys upon and eats another organism (the prey).

PRIMARY PRODUCTIVITY: the rate at which energy from light is absorbed and utilized together with carbon dioxide, water and other nutrients, in the production of organic matter in photosynthesis (see PHOTOSYNTHESIS). Net production is given by the amount of organic matter formed in excess of that used in respiration (see RESPIRATION). It represents food potentially available to the consumers of an ecosystem (see ECOSYSTEM); it can be measured approximately by sampling vegetation (see VEGETATION) at intervals and measuring the dry mass produced per unit area per unit time. (As opposed to SECONDARY PRODUCTION - the amount of consumer (animal) tissue produced per unit area per unit time in any ecosystem (see ECOSYSTEM.)

PROKARYOTIC: of, or relating to, cells (see CELL) having the genetic material (see GENE; GENETIC) in the form of simple filaments of DNA (see DNA) and not separated from the CYTOPLASM (all the protoplasm of a cell excluding the nucleus) by a nuclear membrane. The cells of bacteria (see BACTERIUM) and of blue-green algae (see ALGA) are of this type, distinguishing these organisms from all others which are eukaryotic (see EUKARYOTIC).

PROTEIN: usually taken as the total nitrogenous material in plant or animal substances; extremely complex combinations of amino acids, essential components of all living cells (see CELL).

RESPIRATION: the process of biological oxidation (breakdown) of food materials of stores by all living organisms (see ORGANISM), which releases energy required for daily maintenance.

RESOURCE: a feature of the environment that contributes to an organism's (see ORGANISM) fitness (see FITNESS). Also, often used to describe a source of natural wealth or revenue which can be biotic (see BIOTIC) and renewable (e.g., fish stocks in the ocean) or abiotic and non-renewable (e.g., gold).

RIPARIAN: of, or relating to, rivers.

RUMINANT: any of a group (Ruminantia) of even-toed, hoofed animals (such as sheep, cattle, giraffes, antelopes and camels) which chew the cud (chew again what has been swallowed previously) and have multi-chambered stomachs.

SAPROPHYTE: (saprophytic); growing on decaying organic matter, as do many bacteria (see BACTERIUM) and fungi (see FUNGUS).

SAVANNA: a type of vegetation (see VEGETATION) characterized by scattered trees with a grassy understorey.

SERAL: see SERE.

SERE: the whole series of plant changes in an environment leading from a bare area of land or water to a climax (see CLIMAX) of maximum development; the adjective "seral" applies to transitional phases of this process. Thus, a seral community is a biotic (see BIOTIC) community (see COMMUNITY) that is of transitory nature, in the sense that it will ultimately be replaced owing to changes in the environment (see ENVIRONMENT).

SIBLING: one of two or more individuals having a common parent.

SPECIATION: the process whereby new species are evolved (see EVOLUTION; SPECIES).

SPECIES: a group of actually or potentially interbreeding living organisms (see ORGANISM) more or less isolated from other such groups; in simple terms, a "kind" of plant or animal (see TAXON).

STOCHASTIC: process involving a random variable; used to describe a model (a description or analogy used to help visualize something that can be observed directly) involving chance or probability.

SUBSTRATUM: (plural: SUBSTRATA) a term used to denote the underlying support or the base (ground, soil) on which an ORGANISM lives, as opposed to substrate/substrates which are terms strictly applied to biochemical reactions.

SWIDDEN (more correctly, SWITHERN): slash and burn clearing of tropical woodland for crop cultivation; more generally, using fire to make ground available for agricultural and husbandry purposes.

SYMBIOSIS: the living together in more or less close association of two dissimilar organisms (see ORGANISM), both of which derive mutual benefit from the relationship (see MUTUALISM).

SYMPATRIC: having the same, or overlapping areas of geographical distribution (opposite ALLOPATRIC).

TAXON: (plural: TAXA) a term for any category used in classification. TAXONOMY is the science of the classification of plants and animals. The fundamental taxon in biology (see BIOLOGY) is the species (see SPECIES), which represents a real biological entity; this category can be defined generally in objective terms, whereas all other taxa are either subdivisions of the species or groupings of species, which cannot be defined except in terms involving subjective judgements.

TECTONIC: of, or relating to, forces involved in deforming the crust of the earth.

TELEOST: any of a group (Teleostei) of fish characterized by bony skeletons.

TERRESTRIAL: of, or relating to, the land.

TRAIT: a recognizable entity that represents a unit upon which natural selection (see NATURAL SELECTION) can act.

THEORY: a generalization based on certain knowledge which explains some class of phenomena; in turn used as the guide to gathering additional information.

THERMOCLINE: the abrupt change in water temperature which occurs in relation to depth; occurring seasonally, and separating the warm upper epilimnion (see EPILIMNION) (which usually lies within the euphotic (see EUPHOTIC) zone) from the cold, deeper hypolimnion (see HYPOLIMNION).

TISSUE: an aggregation of similar cells (see CELL) into a functional unit within an organism (see ORGANISM).

TROPHIC: of, or relating to, nutrition; often used as "trophic level." One of the hierarchical strata of a food web (see FOOD WEB, CHAIN) characterized by organisms (see ORGANISM) which are separated by the same number of steps from the primary producers (see PRIMARY PRODUCER).

VEGETATION: the total plant cover of an area.

VERTEBRATE: any of a major group (Vertebrata) of animals (fish, amphibians, reptiles, birds and mammals) with a segmented spinal column (backbone).

VICARIAD: one of a group of (vicarious) closely related species (see SPECIES) whose distribution is allopatric (see ALLOPATRIC) (i.e., not occurring together).

VIRUS: any of a group of infective agents (for disease) regarded either as the simplest micro-organisms or as complex molecules containing a protein (see PROTEIN) coat enclosing a core of genetic (see GENETIC) material.

VULCANISM: of, or relating to, volcanic eruptions.

WATERSHED: area bounded peripherally by waters parting and draining to one or more watercourses; a dividing point or line.

WETLAND: temporarily or permanently inundated terrestrial systems bordering on aquatic systems and including shallow systems such as estuaries, salt marshes, vleis, dambos, bogs, sponges, mires, swamps, floodplains and many coastal lakes and lagoons. Systems which essentially are driven by littoral (see LITTORAL) processes.

ZOOGEOGRAPHY: that branch of biology (see BIOLOGY) that deals with the geographical distribution of animals.

APPENDIX 1. NAMES AND ADDRESSES OF INVITED WORKSHOP PARTICIPANTS

HUNTLEY B J (Mr), CSP : CSIR, P O Box 395, Pretoria 0001
(Workshop Chairman)

BOTKIN D B (Prof), Environmental Studies Programme, University of
California, Santa Barbara, California 93106, USA

BOWMAKER A P (Prof), Oceanographic Research Institute, P O Box 736,
Durban 4000

BRAIN C K (Dr), Transvaal Museum, P O Box 413, Pretoria 0001

BREYTENBACH J (Mr), Saasveld Forest Research Station, Private Bag X6531,
George 6530

CHILD G (Dr), Department of National Parks and Wildlife Management,
P O Box 8365, Causeway, Harare, Zimbabwe

COOPER K H (Mr), Wildlife Society of Southern Africa, P O Box 2985,
Durban 4000

COTTRELL C B (Dr), Division of Biological Sciences, University of
Zimbabwe, P O Box MP 167, Mount Pleasant, Harare, Zimbabwe

DAVIES B R (Dr), Department of Zoology, University of Cape Town,
Rondebosch 7700

DIAMOND J M (Dr), Department of Physiology, University of California
School of Medicine, Los Angeles, California 90024, USA

EDWARDS D (Dr), Botanical Research Institute, Private Bag X101,
Pretoria 0001

FROST P G H (Mr), C/o Savanna Ecosystem Project, P O Boekenhout 0561

FRYER G (Dr), Freshwater Biological Association, The Ferry House, Far
Sawrey, Ambleside, Cumbria LA 22 OLP, England

GIVEN D R (Dr), Botany Division, Department of Scientific and Industrial
Research, Private Bag, Christchurch, New Zealand

GREIG J C (Mr), African Wildlife, P O Box 537, Somerset West 7130

GRINDLEY J R (Prof), School of Environmental Studies, University of Cape
Town, Private Bag, Rondebosch 7700

HALL A V (Dr), Bolus Herbarium, University of Cape Town, Private Bag,
Rondebosch 7700

HALL M (Dr), Department of Archaeology, South African Museum,
P O Box 61, Cape Town 8000

HEYDORN A E F (Dr), National Research Institute for Oceanology,
P O Box 320, Stellenbosch 7600

HUTCHINGS L (Dr), Sea Fisheries Institute, Private Bag, Sea Point 8060

LUCAS G L (Mr), IUCN Threatened Plants Committee, Royal Botanic Gardens,
Kew, Richmond, Surrey TW9 3AB, England

MACDONALD I A W (Mr), Hluhluwe Game Reserve, P O Box 25, Mtubatuba 3935

MILLER K R (Dr), IUCN Commission on National Parks and Protected Areas,
School of Natural Resources, University of Michigan, Ann Arbor,
Michigan 48105, USA

NEWMAN G (Dr), Fisheries and Wildlife Division, Ministry for
Conservation, P O Box 41, East Melbourne, Victoria 3002, Australia

NOBLE R G (Dr), CSP : CSIR, P O Box 395, Pretoria 0001

OWEN-SMITH R N (Dr), Centre for Resource Ecology, Department of Botany,
University of the Witwatersrand, P O Box 1176, Johannesburg 2000

PRESCOTT-ALLEN R (Mr), IUCN, Avenue du Mont-Blanc, 1196 Gland,
Switzerland

RABINOVITCH-VIN A (Dr), Nature Reserves Authority, 16 Hanatziv Street,
Tel Aviv, Israel

RAY G C (Dr), Department of Environmental Sciences, Clark Hall,
University of Virginia, Charlottesville, Virginia 22903, USA

RIBBINK A J (Dr), Fisheries Research Station, P O Box 27, Monkey Bay,
Malawi

ROBINSON G A (Dr), National Parks Board, P O Box 787, Pretoria 0001

SCHEEPERS J C (Dr), Botanical Research Institute, Private Bag X101,
Pretoria 0001

SIEGFRIED W R (Prof), Percy FitzPatrick Institute of African Ornithology,
University of Cape Town, Private Bag, Rondebosch 7700

SHAUGHNESSY G (Mrs), 3 Lloyd Court, Lloyd Street, Toorak Gardens, SA5065
Australia

SHAUGHNESSY P (Dr), 3 Lloyd Court, Lloyd Street, Toorak Gardens, SA5065
Australia

SOULé M E (Dr), Institute for Transcultural Studies, 905 South Normandie
Avenue, Los Angeles, California 90006, USA

SPECHT R L (Prof), Department of Botany, University of Queensland,
St Lucia, Queensland 4067, Australia

THODAY J M (Prof), Department of Genetics, University of Cambridge,
Downing Street, Cambridge CB2 3 EH, England

TINLEY K L (Dr), Blue Bend, P O Box 2021, Beacon Bay, 5205

VAN DER ELST R (Mr), Oceanographic Research Institute, P O Box 736,
Durban 4000

WALKER B H (Prof), Centre for Resource Ecology, Department of Botany,
University of the Witwatersrand, P O Box 1176, Johannesburg 2000

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