In Ecology, Change Brings Stability

Managers of reserves are faced with the challenge of preserving species diversity; counterintuitively, the best policy to prevent long-term change is to allow short-term change

THE Chobe National Park in northern Botswana is typical of many ecosystems in southern and eastern Africa. It has a large population of resident and migratory herbivores, which includes giraffe, impala, buffalo, elephant, zebra, and wildebeest. Some of the more notable predators are lions, hyenas, wild dogs, jackals, and servals. These, together with a rich array of bird and insect species, live among a mosaic of grassland and acacia woodland habitat. In other words, Chobe is a model of the kind diversity of species that many people have in mind when they think of "wildlife" and that many conservationists are trying to protect. Chobe, however, is apparently in trouble.

The acacia woodlands, which seem to be about as attractive to ungulates and tourists alike, are on the verge of destruction. For years now, no new stands of acacias have become established, and the existing trees are suffering badly from heavy browsing pressure and damage by elephants. Not surprisingly, park managers are extremely concerned about the potential loss of a valuable and attractive piece of habitat for which they have a responsibility to preserve. If the woodlands shrink to mere remnants of their former expanse, the managers will consider that they have failed. But, argues Brian Walker, of the Commonwealth Science and Industry Research Organization, in Canberra, Australia, the managers would be wrong to think that way.

Speaking at a recent meeting in New York,* Walker argued that park managers and conservation biologists not only should expect to see change in the habitats in their charge, but also should welcome it. "Rather than being a threat to the biodiversity that managers want to preserve in their parks, the sorts of short-term changes you see in Chobe are actually essential to the maintenance of species diversity," he said.

The meeting, which was organized for the New York Zoological Society by African ecologist David Western, addressed the problems of conservation biology in the next century. And as effective conservation depends critically on an understanding of the biological processes underlying ecosystems, part of the meeting was concerned with the basic issues underlying species diversity.

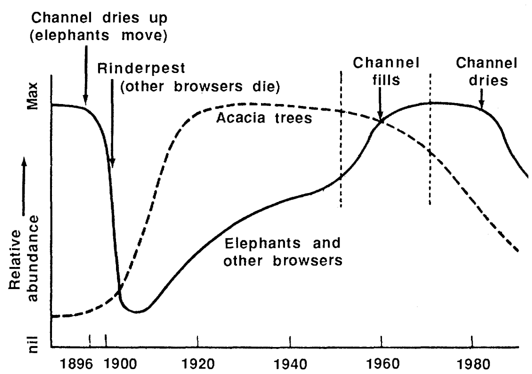
The causes for the radically different perspectives relating to the maintenance of species diversity are several. One of them has to do with the problem of time scales, while another stems from an apparent confusion over what ecological theory really is saying about ecosystems.

"Many people simply have a distorted appreciation of the kind of environmental and ecological changes that have occurred through time," said John Eisenberg, of the University of Florida. "Everyone knows that if you look at the fossil record you see things that don't now exist, things that went extinct. And many people are aware of the tremendous faunal and floral changes in the neotropics that happened 12,000 years ago, when the Pleistocene glaciation collapsed. But when faced with a modern ecosystem, there seems to be a tendency to assume that that's how things should be. And that attitude is bound to affect the way you might approach conservation: it distorts it."

On the larger scale of things, change within ecosystems should therefore be seen as natural and inevitable, even if it sometimes leads to local extinctions. Resisting such change through human intervention is not maintaining the status quo, which is what park managers and conservationists often believe, but rather the opposite.

The second source of confusion over the nature of change comes from ecological theory, specifically, according to Walker, from a misapprehension of ecological theory.

For several decades ecologists have debated the relationship between the diversity of an ecosystem and its stability in the face of perturbation. Initially, there was the intuitively attractive conclusion that increased diversity enhanced stability. But mathematical analysis of the problem, principally by Robert May, of Princeton University, and later by others, including Stuart Pimm, of the University of Tennessee, showed that there was no necessary connection between diversity and stability. It is true that, in the mathematical models, ecosystems that were at or near equilibrium and displayed certain feedback relations between the system's components could be stable in the long term. Generally, however, the relationship between diversity and stability is at best rather loose.

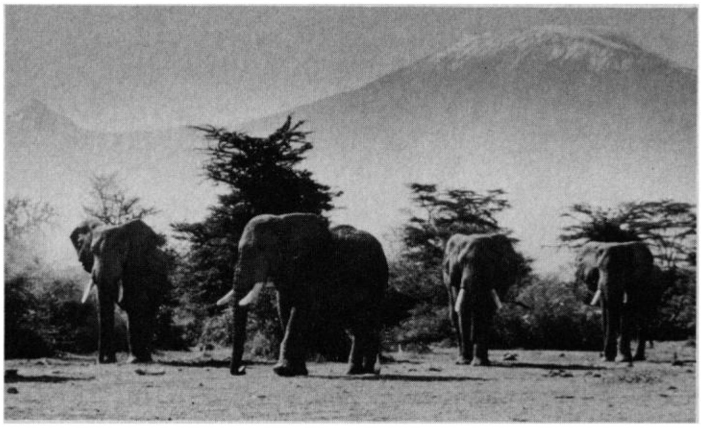


Dynamics of acacia woodland *and browsers in the Chobe National Park, Botswana. The acacias became established when populations of elephants and other browsers collapsed because of hydrological changes and disease.*

Perhaps because the debate was, and continues to be, somewhat esoteric, or perhaps because old, intuitively attractive ideas die hard, the notion of a necessary link between diversity and stability has remained popular. As a result, says Walker, because the goal of most conservation areas is to maintain a high diversity of species, "most management activities are aimed at stabilizing the ecosystems concerned."

This, as Walker sees it, is just the first part of the problem. The rest of it stems from a different use of the notion of stability between the theoretical ecologists and the park managers. When theoreticians talk about stability in their model ecosystems they are typically considering the stability of the number of species: if the number of species remains the same, the system is stable. This

*"Conservation 2100," a Fairfield Osborn Symposium, Rockefeller University, New York, 20–23 October.



Elephants *often live in a delicately balanced relationship with acacia woodland.*

A changing water table *is driving habitat changes in the Amboseli National Park, Kenya, changing acacia woodland into scrub.*

more recently and more precisely has been called *persistence*.

For people in the field, says Walker, stability generally means something different. "They are concerned with what they can see coming and going in the ecosystem. And what they generally see is not species as such, but populations of particular species. If a population size stays the same, it's stable, but if it fluctuates it's unstable." Stability of population size is what ecologists now call *constancy*. "I hardly ever use the word 'stability' now, because it means at least five different things," warns Pimm.

Conservationists should be interested in persistence, not constancy, says Walker—that is, the number of species within an ecosystem, not the number of individuals within any particular species. "The irony is that in order to achieve persistence you need to have the species' populations fluctuating." What has often happened, however, is that park managers have striven to keep populations of a species constant, thus endangering the very diversity they want to protect.

The reason that constancy of populations within species often works against maintaining high species diversity overall relates to the usual state of natural ecosystems, and again is counterintuitive or at least has been misunderstood. In practical terms, the issue is whether ecosystems are or are not at equilibrium. In the realm of theory, the problem is less clear-cut.

For reasons of tradition and mathematical expediency, most of the models of ecosystem behavior are equilibrium models. In other words, left to run their course, the components in the system will eventually come to rest at some sort of steady state in relation to each other. Pimm acknowledges that these models present a somewhat simplified picture of the real world, but, he says, "they do have the ability to capture rather broad-scale phenomena." Some predictions of the models might include the rate at which certain ecosystems recover from severe perturbation and the relative devastation inflicted by an invading generalist herbivore into a system as opposed to a specialist herbivore.

If natural ecosystems were typically at equilibrium, like the mathematical models that are used to portray them, then several consequences would follow. The most important one in the context of conservation, however, would be that the high species diversity that is typical of many of the national parks in the tropics could be inferred to be a stable phenomenon. And maintenance of that diversity could indeed be achieved by ensuring that external factors do not perturb the system.

Now, theoreticians do not necessarily assert that the real world is in equilibrium just because they use equilibrium models in trying to understand it. "The models are a useful way of making generalizations," says Pimm. Nevertheless, says Walker, field biologists have frequently assumed that because theoreticians use equilibrium models, this is the way the real world works.

In fact, ecosystems are rarely if ever at equilibrium. They are continually being perturbed—particularly by shifts in the environment—and are therefore in a permanently unstable state, constantly seeking an equilibrium that is always moving. "Most of our wildlife systems are inherently unstable, in the sense of persistence," says Walker. "And they have been that way for thousands of years. If they ever did come to equilibrium I don't think we would like them very much. The reason is that, in coming to equilibrium, the rich ecosystems we see today would inevitably lose many of their species."

The plight of the acacia woodlands in the Chobe Park illustrates this. Mature acacia trees offer a nutritious and obviously palatable food for many large browsers, and unless they are completely physically destroyed by, for instance, elephants, they can survive for several decades. Seedlings, however, will usually be killed if the browsing pressure is anywhere near high. Walker explained that the major stands of mature acacias owe their existence to a confluence of events at the beginning of the century.

In the 1890's the Savuti channel, which is the major supply of surface water, dried up, which encouraged much of the elephant population to search elsewhere for water. Soon afterward a massive outbreak of rinderpest devastated the ungulate population. The result of these two external factors was that browsing pressure, which had been high, suddenly plummeted, and as a result acacia seedlings survived and thrived through to maturity. As the ungulate population slowly recovered, with the disappearance of rinderpest and the renewed flow of the Savuti channel, browsing pressure once more returned, thus preventing the further establishment of new acacias.

"The coexistence of a large ungulate population and a thriving acacia woodland is therefore essentially unstable," explains Walker. "For the two to occur together you have to have periodic, severe perturbations of the system. Keep the system stable and the large acacia woodlands will disappear, thus reducing the overall diversity." Walker suggests that in order to reestablish the woodlands the park managers would have to recreate the conditions that nurtured the trees at the beginning of the century, namely the absence of a large population of elephants and other browsers for at least 10 years. "The question is, of course, whether the managers and tourists are prepared to accept a 10- to 15-year period with no animals to see."

It is perhaps natural that conservationists and park managers should concentrate on the most prominent aspects of the ecosystem for which they are responsible, namely the species of animals and plants that make up the system. But, argues Walker, this puts too much emphasis on interactions between the species—such as the ungulates eating the acacias—and not enough on the external, abiotic processes that ultimately drive the system. "The most important processes, in addition to disease, are hydrological and mineral cycling," suggests Walker. "For instance, when an area is burnt you can get a decrease in the proportion of infiltration versus runoff of rain water, and this can change a woodland to a shrubland. This is a bigger change than you can usually get just by a normal interaction of species within the system."

Ecosystems should therefore be seen to be in a constant state of turmoil, in both space and time. "In any one year, one or more of the species in the system will be on a path declining toward extinction, but the conditions for that to occur usually don't last long enough," says Walker. "The environment changes, and those endangered species recover, only to be replaced by some other species that is now in decline. Constant change in the relative favoring of different species in the system enables all of them to persist for a long time."

The question for park managers and conservationists, therefore, is how to act in the face of change. If a reserve were immense in size, then no action would probably be the best action, because natural species declines in one area would probably be compensated for by species booms in another. But, as was noted by a constant refrain at the New York meeting, most reserves are going to be too small and fragmented to be maintained without the loss of species. "We will have to learn to compensate for the changes that will inevitably occur," says Walker. "We will have to learn how to manipulate the systems in the directions we want them to go, but we don't know enough about them yet to be able to to that."

Eisenberg made the point that, uncertain though the present may be, it pales against potential changes in the future. "There is a global warming trend," he said, "and this is certain to affect habitats available for conservation. Rainfall patterns will change, and so some areas will become wetter and some drier. Some areas that are now marginal habitats, such as the Central African Republic and Chad for elephants, may in the future be optimal habitats." Flexibility is therefore essential in planning the conservation areas of the future, flexibility on the scale of decades and of centuries. "The trouble is," says Eisenberg, "people are just not used to thinking about problems on that kind of time scale." Which is perhaps one reason why the crisis in biodiversity is facing the world today. ■ Roger Lewin

Zoos and Botanical Gardens

"No large wild terrestrial animal will persist long into the future unless cared for in some way by man." So says William Conway, of the New York Zoological Society. "There will be insufficient habitat for most large species and protected habitats will often be in pieces too small or too unstable to sustain viable populations of the plants and animals they seek to protect." For these and other reasons, argues Conway, conservation biologists will be forced to depend more and more on ex situ care and biotechnology to help protect diversity, at both the species and the genetic levels.

Faced with the imminent extinction of many thousands of species—both large and small—during the next century, mainly through human economic activity, ex situ care and biotechnology may represent the only way to rescue at least a few of them. "Ex situ refuge for a human generation or two may enable species reestablishments even after extinction in nature, when local educational, economic and cultural progress may encourage their return," speculates Conway. At its most extreme, this scenario might involve the long-term cold-storage of plant and animal gametes or zygotes, to be retrieved and propagated when—and if—the human species is willing and able to coexist amidst a diversity of other species. Ex situ gene banks are of course safe from local disease outbreaks that would otherwise devastate a small, local population.

More down to earth, however, ex situ care and biotechnology as currently practiced involve a wide range of intervention activities, which so far have usually been applied as crisis responses to immediate threats of extinction. In the realm of ex situ care, these might include the capture and translocation of wild populations, the breeding of captive populations in zoological gardens, perhaps related to programs of reintroduction into the wild, and the management of a habitat with the goal of protecting a particular, endangered species. Biotechnology offers the possibility of techniques such as artificial insemination and embryo storage and transfer. To date, however, barely 20 species of wild mammal have been successfully reared following artificial insemination, and embryo transfer has been achieved with even fewer.

Although most attention is given to animals in discussions of this kind of human intervention, plant species are often in just as much danger as animal species. For several obvious reasons—including their immobility and their natural potential for seed dormancy—plants nevertheless represent better subjects for biotechnology options. So far, however, "serious attempts to preserve a major representation of botany's genetic building blocks, either in nature or ex situ, are discouragingly rare," comments Conway.

During the past few years, zoos have bred more than 19% of all species of mammals and 9% of bird species, which is impressive. But applying this kind of achievement to the practicalities of preserving threatened diversity immediately generates immense problems, not least of which is space. As Conway pointed out, zoos today contain a little more than half a million individual mammals, birds, reptiles, and amphibians. Given the need to maintain a degree of genetic diversity in a breeding population, zoos would need to have between 100 and 300 individuals of any individual species for long-term preservation programs. "Less than 1000 forms of mammals, birds, reptiles, and amphibians could be cared for on a long-term basis with current technology and facilities," concludes Conway. And, because many species exist as several subspecies and races, there would be the question of which ones would be chosen to be preserved, and on what basis?

For some species, ex situ care is simply not an option, and these include creatures both great and small. Many whales, for instance, simply consume too much food to make possible any kind of artificial preservation. At the other end of the size scale, many insect species have bizarre and complex life histories that defy replication in captivity.

Zoos and botanical gardens are for many people their only contact with living biological diversity. "It is time for them to be devoted to the maintenance of vanishing species and to become more compelling tools in the essentially cultural effort to link human communities with natural communities," argues Conway. Zoos and botanical gardens "must play a role in shaping the fundamental human values essential to the preservation of natural life." ■ **R.L.**