4. WHAT CONSTITUTES A KEY SPECIES?

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4.1 Introduction

This background document has as its brief the general question of what constitutes "a key species for its role in conservation and socio-economic development", from the perspective of an experimental ecologist. I was asked to address two particular points.

a) To what extent should the consideration of ecological stability guide selection of key species (a) in what direction, and (b) by what criteria?
b) Should particular types of ecosystems, and/or particular taxa, be systematically favoured? If so, using what criteria, e.g. rarity, threat of extinction, utility, etc.?

The first section of this paper explains what ecologists mean by 'key species', and what we know about their role in plant and animal communities. I then extend the concept of a key species by developing a new theoretical argument, and present ways in which the importance of a key species might be measured and assessed. These are purely scientific arguments, couched in ecological terms, and stressing the role of individual species in creating and maintaining habitats for others. The second part of the paper considers ways in which ecological ideas about key species and the diversity and stability of ecosystems might be used to select 'target' species for conservation. I am not hopeful that theoretical and experimental ecology have much to contribute to the selection of key species for conservation; the scale of ecosystem destruction and species extinction is now so great, and accelerating so quickly, that we cannot hope to identify more than a trivial proportion of key species in the world's major ecosystems, before they are lost forever. Most species conservation is, and will continue to be, pragmatic and dominated by 'aesthetic' and 'moral' considerations, bolstered occasionally by economic arguments. We have neither the time, the money, nor the resources to fiddle with key species whilst Rome burns; or, more aptly, while the ark sinks.

The science of ecology can contribute to species conservation by specifying minimum viable population sizes, helping to formulate management policies for reserves and parks, and so on. However, there is no set of magic scientific criteria for identifying key species that must be saved.

An alternative, and probably the only practical approach if our goal is to conserve as many species as possible, is to use key groups of species to pinpoint, albeit crudely, major centres of global diversity, and then to make great efforts to protect those areas.

4.2 The ecological definition of a key species

The American ecologist R. T. Paine seems to have been the first to use the term 'keystone species' to describe species that play a critical role in determining

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community structure (Paine 1969). Reviewing the concept, Krebs (1978) gives as examples Paine's own work on the starfish *Pisaster ochraceus*, that maintains species diversity on rocky intertidal sea shores by preying on mussels; lobsters that play a similar role as predators in subtidal communities off the east coast of Canada; and African elephants that promote the establishment and maintenance of grassiness by feeding on woody shrubs and trees. In current technical usage, 'keystone' and 'key' species seem to have identical meanings.

In his brief review, Krebs expresses the opinion: "Keystone species may be relatively rare in natural communities, or they may be common but not recognised. At present few terrestrial communities are believed to be organised by keystone species, but in aquatic communities keystone species may be common." Ecological thinking about key species has advanced very little in the subsequent ten or more years. The third edition of Krebs (1985) simply adds one more example of a key species (the sea otter, *Enhydra lutris*), but leaves his conclusions intact. One of the most up to date, and arguably the best recent major ecology text (Begon *et al.* 1986) does not even have the concept in the index, and has nothing explicit to say about the problem! In other words, the study of key species is hardly in the mainstream of contemporary theoretical and experimental ecology.

In its present form the idea is basically trophic: key species exert their effect primarily by feeding on other plants or animals. By reducing the abundance of victims lower in the food chain, key species create space and resources for other organisms, and thereby promote the existence of these other species in the community. The impact of key species is most easily gauged by a deliberate or accidental removal experiment. Only if the effects of removing a species are dramatic and easy to see does it qualify for the term 'key species'. Interestingly, a number of recent studies have identified what are essentially key species in particular ecosystems, without using the term, and without reference to the earlier literature. Carpenter *et al.* (1987) is a good example. They describe a 'trophic cascade' in which manipulation of fish populations in freshwater lakes has major effects on phytoplankton and lake primary productivity, via intermediate links in the food web. Predatory fish in these systems are clearly key species, and the trophic cascade is simply a good way of describing the extent of their impact.

There are at least two things wrong with the notion of a key species in its present form. First, by focusing primarily upon trophic interactions it misses a huge range of ecological effects and species that may be vital to the maintenance of ecological diversity in most ecosystems. And second, it provides no objective criteria for measuring the impact of a species, and deciding whether it is, or is not, 'key'.

4.3 Towards a broader and more rigorous measure of key species: the concept of organisms as ecosystem engineers

With Clive Jones at the Institute of Ecosystem Studies in New York, I have been attempting to broaden the idea of a key species to embrace processes other than trophic interactions, whilst at the same time sharpening our own perception of the problem. Our ideas are at a very preliminary stage, but I hope they may at least serve as a stimulus for debate in the present context.

Ecological processes, by definition, are driven by interaction between organisms and their environment. Pick up any ecology textbook and it will tell you what these important interactions are: interspecific competition; predation; parasitism; mutualisms of various kinds and; if you are lucky, something on diseases. There will also usually be chapters describing ecosystem processes, energy flow, nutrient cycling and so on.

On the one hand, we try to understand and model these processes by taking the community or ecosystem within which organisms occur as given; we study interspecific competition between voles in a meadow, and predation by sharks on a coral reef. On the other hand we describe processes such as energy flow in a pond, or nitrogen flux in a pine forest, and treat the organisms as black boxes. Missing from virtually all ecological textbooks (and, I suspect, from the day-to-day thinking of most ecologists, though many would deny it!) is any consideration of the major role played by organisms in the maintenance and creation of entire habitats and ecosystems. We do not even have a particular word, or words, to describe the process. The concept of a key species comes closest, but it is too restrictive because of its emphasis on trophic interactions. For want of anything better, Jones and I have coined the term 'organisms as ecosystem engineers'.

Some of the processes that fall within the scope of the term ecosystem engineering are simple, familiar, even trite. The growth of trees, for example, creates a complex habitat for thousands of other species; coral reefs play a similar role in the sea. But there are many other ways for one or a small group of species to influence hundreds if not thousands of other species by creating habitats, sometimes by trophic interactions (as in the classical concept of a key species) but often in many other ways. Take these habitat engineers away, and the ecosystem or community changes, perhaps drastically. Surprisingly, ecologists have no formal language to describe and measure the impact of species as ecosystem engineers, and no formal theory to organise our understanding. Examples range from beaver dams to gopher, ant and termite mounds, and from nitrogen fixing plants that shape succession to rock-eating snails that regulate nitrogen cycling. Honey fungus, chestnut blight and Dutch elm disease create worlds for hundreds of species reliant on dead or dying trees. Earthworms and termites create soils, *Sphagnum* makes blanket bogs, and so on. All these organisms create and maintain, that is they engineer, habitats for a host of other species, and hence have major impacts on energy flow, nutrient cycling, and other ecological processes. The systems we study and may wish to conserve are there, to a greater or lesser extent, because key organisms, the ecosystem engineers, contribute to their creation and maintenance.

Important questions, for which ecology currently has no generally agreed answers, include the following.

a) Do all major ecosystems have key organisms that engineer their structure? What functions do they fulfil and why? What would happen if we took them away?

b) Within the fossil record, can we identify major evolutionary breakthroughs that gave organisms new tools to engineer novel ecosystems? When did these events take place? What effects did they have on the subsequent evolution of species and the development of the world's ecosystems?
c) How can we model the impact of these natural engineers on other species? What currency should we use? Are there any useful, general ways of doing it, or is each case special?

One way to think of the role of natural engineers, and to measure their impact, is as a 'gate' or 'control point'. One measure of importance is then to estimate how many other species would disappear entirely from the area, habitat or ecosystem in question if the gates were closed. For example, alligator-wallows in the everglades are vital reservoirs during dry weather for large numbers of species of fishes, birds and probably invertebrates. Remove the alligators, allow the wallows to silt up, and there will be a cascading loss of species throughout the entire ecosystem that is measurable, at least in principle. Sea otters are key species because their demise leads to the collapse of offshore kelp beds, brought about by a ten-fold increase in grazing sea urchins, an important food for the otters (Estes *et al.* 1978). The effects of removing the kelp reverberate throughout offshore and coastal environments. But we can now see that the classical effects of these key species, driven by trophic interactions, are only one way in which species may engineer and create habitats for other organisms.

A simpler measure of the importance of any species as a habitat engineer, by whatever means, is the number of other species that would be lost from the area, community or ecosystem in question if the 'target' species were removed, or greatly reduced in abundance. In practice, such a measure may be difficult to achieve, but in principle it provides an objective measure of the importance of any particular species for the continuing existence of others. A broader and more useful definition of a key species is therefore one whose presence controls community diversity, by creating and maintaining, that is engineering, habitats for other organisms. (Usually key species will greatly amplify diversity, but we must also keep in mind the possibility that some key species reduce diversity, for example by favouring a small number of dominant taxa).

4.4 Application to conservation

In theory, it clearly makes sense to conserve key species of plants and animals, thus ensuring the continuing existence of the habitats and conditions necessary to sustain large numbers of other organisms.

In practice, conservation already relies heavily on the implicit notion of organisms as habitat engineers in selecting and managing parks and reserves. We know that we cannot conserve particular species without conserving their habitat. At its most simple, we therefore set aside particular kinds of forests to conserve particular kinds of birds or butterflies, dependent upon the forest for habitat. (We have already noted that treating plants as habitat engineers is trite; but that does not mean that it is a false argument, just a very simple one.) Things get more complex when man himself has to engineer the habitat to maintain particular species, or communities; by lighting fires, by controlling grazing regimes, by culling herbivores or by manipulating water levels. Many reserve and park managers are acutely aware that particular species of plants or animals play a vital role in maintaining habitats within their domain, and go to great lengths to ensure their correct management; sometimes with considerable controversy over what constitutes the pristine state, and how it should be maintained! There is therefore nothing new about recognising that key species (now defined in the broader context as species whose presence controls and maintains local diversity) must be conserved if we wish to conserve many other ecologically less important taxa, and entire communities. But in the main, the concept is implicit in what we do, not explicit.

Would more explicit use of the key species concept be useful in framing future conservation strategies? I wish the answer was 'yes', but believe that it will usually be 'no'. As an ecologist I would like to know whether there are rules and general principles in the game of ecological engineering. I would like the idea of trying to measure 'species amplification' across a variety of taxa and communities. It is obvious that if we only knew a great deal more than we now know about key species, conservation would benefit greatly, but I see no prospect of getting this information fast enough to help conservation organisations significantly over the next decade and beyond.

Given the rapid and accelerating pace at which we are currently exterminating species and destroying entire ecosystems (e.g. Roberts 1988), there is really only one way in which application of an ecologically sound keys species concept might aid selection of species for conservation. This is if there already existed some easily identifiable criteria for recognising key species and what they do. But as we have seen, this is not the case; ecologists have hardly studied key species in a formal sense, and there are no useful generalisations about where key species occur, or about what they do, or how they can be recognised. Hence we are reduced to studying each case individually, guided by natural history observations, insight and inspired guesses. In principle it is not difficult to do experiments to discuss whether this fish, that snail, or the other snake is, or is not an important amplifier and maintainer of local diversity. But such experiments take time, and time is not on our side. Where the role of key species can be deduced by simple observation and common sense by all means use the idea to promote conservation. But I see no prospect of ever gathering sufficient hard, experimental information about most threatened communities and ecosystems to use the key species concept as a practical tool for conservation. We have neither the time, the money nor the resources for this.

One example will suffice. I have twice referred to snails as key species. They seem an unlikely choice, but the example is deliberate. Several years of careful research in the Negev desert by Clive Jones and Moshe Shachak have revealed a remarkable food chain. Endolithic lichens (lichens growing under the surface of rocks) are consumed by two closely related species of desert snails, *Euchondrus albulus* and *Euchondrus desertorum*, both able to rasp away the surface of the limestone. The snails are so abundant that their faeces (ground up rock) are a major contribution to soil formation in the desert (Shachak *et al.* 1987), and also liberate significant quantities of nitrogen 'locked up' in the lichens, with major effects on ecosystem productivity (C. G. Jones & M. Shachak, unpublished MS). Extinction or marked reduction in the abundance of the snails would probably have a cascading effect throughout the Negev ecosystem, with loss of many dependent species, and considerable reduction in productivity (I say 'probably', because the experiment has not been tried, and might in any case take many years before the full effects were noticed).

Clearly, *Euchondrus* snails are key species, acting as significant, if unexpected, habitat engineers. Now we know this, conservation of the Negev must ensure that snail populations are maintained; it is difficult to envisage many significant threats, but introduction of an alien predatory snail would be one possibility. Having said all this, it is inconceivable that the establishment of existing or planned reserves or conservation areas in the Negev might have been influenced by earlier recognition of the role of *Euchondrus*. Snails inspire neither the public, nor politicians: desert gazelles and leopards do. We may now know that we need snails to conserve gazelles and leopards, but my money is on the mammals, not the molluscs, in trying to win over public opinion in the battle to conserve more than tattered remnants from the ark. It would also be manifest stupidity to suggest that before we identify any habitat or species for conservation, we must know on the one hand what the key species are, or on the other hand whether that particular bird, mammal, or what have you is, or is not, a key species. In other words, I do not see how a drive to identifying key species will help practical conservation significantly.

4.5 The problem of ecological stability

Although the direct application of the concept of a key species seems to offer little immediate help in the race to conserve biological diversity, to what extent should the consideration of ecological stability guide selection? To answer this part of the brief, we again need to clarify what ecologists mean by stability, before deciding whether the idea is practically useful.

Stability has several distinct meanings (Pimm 1984) in the ecological literature. These ideas are not interchangeable; a population or community may be unstable under one definition, but stable in the sense of another. Hence vague reference to 'stability' is meaningless. There are three principal usages.

a) Stable populations vary, or fluctuate, less than unstable ones. It is not easy to see how this idea could be used to select species for conservation. However, minimum viable population sizes will be larger for species with widely fluctuating populations than for species with more constant population sizes, other things being equal (Soulé 1987).
b) Stable populations return to equilibrium after a disturbance; unstable populations do not. Populations stable to 'small' perturbations are said to be locally stable; populations that will recover from any perturbation short of complete extinction are said to be globally stable. We know rather little about global stability in either theory or practice in ecology and the idea has little to contribute to the

present debate. Local stability analysis, in contrast, is the basis of a great deal of mathematical modelling in theoretical ecology (e.g. May 1974; Pimm 1982). One of the central assumptions of these endeavours is that most of the persistent populations, food webs and communities of plants and animals that we observe in the real world are, by definition, locally stable (otherwise they would not long persist in the face of repeated environmental shocks). If this central assumption is true, all species have stable populations, and the concept provides no basis for selecting species for conservation.

However, it is not actually this simple. A growing body of theoretical and experimental work suggests that a number of major types of communities may exist very far from mathematical equilibrium. Instead, they are formally unstable, and diversity is maintained, not damaged, by repeated disturbances. For example, a good case can be made that both the diversity of tropical rain forest trees and the diversity of corals on tropical reefs are both maintained by repeated disturbance, with neither kind of system being either close to equilibrium, or formally locally stable (Connell 1978). Clearly, if this hypothesis is correct, it has profound implications for the size of reserves necessary to maintain diversity, and for reserve management. But I do not see how it would help us to identify key species.

c) The third, and potentially most pertinent definition is termed species-deletion stability, which measures the capacity of a system to withstand the selective removal of particular species (Pimm 1982, 1984). Theoretically, it can be shown that certain types of food webs, or certain types of communities, are robust to species deletion, and others are not; and that removing certain types of species (top predators for example) is likely to have much greater impact on the remaining species in the system than removing, say, one of several alternative host-plant species for herbivores. A moment's thought, however, shows that if a system is drastically changed by deleting a component population (the system is not stable to species deletion), then the deleted species is, by definition, a key species. In other words, stability (or lack of it) to species deletion and key species are different facets of the same problem, and we are back where we started.

Drawing these arguments together, we must conclude that consideration of ecological stability in its various (and very different) usages is extremely unlikely to help in the selection of species for conservation.

4.6 Other considerations

Should particular types of ecosystems, and/or particular taxa, be systematically favoured? If so, using what criteria? This part of my brief is at one and the same time the easiest to deal with, and the most difficult. It is the easiest because from the point of view of experimental (or for that matter theoretical) science, there is rather little to say. The question, what criteria should we use to select species for conservation (for example rarity, threat of extinction, potential medicinal use, potential as a food resource, multiple use species, or beautiful species) is not a scientific question, and it is not one to which science can provide an answer, except in marginal cases. One such marginal case may be in identifying populations that are so reduced that they are no longer viable in the wild (Soulé 1987). But even this limited application of ecological science presupposes that we have already identified the species worthy of conservation; and that major, initial choice has little or nothing to do with science.

We select species for conservation for all kinds of mixed, often confused, and certainly rarely expressed reasons. Let me make my own position clear, as a citizen, not as a scientist. I care passionately about conservation, and am horrified by the current scale of species' extinction, and the prospects of much, much worse to come during the rest of my lifetime. I care because wild plants and animals, and the places where they live give me, and the people about whom I care most dearly, enormous pleasure. They enrich my life, just as medieval cathedrals, Mozart and Monet enrich my life, and the lives of others. It has been a powerful notice for conservation ever since it began to dawn on thinking people that wholesale destruction of nature impoverishes mankind (Leopold 1949). In other words, one great notice for conservation is 'moral' or 'aesthetic'. That is why we plan to conserve gazelles and leopards, and accidentally conserve snails at the same time. Gazelles are beautiful and leopards are exciting; it takes time to love snails. Put bluntly, we select species for conservation on emotional grounds; science has little or nothing to do with it.

Interestingly, what I have just outlined is a new type of 'key species', but not in the scientific sense defined earlier. They are political, or emotional key species, for which a conservation case is relatively easily constructed because they are spectacular, exciting, intelligent, beautiful, cute or pretty, – grizzly bears, lions, chimpanzees, pandas or butterflies to select a handful of examples. By coincidence some of these organisms may also be key species in the ecological sense of the word, but this is a bonus. The two definitions of key species may coincide most often in dominant large predators, big cats, wolves, eagles, sharks, and so on. So that if I had to target money and resources on any ecological group, it is here that I would put greatest effort, in full realisation that it is at best a crude, first approximation. The reasonable hope is that by conserving viable populations of these kinds of organisms in the wild, thousands of other more humble creatures get a ride into the twenty-first century.

Unfortunately, as pressures mount, and nature shrinks, these arguments frequently fail in the face of pressing and very real human needs, and other arguments come to the fore, or are used to bolster the aesthetic and moral case for conservation. It is clearly desirable that nations conserve species with the potential to pay their way in the world, be it via tourism, or sources of potential medicines, or food, or some other trade.

But these are matters of common sense, politics, economics and luck. (Luck because we have no idea, for example, how many plant species offer the potential for new drugs, or new pest resistant genes for our crops, and currently no simple and quick ways of recognising them; it will therefore be a matter of luck how many such species survive to be useful.) So as a scientist, I have little or nothing to contribute to the selection of 'key species' because they are, or may be, in some way useful. It is not a scientific problem.

It is not to say that ecological principles cannot be applied to pressing human and environmental problems in both the developed and developing world. Obviously they can, they are, and must increasingly be. Application may involve promotion of new plant species for shelter, firewood or food, or different way of using semi-natural ecosystems, or what have you. Each such project may involve 'key' species, vital to its success. But I see no general set of theoretical ideas linking these numerous efforts. Once pressing problems have been identified, we can use science to help solve them. But it is not easy to see how science (ecological or any other) can ever identify particular types of ecosystems and/or particular taxa that must be conserved.

A major exception to these generalisations may lie in discovering, as quickly as possible, where the world's exceptionally rich ecosystems are located. We already know some of them; they include the Cape Floral Region, and parts of the western Amazon basin. Then, if our aim is to conserve as much as possible of global diversity, we must ensure maximum protection for taxonomic 'hot spots'. Identification of such areas must rely on surveying a limited range of organisms; there is not time to do otherwise. Butterflies, freshwater fishes, woody plants, birds and other vertebrates have been suggested as suitable representative taxa (Roberts 1988). The hope is that these groups of species can serve as the nominated representatives of a silent and largely unknown majority.

Last but not least, it is obviously a valid scientific question to ask whether the planet as we know it will continue to function, that is continue to support and sustain our people, our cultures and our civilisations, in the face of massive species' extinction. Since we do not know the answer, I personally believe it would be prudent not to do the experiment! Unfortunately, this is a powerful, but somewhat two-edged scientific reason for conservation of species. It is two-edged because I cannot say with any confidence that the world would not be a perfectly acceptable, albeit rather dull place to live, even without 95% of current species; and indeed there are those who believe that a simplified planet would still "work". To put it bluntly, even at this level, the case for conservation lacks hard scientific support, provides those who do not care about gazelles and leopards, still less about snakes and snails, with a powerful argument to do nothing to prevent their demise.

4.7 References

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