Conservation of threatened natural habitats

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

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INTRODUCTION

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

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

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

Real-conserv is a philosophy of conservation based on an integration of conservative goals and social reality. It shares with Realpolitik a healthy respect for pragmatism and an admiration for decisive action. Unlike Realpolitik, however, which is basically amoral and concerned with ends, not means, real-conserv rests on the same scientific, economic and moral foundations as does 'normal' conservation or conservation-as-usual. Actually, the difference is one of degree only – the degree to which planning and implementation of programmes takes into account the impact of probable social, political and economic events.

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

Three scenarios

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

Dystopia had arrived by 2020. While nuclear war had somehow been avoided, society had gradually become meaner and anarchic. The trends were already established and could have been extrapolated from the then existing patterns of international, economic and civil behaviour. These trends included: 1. Continuation of the costly arms race among the superpowers; 2. Increasing inflationary pressures and economic instability; 3. Decline in real income and living standards in industrialized countries due to increasing pollution and the cost of energy and raw materials; 4. No real increase in international aid; 5. No change in the frequency of civil and international warfare in the tropical countries. (In sub-sahara Africa, between 1945 and 1980, at least one-third of the nations had been totally involved in at least one war with a significant loss of wildlife in nature reserves. Among these were Angola, Mozambique, Rhodesia, the Central African Republic, Uganda, Somalia, Ethiopia, Burundi and Nigeria. On the average, each African nation had a war with significant impact on wildlife every 75 to 100 years);
6. Failure of the United Nations to effectively enforce peace and stability in the world;

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

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

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

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

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

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

3. A rise in average temperature of 1.5-9 degrees Celsius and a consequent rise in sea level, causing the drowning and abandonment of many coastal cities and most ports; and

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

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

The World Famine of 2014-17 has left 2.5 billion dead, four billion starving and has caused the total collapse of most public services in Asia, Africa and Central America. All national parks and reserves were plundered, and have virtually ceased to exist, except in Europe, China and North America.

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

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

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

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

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

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

In stark contrast, others, such as Norman Myers (1979) and the Ehrlichs (1981) are warning of impending ecological disasters such as already described. It is our job as conservationists to awaken the more optimistic
As the forests and other habitats matured, captive-born and wild-caught animals were introduced. In one hundred years, the Maritopians had successfully established quasi-natural, but intensively managed ecosystems that closely resembled those that had once existed on the nearest continent, but which had been virtually destroyed between 1980 and 2050.

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

A major role for ex situ conservation?

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

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

Why indulge in such fantasies in the first place? My reason is that much, if not most, of conservation planning today is based on equally unrealistic fantasies, on specious assumptions about what the future holds, and that we thereby do a disservice to our descendants. We owe future generations of scientists the continuing survival of the majority of tropical macrofauna and macroflora (trees) be eliminated, but ecosystem services will not.

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

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

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

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

The following section may provide a useful rubric for such action. It should be noted, however, that an implicit and very speculative assumption of this section is the continuing survival of the majority of tropical nature reserves.
A DECISION FLOW-CHART FOR THE GENETIC MANAGEMENT OF ANIMAL POPULATIONS IN NATURE RESERVES

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

A two-level process

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

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

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

Figure 1. A decision flow-chart for management of numerically endangered populations in nature reserves. \( n_0 \) is the effective number of breeding individuals in a population of a species.
or technicians may be found across an international border. Even before such a transfer is made, a whole battery of scientific questions may have to be answered, including the possibility that karyotypic differences exist between the stocks. The country in which this operation is to be carried out may or may not have the facilities and personnel to carry out such research.

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

Criteria for minimum population sizes

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

It is necessary to caution again that the employment of any number is subject to many qualifications, namely that effective size translates into a much larger number of breeding adults when dealing with real, not ideal, populations. For example, when populations decline or 'crash', the survivors constitute a genetic 'bottleneck' in the history and evolution of the population. Any deviation in the genetic makeup of these survivors from the gene pool of the original population will be reflected in future
generations. More particularly, if the progenitor's gene pool is less diverse than that which existed in the original population, future-generations will have a corresponding deficit in genetic diversity. If the minimum population size is very small, due either to normal fluctuations or to an environmental change or catastrophe, it is tantamount to squeezing the genetic variability of the source population through a very narrow channel and eliminating a significant amount of this variability. Bottlenecks inevitably accompany the establishment of a captive stock for breeding purposes.

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

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

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

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

Instead of emphasizing rare alleles, zoologists have tended to worry about conserving quantitative variation (Franklin 1980). For this reason, the minimum population size recommended for animals has been lower (Franklin 1980; Soulé 1980) than those suggested for plant germ plasm collections. Biologists should probably be more conservative in this regard. For example, from experience with resistance to pesticides in insects, we know that some resistance alleles occur at very low frequencies in natural populations. Such genes are likely to be lost during a bottleneck. Therefore, it would be expected that populations passing through bottlenecks might not be noticeably affected until a disease epidemic swept through the population, and by then it would be too late. (Frankel and Soule 1981, chapter 2).

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

Management at the local level

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

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

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

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

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

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

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

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

The transfer controversy

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

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

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

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

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

Ex situ build-up

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

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

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

Mercy extinction

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

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

THE GENETIC EVOLUTIONARY CONSEQUENCES OF DESIGN AND MANAGEMENT TACTICS

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

Corridors

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

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

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

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

In most parts of the tropics the areas surrounding reserves and corridors will be settled and the corridors will pass through developed regions. Ultimately, these regions cannot be policed effectively. Furthermore, there will be a tendency for many species, including large mammals, to move into the corridors during their dispersal stages, and it is likely that in a reserve of a moderate size, (less than 2000 km²), many, if not most of the individuals of a particular species, will, by chance, at one time or another, enter a corridor and have to face an obstacle course of guns, snares, traps and other weapons along its route, not to mention diseases from direct and indirect contact with domestic animals.

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

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

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

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

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

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

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

Rational habitat manipulation

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

Structural criteria for nature reserves

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

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

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

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

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

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

**SUMMARY**

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

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

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

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

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

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

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

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

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

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

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