

KEYSTONES, FLAGSHIPS, UMBRELLAS AND INDICATORS –
THE ROLE OF CHARISMATIC SPECIES AND ECOLOGICALLY INFLUENTIAL SPECIES IN PROTECTING
WHOLE ECOSYSTEMS

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“Something about the brink of extinction - at least for charismatic species - seems to wake people up and motivate them to do something” - Noss et al. 1997

Is it possible that some species are so ecologically influential that their loss results in dramatic changes to entire ecosystems and landscapes? Are other species so popular with the public and are their habitat needs so extensive that they can be used to focus attention on important conservation issues? Are there species with wide-ranging habits over a diverse landscape that can be singled out and managed so that all other native species and ecological processes benefit? Are there still other species that exhibit such ecological specialization and restricted distribution that they can be used to measure the integrity or “health” of a particular ecosystem or habitat type? Of course, the answer to all of these questions is a qualified “yes,” with each designation carrying its own set of evolutionary, political, and socioeconomic baggage. Each can be useful in either understanding or managing the planet’s dwindling biodiversity, so all of them are important from a conservation perspective.

Although ecosystem management has received increasing attention in recent years (Salwasser 1991, 1992, Frissell et al. 1992, Noss and Cooperrider 1994) the concept has been hotly debated by conservation practitioners (Simberloff 1997). Individual species are not an explicit target of this form of management, yet ecosystem processes are poorly understood even by the scientists who study them. This makes it very difficult to enlist the layperson and politician as proponents of large-scale conservation programs. Regardless of one’s perspective, ecosystem management stresses entire ecological systems and their restoration. More recently, the ecosystem approach has been criticized as insufficient to maintain important ecological processes ranging from energy flow to evolution (Harris et al. 1996a, 1996b, Maehr et al. 2002). These authors and others recognize the need to manage entire landscapes and regions to maintain and restore essential biotic processes. The Wildlands Project of North America (Soule and Noss 1998) and the Florida Greenways Project (Carr et al. 1998) are products of this change to a landscape perspective. Regardless, both approaches stress the importance of keystone species, especially carnivores, in designing regional and continent-spanning conservation blueprints. The three features of such planning are cores, corridors, and carnivores (Soule and Noss 1998). The latter feature encompasses the notions of flagships, umbrellas, and keystones - concepts that will be addressed further below.

Humans have a natural tendency to reduce complex concepts to their simplest common denominator. For many people, the species is the most logical element for understanding the natural world (Meffe and Carroll 1997:82), and most biologists, especially those working for natural resource agencies, focus on single species for research and management. Trends in subject matter of biological journals suggest that a focus on species is unlikely to change, so strong is the human tendency to reduce complexity to understandable units. Species with

keystone, flagship, umbrella, and indicator status may well be the bridge between the approach that we should take (the landscape) and the one that we seem helpless to avoid (the species).

Definitions

A **keystone** is a species that influences ecosystem or landscape function and biodiversity in a way that is disproportional to its abundance. Decades before the advent of the science of conservation biology, Aldo Leopold (1949) recognized the work of wolves in maintaining the protective blanket of vegetation on a mountain in the western United States. In the absence of the top predator, he observed “every edible bush and seedling browsed, first to anaemic desuetude, and then to death” as deer populations grew beyond the ability of the land to support them. This is the work of a keystone species, which is uncommon relative to the other organisms and processes that it influences. Implicit in this definition is that the loss of keystone species will also result in “shock waves” on other species (Orians and Kunin 1991), communities, ecosystems, or landscapes. Other examples of keystone species include the gopher tortoise (*Gopherus polyphemus*) in providing habitat for fossorial commensals, the sea otter (*Enhydra lutris*) in maintaining kelp bed structure and associated marine communities, and the African elephant (*Loxodonta africana*) in maintaining savanna landscapes. Abundant species that play important roles in ecosystems are not keystones, but are considered dominants (Fig. 1) (see also Navarette and Menge 1996, Piraino and Fanelli 1999). Examples of dominant species include some social insects, coral, salmon (Soule and Noss 1998), and Dipterocarp trees in tropical rain forests (Blundell 1999).

Umbrella species are sufficiently widespread to encompass the spatial requirements of many other native species. An umbrella species does not have to provide keystone services, but its successful management must translate into benefits for other species and ecosystem processes. The black bear (*Ursus americanus*) is a wide-ranging species that lives at relatively low density at the landscape scale (Maehr 1997) and incorporates many ecosystems at the individual and population levels. In Florida it is sufficiently widespread that virtually all terrestrial and aquatic ecosystems fall within the boundaries of its distribution. Its pre-Columbian distribution even included coastal beaches and the Florida Keys. A regional approach to black bear management in Florida would require a metapopulation perspective and would provide many organisms and processes increased security. In the Eastern Hemisphere, the tiger (*Panthera tigris*) ranges from the near-arctic reaches of Siberia to Indonesian tropical islands. Its extensive distribution and the large home ranges of individual tigers make it ideal as a conservation umbrella (Tilson and Seal 1987).

An **indicator** is a species with specialized habitat requirements that is often used to reflect the health of a particular habitat or ecosystem. Much like the canary in the coal mine, an indicator species is examined for demographic or physiologic stress that may be the result of toxins in the environment, habitat fragmentation, or other anthropogenic influences. An example of an indicator species is the northern spotted owl (*Strix occidentalis caurina*) that is associated with forests of coniferous old-growth in the Pacific Northwest region of the United States. Another might be the goshawk (*Accipiter gentilis*), an inhabitant of large tracts of boreal forest in North America, Europe and Asia. Amphibians are often suggested as indicators, because they are perceived to be ultra-sensitive to environmental damage (Primack 1998). Less ambiguous environmental indicators include rock lichens (Hawksworth 1990) and mussels (Master 1990),

organisms that are directly affected by environmental contaminants and changes in the local environment.

Flagship species may possess characteristics of keystones, umbrellas, and indicators, but they are especially important as ambassadors of conservation causes. Such species are usually charismatic and popular with some segment of the human population. The emblem of the World Wildlife Fund, the giant panda (*Ailuropoda melanoleuca*), is probably the best known flagship species on the planet. Its charisma has not only served to benefit China's dwindling forests, but has generated interest in conservation causes world-wide. A more typical, regional example is the American kestrel (*Falco sparverius*), a small, charismatic falcon that is used by Pennsylvania's Hawk Mountain Sanctuary to promote education and nature conservation in the central Appalachian Mountains (Fig. 2). In central Europe the red deer (*Cervus elaphus*) is a common icon of rich regional cultures and is revered as a game animal. The maintenance of healthy red deer populations in highly altered cultural landscapes serves not only other wildlife species but the perpetuation of living folklore.

All but one of these categories are abstractions that are intended to help articulate environmental problems and to justify conservation action. Only the keystone species concept reflects the results of evolutionary processes, and is supported by compelling empirical evidence that these species are indeed critical to ecosystem function. Experimental research on marine invertebrates demonstrated the profound influence of top-down predation on community dynamics (Paine 1966, 1974, Paine and Vadas 1969), and led to the creation of the ecological keystone concept. Paine observed that the predatory starfish, *Pisaster ochraceus*, prevented a mussel (*Mytilus californianus*) from dominating the intertidal zone and that it actually facilitated coexistence among competitors. Removals of the starfish resulted in reductions or elimination of at least 25 species of invertebrates and algae. Similarly, local extinctions of the gopher tortoise create a cascade of impacts to other species because it excavates burrows that are used by many other species. Populations of Florida mouse (*Peromyscus floridanus*), gopher frog (*Rana capito*), diamondback rattlesnake (*Crotalus adamanteus*), indigo snake (*Drymarchon corais*), pine snake (*Pituophis melanoleucus*), gopher cricket (*Ceuthophilus* spp.), and thousands of other invertebrates would all suffer as a result of losing the services that this habitat-altering keystone provides.

Simberloff (1997) has stressed the need to develop empirical evidence in support of the validity of single-species management in an increasingly landscape-conscious world. In an effort to make the keystone concept more consistently applied, Power et al. (1996) developed several algorithms based on a single equation that represents "the strength of the effect of a species on a community or ecosystem trait." The community importance (CI) of a species can be described as,

$$CI = [d(\text{trait})/dp] [1/(\text{trait})]$$

where p is the proportional abundance (usually biomass of a species/total community biomass) of the species whose abundance is modified. Trait refers to a quantitative trait of a community or ecosystem such as productivity, nutrient cycling, species richness, etc. Based in part on this algorithm, Knapp et al. (1999) concluded that with a CI value ranging from 6 to 25, the

American bison (*Bison bison*) is a keystone species in tallgrass prairie. In this study, bison increased plant diversity by 10-30%, but were estimated to equal only about 1% of the total vegetative biomass (11-12g/m²).

Keystone species are recognized as critical components of effective conservation plans for ecosystems and landscapes (Noss et al. 1997:15) even though the identification of keystones is often difficult (Simberloff 1997). In post-Pleistocene North America, modern keystone species tend to be first order carnivores. The gray wolf (*Canis lupus*), for example, not only has direct effects on prey species such as moose (*Alces alces*) and elk, but its top-down influence benefits omnivores and opportunistic scavengers such as the bald eagle (*Haliaeetus leucocephalus*), common raven (*Corvus corax*), and grizzly bear (*Ursus arctos*), species that can also be considered flagships or umbrellas. In addition, large carnivores have been shown to affect patterns of tree growth through predation on large herbivores (McLaren and Peterson 1994). Terborgh (1988) described these indirect effects in the New World tropics where jaguar (*Panthera onca*) and puma (*Puma concolor*) control seed-eating herbivores at population levels that facilitate reproduction in certain large-seeded forest trees. Forest fragments that lack these top order predators may experience altered patterns in tree reproduction because herbivore populations are up to 10 times higher than in intact forests.

When viewed from an evolutionary perspective (see Box 1), the mountain lion (*Puma concolor*) is more than the flagship of conservation organizations and children who made it the official state animal, and it transcends the role of umbrella that agencies embrace in order to maintain funding for research and management. It is an animal that has spawned 5 non-fiction books and at least 2 novels in the last 6 years - there is most definitely some charisma here. But it is virtually overlooked for the role it has in life itself. As Darwin (1859) observed in *The Origin of Species*, "...Natural Selection...is a power incessantly ready for action, and is immeasurably superior to man's feeble efforts, as the works of Nature are to those of Art." Most of eastern North America has been without the power of the mountain lion for more than two centuries, but it is an ideal centerpiece for ecological restoration, whether it is viewed from a scientific or lay perspective. To succeed in such efforts, vast areas of the eastern United States and Canada would need to be set aside or otherwise managed to accommodate the spatial needs of *Puma concolor* populations. Noss (1991) concluded that individual reserve networks capable of supporting a mountain lion population would need to encompass from 6.9 to 13.8 million acres. Private conservation organizations could embrace the mountain lion as a charismatic flagship, agencies could find comfort in choosing a logical umbrella, and biodiversity itself would benefit through the return of an evolutionary keystone. Such species can be found throughout the world - disappearing, top-order, keystone carnivores. Tigers, clouded leopards (*Neofelis nebulosa*), jaguars and other large carnivores all have the potential to serve as flagships for conservation efforts targeted at dwindling global forest resources.

Keystones of the Future

The late Pleistocene extinctions resulted in a world with many fewer large mammals and the keystone services that they undoubtedly provided. Should today's keystones disappear, will tomorrow's society settle for the services that habitat generalists provide? At least two leading paleontologists have suggested that because the disappearances of woolly mammoth (*Mammuthus primigenius*) and mastodon (*Mammuthus americanum*) were caused in part by

humans, and because they provided important keystone services, elephants should be returned to the North American southwest (Martin and Burney 1999). Others have suggested that because proboscideans are second only to humans in the ability to alter habitats and landscapes, they should be considered “superkeystones” (Shoshani and Tassy 1996). A variety of large-seeded trees (e.g., mesquite, osage orange, honey locust, black locust, and Kentucky coffeetree) remain in North America as reminders of the very large animals that once acted as their dispersal agents. The restoration of the keystone services that proboscideans once provided in North America would certainly be controversial. African elephants are certainly charismatic and popular with the public, but is the idea practical in light of the perceived danger that they would present to humans and their property?

Single-species Pitfalls

Single-species approaches to biodiversity conservation can be criticized because of their potential to divert attention and funding away from holistic approaches to landscape management and restoration. However, a species-by-species approach is viewed by some conservationists as essential because there are so many species in need of emergency attention (Noss et al. 1997). In the worst case, a lost-cause species may be so popular with the public and natural resource agencies that it might be managed into extinction even though conservation dollars could have been better spent elsewhere (Simberloff 1997). In addition, a focus on species may create barriers to effective environmental education programs if ecological processes and trophic interrelationships receive limited instructional attention as a result. Advocates of single-species approaches must stress the ecological and evolutionary importance of target species and their surrogate roles for ecosystem or landscape management. All too often, managers reduce their interests to a species’ needs in the absence of understanding its community role or without considering the impacts of its management on other species or processes. A dilemma created by this approach is exemplified by autecology of the south Florida flagship species wood stork (*Mycteria americana*), and snail kite (*Rostrahamus sociabilis*) - both inhabitants of shallow freshwater wetlands. The former is a wading bird that reproduces when dry season water levels concentrate prey, whereas the latter is a raptor that requires less water level variation to support its mollusk prey. Current restoration plans for the Everglades must reconcile the opposing ecological needs of both species because management targeted at only one would cause problems for the other (Harris et al. 1996b). In this case a landscape approach must be taken that incorporates sufficient habitat in space and time that both species’ long-term needs are met.

A species that is chosen as a flagship must truly represent the landscape of interest or misguided management may ensue. For example, the Florida panther is often used as a flagship for Everglades restoration despite the fact that this national park and its environs are poor panther habitat and that successful restoration of this herbaceous wetland will further reduce the ability of southeastern Florida to support a panther population. The Florida panther is a forest obligate that prefers uplands (Maehr 1997) - the antithesis of a functioning Everglades. Unless forest restoration becomes a focal point of Everglades restoration, the panther is a poor choice for a flagship - at least in southeastern Florida. In California, the endangered giant kangaroo rat (*Dipodomys ingens*) has developed a mutualistic relation with exotic plants (Schiffman 1994, Noss et al. 1997). Conservation plans that target only the kangaroo rat could encourage the establishment and spread of exotic plants that could do damage elsewhere. For this species, recovery plans must include the restoration of its habitat in addition to the maintenance of its

demography.

Researchers and managers must be careful when proposing species for singular conservation roles. A strong bias toward a favorite study subject may result in management that selects an inappropriate flagship, umbrella, or indicator when a better selection (or none) exists. Similarly, so many species have been proposed as ecologically influential that keystone inflation may be devaluating the concept's usefulness as a management tool. The overuse of the term keystone has become problematic enough for some to recommend that the label be dropped entirely (Mills et al. 1993). Clearly, not every species can be a keystone, but the harder we look, the easier it becomes to assign great importance to each one. Charismatic species are ideal conservation ambassadors only when they provide ecological or evolutionary services, or when they truly are a canopy for the needs of other species and processes. Species flagships will facilitate long-range conservation goals so long as their cargos contain an ample supply of umbrella and keystone services.

Box 1 - keystones and Evolution

One can only imagine the faunal assemblages that typified North America a mere 11.5 thousand years ago. Giant herbivores such as the Shasta ground sloth (*Nothrotheriops shastensis*), woolly mammoth and mastodon were likely powerful instruments in physically altering the landscape, and, like African elephants today were probably preyed upon infrequently as adults. These, and an impressive array of predators including the saber-toothed cat (*Smilodon californicus*), the giant short-faced bear (*Arctodus simus*), dire wolf (*Canis dirus*) and American lion (*Panthera leo atrox*) are thought to have succumbed to human predation at the end of the Wisconsin glaciation (Pielou 1991). In all, more than 40 species of large mammal, many of which certainly provided keystone services, became extinct during a relatively short period that coincided with the colonization of North America by the technologically advanced Clovis people. A similar wave of extinction occurred several thousand years earlier in Australia after human settlement of that continent. Perhaps this identifies stone age humans as the ultimate keystone species. Regardless of the cause for the Pleistocene extinctions, the planet lost many species that undoubtedly provided keystone services. Following these mass extinctions, North America was left much poorer in terms of species diversity and the evolutionary processes that were facilitated by this rich fauna. North America's modern keystone species, while undoubtedly important, probably played relatively minor roles in Pleistocene landscapes and their fauna.

Modern North American species assemblages are dominated by comparatively generalist herbivores and a handful of predators, primarily canids and cats, that exhibit varying degrees of prey specificity. The most specialized of these is the mountain lion, a species that likely co-evolved in North America with deer in the genus *Odocoileus*. Compared with South American deer, the white-tailed (*O. virginianus*) and mule deer (*O. hemionus*) have been characterized as virtually predator proof (Geist 1998) - a hint of the top-down influence that predators can have on their prey. This evolutionary tug of war has served deer of North American origin well. They tend to be the most specialized and resilient of the world's deer (Geist 1998). Perhaps the anti-predator encephalization of the *Odocoileus* brain and its fast-twitch physiology set it apart from the other Pleistocene mammals that so quickly succumbed to stone age technology. The larger and slower megafauna were likely ill-equipped to deal with a new pack-hunting predator with weapons, whereas deer and mountain lion were pre-adapted to deal with this novel threat.

There is likely no greater role for a species than to be a driving force of evolution itself, a distinction that has become increasingly difficult for the Florida panther. Driven nearly to extinction in extreme south Florida, this endangered subspecies is still a vital part of the landscape despite numbers that are fewer than 100. Elsewhere in the eastern United States, the dominant wild herbivore, the white-tailed deer, often exists at near epidemic levels in areas without keystone predators such as the gray wolf and mountain lion. This situation has led to the development of a subdiscipline of wildlife ecology known as the science of overabundance. Problems associated with too many deer do not occur in Florida where the panther still exhibits typical demographics and spatial arrangements. Although it is still widespread in western North America, in the east it can only be found in the southern extremes of subtropical Florida. But it is in these places, landscape matrices of private land, public-owned parks, and preserves that the phenomenon of evolution may still occur. Thus, a species that may be listed as endangered in Florida, vermin in Texas, an umbrella in California, and a flagship in the Everglades, is still a keystone wherever it is found.

Box 2 - Keystone Variations

Keystone Guild - groups of species with similar feeding habits and disproportionately large impacts relative to their collective biomass include desert rodents, and fish in river food webs.

Keystone Mutualist - often referred to as mobile links, animals such as hummingbirds promote the persistence of certain plant species, which, in turn, support entire communities. The species that are serviced by mobile links can also be considered keystone mutualists.

Keystone Modifier - species that significantly alter the landscape can create conditions upon which other species depend. Examples include the North American beaver (*Castor canadensis*), and African elephant.

Keystone Resource - important resources such as figs, palm nuts, and nectar may be seasonally restricted, spatially concentrated, and support many species of insects, birds, and mammals.

Keystone Process - a phenomenon such as seasonal river flooding, or avalanche, that maintains environmental conditions suitable for the persistence of organisms adapted to such conditions.

Keystone Exotic - an introduced or alien species that has the capacity to completely alter ecosystems and landscapes in which it is not native. Examples include feral pigs (*Sus scrofa*) in Hawaii, Kudzu (*Pueraria lobata*) in the southern Appalachian Mountains, and goats (*Capra* spp.) on the Galapagos Islands.

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List of Figures

Fig.1. Keystone species are those that exist in low numbers or biomass, but have proportionally large influences on biotic communities and landscapes. Abundant species with large community and landscape effects are considered dominants.

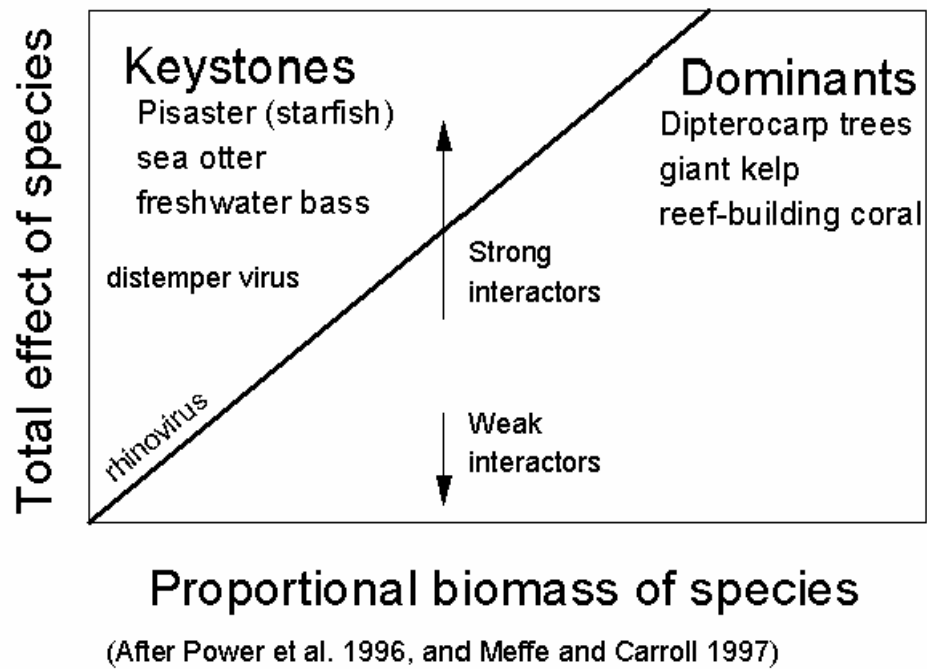


Fig. 2. The American kestrel is a flagship species for raptor conservation and education. Its demeanor and personality in captivity help to educate the public and garner support for regional conservation programs for a variety of resident and migrant hawk species.

