

The Nature of Cumulative Impacts on Biotic Diversity of Wetland Vertebrates

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ABSTRACT / There is no longer any doubt that cumulative impacts have important effects on wetland vertebrates. Interactions of species diversity and community structure produce a complex pattern in which environmental impacts can play a highly significant role. Various examples show how wetlands maintain the biotic diversity within and among vertebrate populations, and some of the ways that environmental perturbations can interact to reduce this diversity.

The trophic and habitat pyramids are useful organizing concepts. Habitat fragmentation can have severe effects at all levels, reducing the usable range of the larger habitat generalists while threatening the genetic integrity of small, isolated populations. The complexity of trophic interactions, and the propensity, or necessity, of vertebrates to switch from one food source to another—something we know little

about—makes using food chain support as a variable for predicting environmental impacts very questionable.

Historical instances illustrate the effects of the accumulation of impacts on vertebrates. At present it is nearly impossible to predict the result of three or more different kinds of perturbations, although long-range effects can be observed. One case in point is waterfowl; while their ingestion of lead shot, harvesting by hunters during migration, and loss of habitat have caused waterfowl populations to decline, the proportional responsibility of these factors has not been determined.

Further examples show multiplicative effects of similar actions, effects with long time lags, diffuse processes in the landscape that may have concentrated effects on a component subsystem, and a variety of other interactions of increasing complexity. Not only is more information needed at all levels; impacts must be assessed on a landscape or regional scale to produce informed management decisions. I conclude that a system of replicate wetland reserves that are allowed to interact naturally with the surrounding landscape will be more effective in preserving biotic diversity than isolated sanctuaries.

The National Environmental Policy Act and similar state legislation dictate the performance of cumulative impact analyses prior to specific environmental manipulations. Still other legislation requires the maintenance of biological diversity on certain Federal lands (e.g., the National Forest Management Act), and “the protection and propagation of a balanced indigenous population of shellfish, fish, and wildlife in the body of water to which the discharge is to be made . . .” [1972 amendments to the Federal Water Pollution Control Act, Section 315(a)]. Although logic and observations dictate that the impacts of repeated, similar actions, or a sequence of different actions, can accumulate to cause severe or irreparable damage to biotic diversity, some suggest that the concept of cumulative impacts is only “an interesting hypothesis.” While it may not be possible to predict cumulative impacts a priori, they certainly exist, can be described, and are critically important. To be effective, assessment of cumulative impacts on vertebrate communities must be done at a

landscape or regional scale of analysis. This means that the wetland manager and program administrator must be increasingly sensitive to the presence and meaning of within-species biotic diversity, not only to among-species diversity. What follows are descriptions of how wetlands maintain vertebrate biotic diversity and of some ways that various impacts have accumulated to reduce biodiversity. The majority of examples cited are from southern wetlands and related systems only because of my familiarity with them.

Hierarchy of Biotic Diversity

A great deal has been learned about genetics over the last 80 years. It is now recognized that the lowest levels of genetically encoded biotic diversity occur at the level of the gene allele. Other important aspects of genetic diversity within a species or subspecies include the proportion of loci that are polymorphic, the number and types of alleles at these loci, and the average level of heterozygosity. Moreover, we now know that the expression of a dominant, heterozygous, or recessive allele at a single locus may determine

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adaptive characteristics such as the presence or absence of a critical enzyme, resistance to malaria, or occurrence of sickle-cell anemia.

Our former understanding of genetics led ornithologists and wetland wildlife scientists to recognize the lesser snow goose (formerly *Chen hyperborea*) and blue goose (*Chen caerulescens*) as distinct species. The same situation was true for the great blue heron (*Ardea herodias*) and the great white heron (formerly *Ardea occidentalis*). In both cases further investigation revealed that the groups were, in fact, only expressions of allele variation within the same genome. Because of rapid progress in the classification of vertebrates during this century, bird species have been reclassified such that the more than 20,000 recognized species in 1920 have been reduced to about 9000 at present (Mayr 1982). Thus, what formerly constituted diversity among species is now considered to be genetic diversity within a species.

Both genetic (genotypic) and environmentally induced (phenotypic) variance may be manifested either as a gradual or clinal change, or as distinct ecotypes because of the separation of populations, with little or no opportunity for interbreeding. Both situations represent legitimate, and ecologically important, aspects of biotic diversity that must be considered.

The number of species (richness) and some measure of their relative abundance (equitability) combine to form the concept of species diversity. Because this concept was so heavily reviewed and debated by ecologists in the 1960s and 1970s, it became the standard by which biotic diversity was monitored and evaluated. Not until this decade have ecologists and regulators realized that it is neither sufficiently broad nor sensitive to assess the complete spectrum of biotic diversity.

Interactive community processes, such as herbivory, pollination, propagule dispersal, predation, parasitism, and competition, all function to influence the distribution, abundance, form, and behavior of organisms. It is the occurrence and magnitude of coevolved processes such as these that distinguish functional biological communities from random collections of species and determine biotic diversity at the community level. Thus, both the occurrence and relative abundance of species, and the relative magnitude of key biological processes, must be evaluated when assessing impacts on wetland biotic diversity. Keystone wetland species such as muskrat (*Ondatra zibethicus*), nutria (*Myocastor coypus*), beaver (*Castor canadensis*), manatee (*Trichechus manatus*), and moose (*Alces alces*) can dramatically alter community vegetation structure, which in turn influences and controls the occurrence of yet other animal species.

Presence, relative abundance, and activity levels of some wetland vertebrates—beaver, alligator (*Alligator mississippiensis*), and to a lesser extent muskrat, and large fish and turtles—may transform the physical structure of a site, altering hydroperiod and water flow characteristics to such an extent that they influence the very presence/absence of wetlands throughout the landscape.

Unless laws and permitting and regulating policies begin to consider biotic diversity across the full hierarchical spectrum, they will not ensure conservation of the wetland biodiversity resource (Noss and Harris 1986). Only regulation and planning strategies that maintain the full gamut of diversity (including processes) to the landscape level and above stand to be effective at maintaining biodiversity at all lower levels. However, even more may need to be done to maintain long-term diversity at the community, ecosystem, or landscape levels.

Wetland Wildlife Habitat and Food Chain Support

Wetland impact analysis procedures frequently revolve around two specific biological functions: the provision of habitat and of food chain support. These are neither simple nor independent concepts, and thus some explanation is warranted.

Wildlife Habitat

At least four different issues are integral to the assessment of cumulative impacts on wetland habitat. These are (1) specialist vs generalist species; (2) alpha, beta, and gamma diversity; (3) component vs compound ecosystems; and (4) animals' need to move. Numerous amphibian and reptile species are habitat specialists: mammals such as bog lemmings (*Synaptomys* spp) and round-tailed water rats (*Neofiber alleni*), and breeding birds such as Swainson's warbler (*Limnothlypis swainsonii*) and prothonotary warbler (*Protonotaria citrea*). Resident species that have specific habitat requirements also usually have small home-range sizes, and thus all their resource requirements may be provided within a single wetland. In the classification scheme of Whittaker (1960), these within-habitat species would constitute the alpha (α) component of diversity. At the other extreme, large, frequently wide-ranging species, such as bald eagles (*Haliaeetus leucocephalus*), mink (*Mustela vison*), or Florida panther (*Felis concolor coryi*), may be no less dependent on wetlands for specific life needs, but they cannot be restricted to, nor contained within, a small tract of wetland. Species

such as these must utilize two or more specific habitat types within a regional landscape in order to meet their life requirements. Thus, they are more appropriately thought of as creatures of the landscape; in Whittaker's scheme they might constitute the gamma (γ) component of diversity.

As noted by Elton (1966), animals higher in the trophic pyramid tend to be less habitat specific. Plants and primary consumers are frequently habitat specialists, but top carnivores rarely are. The principle of the inverse pyramid of habitats suggests that while animals at the higher trophic levels are generally fewer in number, they also generally range over greater distances and derive their life requirements from a greater number of community types or habitats (Figure 1).

The concept of component and compound ecological communities (Root 1973) suggests that regional or landscape-level systems consist of component communities articulated in space by the movement of nutrients, energy, propagules, and organisms. Within any given component subsystem, ecological relations will be dominated by relatively intense, niche-specific and/or host-specific interactions that tend to occur continuously. Presence or absence of a species or interaction within the component will be largely determined by conditions internal to the component, that is, its content.

Wide-ranging vertebrates link various component subsystems spatially and ecologically to help form compound landscape systems. Although transient species that move from one component subsystem to another are frequently generalists, highly specialized "mobile links" are not infrequent in temperate systems and are common in tropical systems (e.g., Gilbert 1980, Terborgh 1986).

The need for vertebrates to move derives from many basic biological functions, ranging from the need to access resources (food, water, or shelter), to the need for sexual organisms to mate and outbreed, and the need to colonize new or disturbed environments (Chepko-Sade and Halpin 1987). Most amphibians require fresh water for their egg and larval stages, but many use dry land as adults. Reptiles require an aerated medium for their eggs, but many then require an aquatic environment as adults. Large resident species such as black bear (*Ursus americanus*) forage in upland environments during summer and fall but depend on lowlands in winter. Migrant species may interconnect subsystems thousands of kilometers apart. Not only does the occurrence and abundance of the wide-ranging animals depend upon the asynchronous functioning of the component sub-

systems, but the long-term viability of the subsystems may well depend upon the presence of these landscape integrators.

There seems to be a gradient in ability (presumably adaptive) and apparent need for the different classes of vertebrates to move. Some vertebrates that occur in frequently or constantly renewed environments (e.g., flowing water) reflect little need for movement. Amphibians fit at this end of the gradient despite their larval (aquatic) versus adult (mostly terrestrial) life-stage differences. Long-lived turtles that spend decades in an aquatic environment but still require a 1-h nesting period in a safe terrestrial environment dramatize both the necessity of diverse component subsystems and the need to move between them.

With few exceptions, terrestrial mammals are highly vulnerable to forces that create impassible barriers between component habitats in the landscape. This derives from the need to range over wide distances while being limited to movement on the ground. Mammals that inhabit wetlands exhibit specific traits that make them highly vulnerable to isolation and habitat fragmentation. Virtually every species of North American mammal weighing more than 0.5 kg that inhabits wetlands is commercially valuable as a furbearer. Only four of the 30 commercially listed furbearers (Deems and Pursley 1983) are herbivorous (Table 1). The remainder of the furbearers (26/30 = 85%) are either carnivores in the strict sense or omnivorous members of the order Carnivora (e.g., the black bear). Because most are carnivores, they have much larger home ranges than herbivores or omnivores of equal size, and because they inhabit the water's edge, their home ranges tend to be long and narrow, aggravating the probability of fatal encounters with humans or human artifacts. Carnivorous mammals are probably the group most vulnerable to habitat fragmentation.

No small population (fewer than several hundred) of vertebrates can maintain its demographic and genetic integrity indefinitely in the face of population fragmentation, genetic isolation, and inbreeding (Frankel and Soule 1981). Thus, modifications to the environment that preclude movement between component subsystems may be as devastating to vertebrates in the long run as are forces that actually destroy the wetland.

This phenomenon can be dramatically illustrated by citing the history of mammal extinction and endangerment in Florida, USA. A strong linear relation between percent of size class now extinct and body size exists for mammals dating from the Pleistocene to the present. While 100% of the very large (>10,000 kg)

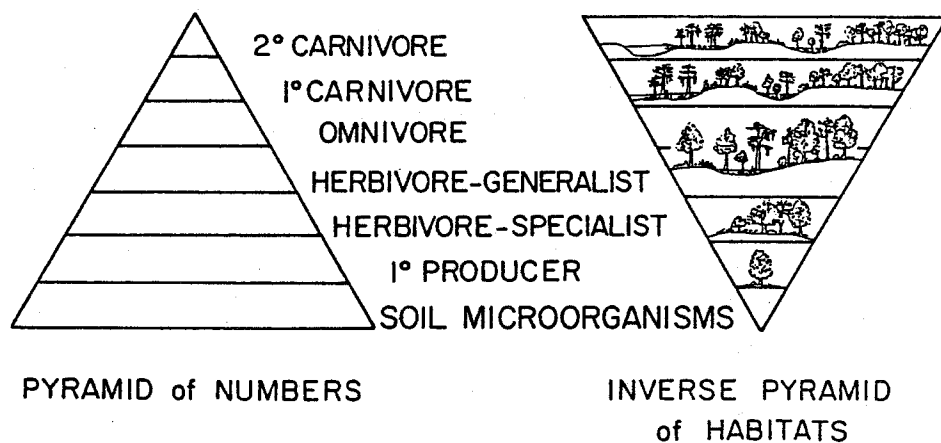


Figure 1. Relationship between the trophic pyramid of numbers of animals and the inverse pyramid of their habitats. The inverse pyramid suggests that while animals of the higher trophic levels are generally less abundant, they range over greater distances and derive their life requirements from a greater number of habitat types. (See Elton 1966)

Table 1. North American furbearers classified by systematics, and trophic and habitat characteristics.

Species	Tropic group ^a	Characteristic habitat
Marsupalia		
Opossum (<i>Didelphis virginiana</i>)	O	Riparian woodlands
Rodentia		
Beaver (<i>Castor canadensis</i>)	H	Slow-flowing forested waterways
Muskrat (<i>Ondatra zibethicus</i>)	H	Fresh and saltwater wetlands
Nutria (<i>Myocastor coypus</i>)	H	Coastal marshes and swamps
Carnivora		
Coyote (<i>Canis latrans</i>)	C	Grasslands, meadows, and open environments
Gray wolf (<i>Canis lupus</i>)	C	Grasslands, tundra, and open woodlands
Arctic fox (<i>Alopex lagopus</i>)	C	Alpine and Arctic tundra
Red fox (<i>Vulpes vulpes</i>)	C	Woodlands and prairies
Gray fox (<i>Urocyon cinereoargenteus</i>)	O	Woodlands and forests
Brown bear (<i>Ursus arctos</i>)	C	Generalist associated with forested landscapes
Black bear (<i>Ursus americanus</i>)	O	Principally hardwood forests
Polar bear (<i>Ursus maritimus</i>)	C	Arctic coast and pack ice
Bassarisk (<i>Bassariscus astutus</i>)	C	Riparian forests in arid environments
Raccoon (<i>Procyon lotor</i>)	O	Riparian forests and wetlands
Marten (<i>Martes americana</i>)	C	Mature conifer and mixed forests

Table 1. (continued)

Species	Tropic group ^a	Characteristic habitat
Fisher (<i>Martes pennanti</i>)	C	Mature conifer and mixed forests
Short-tailed weasel (<i>Mustela erminea</i>)	C	Cool conifer forests with water and openings
Long-tailed weasel (<i>Mustela frenata</i>)	C	Warm conifer forests with water and openings
Mink (<i>Mustela vison</i>)	C	Wetlands generalist
Wolverine (<i>Gulo gulo</i>)	C	Boreal and montane forests
Badger (<i>Taxidea taxus</i>)	C	Prairies and grasslands
Striped skunk (<i>Mephitis mephitis</i>)	C	Forest edges near water
Spotted skunk (<i>Spilogale putorius</i>)	C	Grasslands and meadow edges
River otter (<i>Lutra canadensis</i>)	C	Riparian forests and marshes
Cougar (<i>Felis concolor</i>)	C	Generalist
Lynx (<i>Felis canadensis</i>)	C	Boreal forests and tundra
Bobcat (<i>Felis rufus</i>)	C	Broken forests
Pinnipedia		
Northern fur seal (<i>Callorhinus ursinus</i>)	C	Nearshore marine
Harp seal (<i>Phoca groenlandica</i>)	C	Arctic marine
Hooded seal (<i>Cystophora cristata</i>)	C	Pelagic marine

^aO = omnivore, H = herbivore, C = carnivore.

Prepared in consultation with J. Eisenberg.

mammals are extinct, there is no fossil evidence that any of the very small (c.10 g) mammals are extinct (Harris and Eisenberg 1988). This same pattern still pertains inasmuch as the large mammals have been most dramatically impacted by development. Since Florida's discovery, the bison (*Bison bison*), monk seal (*Monachus monachus*), and red wolf (*Canis rufus*) have been extirpated. The manatee (*Trichechus manatus*), black bear (*Ursus americanus*), Florida panther (*Felis concolor coryi*), and Key deer (*Odocoileus virginiana clavium*) are presently all listed as either threatened or endangered species. With the exception of legal bear hunting in two designated areas, the number one known source of mortality for all of these species derives from vehicular collision. With the exception of mainland white-tailed deer and raccoon, all seven of the native large mammal species in Florida are either extinct or threatened, and by mortality associated with their movement throughout the landscape is a primary cause.

Based on current knowledge, the direct consequences of habitat fragmentation on biodiversity may be assigned to one of the following four categories:

1. *Loss of large, wide-ranging species* (γ species), especially top carnivores or otherwise threatening forms (e.g., bears). Cursorial forms, which are vulnerable to automobile collisions, and aquatic migratory forms (e.g., fish, manatees), which are vulnerable to obstacles to migration, are particularly sensitive.
2. *Loss of area-sensitive or interior species* (α species) that only reproduce in the interior of large tracts of wetland and are therefore vulnerable to reduction in size of the individual component wetlands as well as reduction in total wetland acreage.
3. *Loss of genetic integrity from within species or populations* that inhabit areas too small for a viable population of individuals. This is especially important for large, wide-ranging carnivores or raptors that are territorial and require areas proportional to population number (i.e., are not amenable to population packing).
4. *Increase in abundance of habitat generalists characteristic of disturbed environments* (β species). Often these species serve as competitors (e.g., starlings), predators (e.g., crows and raccoons), or parasites (e.g., brown-headed cowbirds) on native species and accelerate their demise.

The ultimate result of these four classes of impacts is that each region loses its unique and distinguishing biological characteristics and acquires the generalist

species that are already common throughout the human-dominated landscape. Therefore, activities that may increase the number of species and biological diversity of individual component subsystems may in fact cause the demise of some species and homogenize regional differences, thereby greatly reducing the biodiversity of the compound or regional system.

Food Chain Support

While alteration and loss of habitat pose serious threats to wetland fauna, alteration of food chain support may be equally important. Yet, it is impossible to use analyses based solely on biomass or available energy or simple trophic-dynamic models to predict impacts unless we know what does and does not constitute food. For example, the muskrat, which is perhaps the most studied wetland vertebrate in North America, is commonly thought of as an herbivorous habitat generalist. Yet we know little of the conditions under which it can or would prefer to exist as a rhizovore (roots, corms, and tubers), a granivore (seeds), a frugivore (nuts and fruits), a browser (shoots, twigs, and cambium of woody plants), an omnivore, or even a cannibalistic carnivore.

The literature on ecology of terrestrial vertebrates is heavily biased toward the primary producer–primary consumer–carnivore energy pathways, while the role of detritus and the detritivore–omnivore–carnivore food chains are much less well known. Macroinvertebrate detritivore food chains such as those associated with crayfish are probably more important than most vertebrate ecologists acknowledge (e.g., Penn 1950). Aside from the autochthonous detritus produced annually within wetlands themselves, a variable but important amount of organic matter produced elsewhere is generally washed into and perhaps through many wetland systems. In southern wetland systems, such as the Mississippi River basin, these inputs probably exceed on-site production many times over.

As a generality, food-habit specificity of terrestrial vertebrates tends to be inverse to the size and trophic level of the consumer. Specialists tend to be primary consumers with specialization reduced at the higher trophic levels. With some exceptions (e.g., snail kite, *Rostrhamus sociabilis*), carnivorous terrestrial vertebrates are not specialists. Similarly, one of the adaptive advantages of large body size is that the body can serve as a food storage reserve and thus intake rate can be increasingly variable as a correlate of size. Large carnivores (e.g., alligators, snapping turtles, snakes, raptorial birds, Florida panthers, or red wolves) do not

require daily energy input, as is the case with small carnivores such as shrews. This is especially true of the cold-blooded vertebrates. Thus, coupling the relations of food habits and body size together virtually ensures that large, wide-ranging carnivores are not only unpredictable in terms of what they consume, but also when and where they consume it. As observed by Craighead and Craighead (1956), the consumption of prey species by predators seems not so dependent on prey taxonomy or abundance as on its vulnerability.

In addition to these variables, a constant danger of utilizing a food-habits approach to impact analysis is that organisms that do not have clearly identified food habits are neglected, while those that have specialized and well-known food habits tend to be emphasized.

Because of highly significant interactions among spatially defined habitats, food chain type, the predominant consumer group present, and season, impact analyses must be conducted at the landscape level. Because hydroperiod and water level fluctuation are of primary importance in wetlands, special attention must be given to these variables. Ironically, within many wetlands of the deep South, the detritivore pathway may predominate during the growing season when primary productivity is high, and the primary consumer pathway predominates during winter when primary production is low (e.g., Harris 1978). This pattern can be explained as follows:

1. Mammal herbivores are largely driven from a site by rising water levels in spring and early summer (only one, or perhaps two, species of mammal such as muskrat, nutria, round-tailed water rat, or beaver remain).
2. Bird abundance declines as overwintering and migrant species emigrate to northern breeding grounds. Resident birds shift their diet to emergent lifestages of principally detritivorous benthic invertebrates that fed on detritus derived from the previous year's production. Detritus therefore serves to store energy and introduces a seasonal time lag into the production-consumption process.
3. Cold-blooded, detritivorous macroinvertebrates, such as the crayfish, and cold-blooded, carnivorous fish, amphibians, and reptiles increase their metabolic and ecological activities and their abundance in response to warming temperatures. The diversity and abundance of amphibians and reptiles exceeds that of birds and mammals at this season.
4. Macroinvertebrates, shellfish, finfish, and amphibians follow the shallow, migratory edge of

flood water into generally terrestrial areas for reproductive purposes. Most of these organisms are either detritivorous or carnivorous.

5. Primary production that occurs during spring and early summer is physically unavailable to land-based herbivores because of its spatial location vis-à-vis the flood water.
6. As water levels recede, the site is reinvaded by herbivorous mammals. Seeds and fruits rapidly become available for granivorous and frugivorous mammals and for returning migrant birds, most of which were insectivorous during the breeding season.
7. As temperatures decline in fall and winter, the metabolic and activity levels of cold-blooded fish, amphibians, and reptiles also decline. This occurs simultaneously with reinvansion of the wetland by overwintering birds and mammals that are predominantly direct consumers of primary production. In southern Florida, reproduction of wading birds such as wood storks (*Mycteria americana*) and roseate spoonbills (*Ajaia ajaja*), raptors such as the bald eagles (*Haliaeetus leucocephalus*) and osprey (*Pandion haliaetus*), and even the white-tailed deer (*Odocoileus virginianus*) (Richter and Labisky 1985) seems to be synchronized with the winter low water levels.

Only analyses that consider the habitat and wildlife content of the component wetland against the temporal and spatial context within which the wetland occurs will be fruitful. Perturbations to the wetland itself will have direct and measurable effects on the vertebrates that live within it, while low-intensity actions that occur throughout the landscape will have only indirect impacts on this group. Conversely, organisms that occur high in the trophic hierarchy are likely to range over a wide area and depend upon the asynchronous functioning of component subsystems within the compound landscape. Low-intensity landscape manipulations that alter the ratio and configuration of component subsystems will have direct impacts on these species, while the manipulation, creation, or elimination of a component wetland might have only indirect effects. Therefore, whether the impacts resulting from any given wetland perturbation will have direct or indirect effects depends largely upon the trophic level and range requirements of the organism involved (Table 2).

Assessing Accumulation of Impacts

When approaching cumulative impact assessment,

Table 2. Interaction of environmental perturbation with vertebrate species, illustrating that a direct effect on one species might constitute an indirect effect on a different species type.

Species type	Impact type	
	A	B
Stenotopic or habitat specialists (α species)	Direct	Indirect
Eurytopic or habitat generalists (β species)	Indirect	Direct

A = sharp, focused, locally intense, and within a wetland; B = attenuated, diffuse, regionally distributed among wetlands.

it is important to distinguish between the assessment of consequences after the fact and the need to predict them beforehand. The knowledge and expertise to conduct accurate post hoc assessments of cumulative impacts resulting from major projects in the past exists (cf., Brinson 1988),—and increasingly common historical accounts of long-term ecological change (e.g., Cronin 1983, Chase 1986, Crosby 1986) could be profitably dissected and analyzed by ecologists. Multiple independent impact analyses of several different completed projects might be performed to determine when such actions constitute a stress and when they are a benefit. The result will no doubt depend upon the intensity of the action as well as the time frame and scale of the landscape unit analyzed (Odum and others 1979, Barrett and Rosenberg 1981, Rykiel 1985).

The following examples are chosen to represent the fundamentally different ways that wetland vertebrate communities accumulate and/or manifest impacts of different sorts.

Simple Additive Responses

Simple additive responses are likely to result when actions of similar type, such as furbearer or waterfowl harvest, are repeated. These impacts affect the biotic diversity directly with no intervening variables between the act (hunting or trapping) and its effect (population reduction). The responses may accumulate in time (harvesting resident species) or in space (when each province and state along the migration route takes its allocated quota from a population of migratory waterfowl).

Effects may be additive within a season but not necessarily between seasons or over longer periods of time. A large literature attests that all biological populations have some capacity to compensate for variable mortality rates. It is enough to say that the long-term population response will not be a simple linear function of harvesting intensity, and the nature of the re-

sponse curve is fundamentally different for semelparous and iteroparous species.

Additive Responses of Dissimilar Actions

The additive responses of dissimilar actions, such as continuing to trap furbearers after a highway has been expanded to carry heavier traffic loads through a marsh, are not easy to predict. It is possible to add recorded road kill to recorded fur harvest, with the sum representing the true number of animals removed, but it is not possible to add last year's fur catch from a marsh without a road to last year's road kill from a similar marsh not subject to trapping and accurately estimate last year's mortality in a marsh that has been trapped and has a road. Errington (1963) and others have spent decades attempting to understand the intercompensatory nature of responses to such actions, yet it seems beyond our ability to predict the cumulative impacts of three or more simultaneous actions. North American waterfowl populations are impacted by reduction of breeding range wetlands, harvesting during the course of migration, ingestion of lead shot and other toxicants, and loss and disturbance of overwintering habitat in the South. Despite the evidence that impacts are accumulating (Figure 2), it is impossible to pinpoint single-factor effects.

Multiplicative Effects of Similar Actions

The multiplicative effects of similar actions, such as the serial addition of dams to a river, are perhaps most well known. If each of five dams were to exclude 50% and allow 50% of a migrating fish population to pass, the reduction would not be 250%, but rather $1 - 0.5^5 = 97\%$. Three percent would presumably survive the migration around all five dams. A similar geometric response curve would result whenever a constant proportion of the resource is removed or whenever a constant fractional response occurs.

Nonmonotonic or Threshold Responses

Nonmonotonic or threshold responses may occur under certain circumstances. For example, constructing a road through a large tract of bottomland hardwood forest might substantially increase local breeding bird species diversity (see Perkins 1973 for supporting data). If it were a single road, initially only a few forest interior species would be negatively impacted, whereas as many as 20 edge species might typically colonize the disturbed environment along the road. An alien species might parasitize all the nests of a native warbler within a distance of 30 m on each side of the road. This means that roughly 10 ha (25 acres) of native warbler habitat are lost per 1.6 km (1 mile) of road

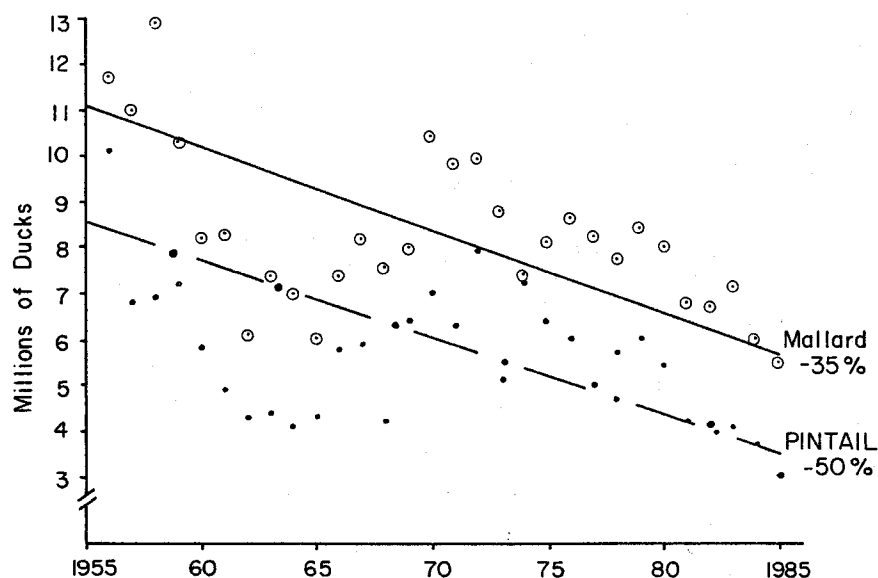


Figure 2. Decline in the number of waterfowl in North America, 1955–1985. This is one manifestation of cumulative impacts that derive from a combination of factors spanning thousands of kilometers of space and decades of time. Slopes derived by least-squares analysis are $-49.6\times$ for mallard and $-93.7\times$ for pintail; percent declines calculated from data are 35% for mallard and 50% for pintail. Data from US Fish and Wildlife Service and Canadian Wildlife Service 1985.

through the bottomland forest. As additional roads are added, the percentage of habitat parasitized increases linearly to 100% when a density of 4 km/259 ha (2.5 miles per square mile) of habitat is reached (Figure 3). Any further increase in road density will have little additional impact on warbler-nest parasitism, since all habitat has already been parasitized. Temple (1986) and Wilcove (1985), among others, have documented the negative consequences of edge-induced predators, competitors, and nest parasites to extend as far as 500 m from the forest edge.

Although similar threshold responses can be described for other perturbations, this form of response curve is probably not sufficiently common to conclude that there are definable or discrete critical levels to which a system can be perturbed before the negative consequences become unacceptable. An agency that hinges permitting or enforcement authority on "critical threshold levels" of acceptable impact will be frustrated by the present inadequacy of data as well as the constant changes in the information base.

Indirect Impacts

Indirect impacts occur when a perturbation directly impacts one wetland component and then proceeds to impact other temporal or spatial components or processes by chain reaction. Indirect effects can also result from perturbations that occur outside the wetland but get carried into the wetland by diverse pathways. The impacts may not be manifest until a later time (time-lag effects) or in a different place (space-lag effects).

Long Time-Lag Effects

Long time-lag effects can be illustrated by noting

that temperature-dependent sex determination (TSD) is a common phenomenon in reptiles and amphibians (e.g., Bull 1980, Morreale and others 1982). Since the gender of individuals is determined by only a few degrees difference in incubation temperature, the sex of entire cohorts of offspring depends on nest and site conditions. If the species involved does not reach sexual maturity for many years (large turtles or alligators), all individuals entering the breeding population in 1988 might be impacted by incubation temperatures of the 1970s. It would be shocking to discover that all breeding adults returning to a site 20 years after birth (e.g., marine turtles) were of the same gender. Under natural circumstances the population sex ratio would be counterbalanced by numerous intersite, interyear, and intervening variables. But such opportunities are rapidly diminishing because of fragmented and isolated habitats and greatly reduced populations. Increasing proportions of a population derive from the production of a single site or a single year.

A second example involves the recent extinction of the dusky seaside sparrow (*Ammospiza maritima nigrescens*). Originally classified as a distinct species, the dusky was merged with other seaside sparrows as a single species in 1973 (Kale 1977). With its natural habitat limited between the 3- and 5-m contour lines in a few hundred square kilometers of Brevard County, Florida, the dusky's restricted distribution was unique among North American birds. The activities that endangered and ultimately exterminated the dusky began with DDT spraying for mosquito control in the 1940s. During the 1950s marsh impoundment was implemented as a mosquito-control and waterfowl-

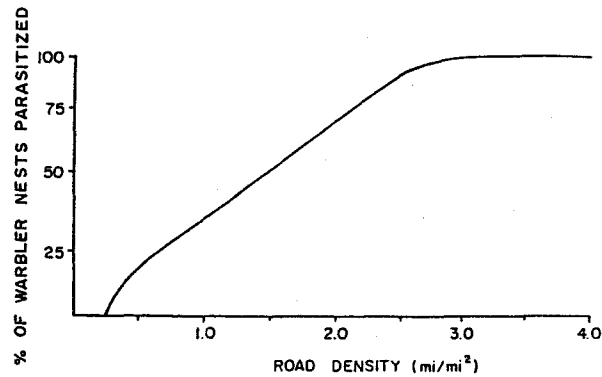


Figure 3. Response curve showing percent of native warbler nests parasitized as roads are constructed through a bottom-land hardwood forest. Threshold response curves characterize a small class of environmental impacts, but this form of response does not seem widespread.

management technique. Impoundment during the breeding season seriously limited nesting and feeding, and the impounded areas of Merritt Island were the first to lose the dusky. Construction of the Beeline Expressway (SR528) through one of the last remaining patches of primary habitat in the early 1970s further fragmented and jeopardized the dwindling population and restricted management of the remaining habitat. Drainage for domestic pasture and the development of residential subdivisions further fragmented and reduced habitat in the St. Johns River marshes. With such a high concentration of roads, subdivisions, and related human facilities, the use of prescribed fire was greatly limited. In the absence of prescribed fire, plant succession occurred, the fuel load of the habitat increased, and fires that were ignited on surrounding rangelands blew into the refuge and caused serious damage (and the loss of human lives as well as wildlife) in the mid-1970s (Kale 1977, Baker 1978, USFWS 1979a).

The final, and fatal, mistake was not due to mismanagement, but rather to the inadequacy of survey methodology. Throughout North America and much of the world, birds are censused by recording the abundance of territorial singing males. It is generally assumed that each territorial male is accompanied by a breeding female. After documenting a decline in relative numbers through the 1960s, the first comprehensive census of duskies was conducted in 1968 (Sharp 1970). The population decline was closely monitored through the 1970s, and when only five territorial males were recorded in 1980 the decision was made to remove the birds from the wild and begin a captive breeding program. Unfortunately, the decision was too late; no female birds remained, and the only dusky seaside sparrows left in the world were the five captive

males. The consequences of manifold activities had accumulated throughout the previous 30 years but had not been adequately monitored. The cumulative effect proved lethal; the last true dusky seaside sparrow died in captivity June 17, 1987.

Similar examples occur when the age structure of a population is significantly but unknowingly skewed and a false security about population numbers is followed by a later catastrophic decline (e.g., the Puerto Rican parrot). These examples illustrate the importance of using more sensitive population parameters (e.g., effective population size) that take into account age and sex ratios, dominance, dispersal, and related characteristics.

Indirect Effects Concentrated in a Component Wetland

Indirect effects may be concentrated in a component wetland imbedded within the compound landscape where the actual environmental perturbation occurs. Three examples of increasing complexity are given. Kesterson Reservoir consists of a series of irrigation drainwater/evaporation ponds totaling about 500 ha in the much larger Grasslands area of Merced County, California, USA, on the west side of the San Joaquin Valley (Ohlendorf 1985, Tanji and others 1986, Ohlendorf and others 1987). As part of the US Bureau of Reclamation's Central Valley Project, Kesterson Reservoir was completed and began to receive surface irrigation tailwater and serve as the terminus for excess runoff in 1972. Although originally planned as a flow-regulation area, the reservoir and adjacent 1900-ha Kesterson National Wildlife Refuge now served as the terminus of the San Luis Drain. Historically, the Grasslands area comprised the largest tract of waterfowl habitat in the San Joaquin Valley and was used by perhaps 65% of all migrating birds in the Pacific Flyway. The average annual harvest of over 300,000 ducks (1966–1980) ranked Merced County as the first or second most important waterfowl hunting county in the US (Ohlendorf and others 1987, Presser and Ohlendorf 1988).

As early as the 1940s, US Department of Agriculture soil scientists had identified high selenium (Se) levels in western San Joaquin soils, and by 1960 a water resources report warned that drainage from the Panoche Fan area was "unusable for beneficial purposes" (Schultz 1985). The excess drainage from irrigated lands contains Se concentrations 400 times the safe drinking water standard (10 ppb) established by the US Environmental Protection Agency (Tanji and others 1986). By 1981, subsurface water from the tile-drained agricultural lands, undiluted by surface water, was being emptied into the Kesterson. By 1983, the

US Fish and Wildlife Service detected toxic poisoning of wildlife.

Bioconcentration of selenium averages less than a 1000-fold increase for algae and plants in the reservoir, but more than 1000-fold for aquatic invertebrates. Mosquito fish (*Gambusia affinis*) from the reservoirs contain selenium concentrations 100 times greater than from nearby unirrigated areas, and high rates of reproductive failure and deformities have developed in American coots (*Fulica americana*), black-necked stilts (*Himantopus mexicanus*), and other species that nest in the reservoir ponds (Ohlendorf 1986, Ohlendorf and others 1986a,b, 1987). Hunters have now been warned not to consume waterfowl that overwinter in the area because they contain Se concentrations of 3.0–9.5 ppm, perhaps 10 times the normal background level. Waterfowl and wading bird mortality became so critical that the Secretary of Interior announced closure of the Kesterson Refuge on March 15, 1985, because of violation of the 1918 International Migratory Bird Treaty (Tanji and others 1986).

The fact that three different ecosystem components are mobile and transient but are artificially concentrated in a single wetland site explains this accumulation of impacts. Irrigation water comes from the Sacramento and San Joaquin rivers and from deep well sources. It is suffused over an agricultural landscape, and then disposed of in the Kesterson ponds. Selenium is leached from the agricultural soils by the percolating irrigation waters. Because the Kesterson serves as a collector and a concentrator, Se becomes readily available there; it is further bioconcentrated by plants and invertebrate consumers as it enters the waterfowl food chain.

Most North American waterfowl production derives from an extensive northern breeding ground, is concentrated along migration corridors, and finally overwinters, in this case, at a man-made and ostensibly human-enhanced wetland site. The loss of 95% of California's historic wetland (Gilmer and others 1982) greatly amplifies the importance of the few remaining sites, such as the Kesterson. Because waterfowl are long lived relative to the organisms they consume, they serve as bioconcentrators of micronutrients from the tissues of thousands of different seeds, plants, and benthic invertebrates. As a consequence of all three anthropogenic concentrations (water, selenium, and waterfowl), the impact of a spatially removed and perhaps low-intensity activity accumulates in the vertebrates in and around the Kesterson.

Actions Occurring within a Component Subsystem

Actions that occur within a component subsystem

may accumulate and be manifest in high trophic level organisms that depend upon the compound landscape system. Organochlorine residues derive from manufactured chemicals used throughout the world, principally as agricultural pesticides. These residues can be concentrated by simple water flow processes such as described above for the inert element selenium. But the phenomenon of biomagnification in vertebrate wildlife populations is an additive process that delays, accumulates, and then amplifies the impacts of the toxic substance. Because many of the hydrocarbon compounds are fat soluble, they can be consumed, metabolized, and stored in fatty tissues of animals, especially warm-blooded vertebrates. It is commonly held that this biomagnification process may result in a 10-fold greater concentration of pesticide in each successive trophic level.

Over 150 species of North American breeding birds migrate to the lower latitudes annually, and over 90% of the bird species of eastern North America are recorded to use southeastern wetlands for one reason or another (Sprunt 1967). Among the raptors, there exists a close correlation between the magnitude and importance of migration and the nature of their primary food source. Fish-eating, bird-eating, and especially insect-eating species are highly migratory and dependent upon southern habitats during the winter months. Small-bodied birds are more heavily dependent on migration than are large-bodied birds.

The American kestrel (*Falco sparverius*) is a small, predominantly insectivorous raptor that breeds throughout eastern North America but overwinters in the southeastern US. Organochlorine toxicity in birds is most dramatically revealed during the reproductive process (or at other times of severe physiological stress) when fat reserves are mobilized and the toxin reenters the systemic system. By affecting calcium metabolism, it becomes manifest as eggshell thinning, whether the adult females acquire the pesticides on the breeding or overwintering grounds. (Eggshell thinning is caused by food-chain accumulation of dichloro-diphenyl-dichloroethylene, DDE, which is formed from DDT by organisms lower in the food chain. DDE is both more persistent and more biologically active than the chlorinated organic pesticide DDT.) Although a 20% thinning of the eggshells is sufficient to cause serious reproductive failures among most bird species, there is perhaps a 10-fold difference in DDE levels necessary to cause different taxa of birds to reach this threshold level (Figure 4). After cessation of the use of organochlorine pesticides in New York State, American Kestrels continued to exhibit high tissue concentrations of DDE residues:

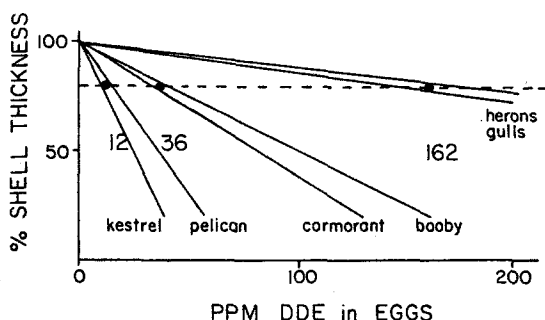


Figure 4. Relationship between the amount of dichloro-diphenyl-dichloroethylene (DDE) in eggs and shell thickness, for selected bird species. Variable concentrations of toxin may be tolerated before a specified level of impact, such as 20% loss of eggshell thickness, occurs. A 20% loss is sufficient to cause serious reproductive failures in most bird species. Modified from Keith and Gruchy 1970.

The sources of the high DDE residues in eggs of local wild kestrels and the degree of shell-thinning cannot be fully explained by the low residue levels in prey items on the breeding grounds. The fact that breeding kestrels, feeding on a relatively uncontaminated food chain, can produce highly contaminated and thin-shelled eggs points out the importance of the quality of the wintering grounds to this and other migratory species. The disastrous role played by the far-removed, but inordinately contaminated, winter prey once again dramatically points out the global nature of the biocide problem (Lincer and Sherburne 1974).

As in other cases, the effect of the environmental toxicant was delayed in time, magnified in the trophic pyramid, and offset in space. Effects that appear as direct and immediate within a component subsystem may well accumulate as indirect time- and space-lagged impacts in the larger compound system. It can reasonably be predicted that additional chain reaction effects will reverberate downward to component subsystems in response to population reductions and/or elimination of landscape integrators (top carnivores). Processes that are diffuse or only weakly operative among numerous landscape components may well appear as, or engender, more concentrated and tangible effects within a component subsystem.

Diffuse Processes in Compound Landscape

Diffuse processes in the compound landscape may have concentrated effects within component subsystems. Throughout the 19th century perhaps 2.5 million wading birds (principally Ciconiiformes) inhabited the Everglades area at the southern end of the Florida peninsula (Robertson and Kushlan 1974). A key characteristic of these birds is that most return nightly to colonial roosts and also concentrate their nesting and reproduction in such colonies. One authoritative reviewer of 19th century conditions stated:

... some fifty nesting rookeries were visited, some of them containing upwards of one hundred thousand nests. ... The island, upwards of eight acres in extent, was nearly all occupied by the rookery. A count of all the nests in a small section showed that there were many more than one hundred thousand nests of birds of all kinds on the island (Ward 1914).

As late as 1934, one mixed-species nesting colony was estimated to contain as many as 250,000 pairs (Allen 1958, in Ogden and others 1987). Roosting and nesting generally occur in trees, with colonies ideally located on isolated islands or sites that provide protection from predators. Diurnally, the birds disperse over the shallow marshes and Florida Bay to forage on aquatic animals (Ogden 1978, Kushlan and others 1985).

Using recent wading bird relative abundance data (Kushlan and White 1977), a weighted average food consumption rate of 100 g/day (Schramm and others 1987), and a mineral ash food composition of 2.2% (Rottiers and Tucker 1981), it follows that the average wading bird withdraws 0.8 kg of minerals per year from the aquatic environment:

$$(100 \text{ g food/d}) \times (365 \text{ d/yr}) \times (0.022 \text{ g ash/g food}) \\ \times (10^3 \text{ g/kg}) = 0.8 \text{ kg ash/bird/yr}$$

A population of 2.0 million wading birds would withdraw 1.6 million kg of mineral ash from the aquatic environment per year. Assuming that 50% of the excrement (i.e., half of daily intake) and 50% of all bird mortality occurred within the colony site, then 25% of the total mineral ash withdrawal would be translocated from the aquatic environment to the colony sites annually. By conservative estimates, a population of 2.0 million wading birds would translocate 400 metric tons (400,000 kg) of mineral ash per year. In the 100 years since 1885, this translocation would have amounted to 40,000 metric tons of mineral ash.

Whereas numerous studies (Gillham 1956, Leentvaar 1967, Dobrowski 1973, Smith 1979) have addressed the consequences of avian guano translocation, only a few have been directed at Florida environments (Odum and Heald 1972, Onuf and others 1977, Watson 1986). Nonetheless, it has been demonstrated that insect herbivory in bird-fertilized red mangroves (*Rhizophora mangle*) increased fourfold over that of unfertilized stands and that the difference disappeared when the birds migrated from the area (Onuf and others 1977). Watson (1986) demonstrated that taller and sturdier black mangroves (*Avicennia germinans*) were preferentially utilized as colony sites by brown pelicans (*Pelicanus occidentalis*) and that these trees were on average 1.7 m taller and grew significantly more in circumference per season than did the mangroves not

utilized by pelicans. Thus, while notable accumulations of guano only occur in dry, cold, or sheltered environments, the effects of guano translocation between different components of wetland landscapes may be no less significant to ecosystem function. This is particularly true in nutrient-poor areas such as the Everglades.

If the magnitude of the process involved only a few kilograms, the impacts might be negligible, but it seems highly unlikely that a process involving the redistribution of 400 metric tons of nutrient per year or 40,000 tons during the last century could be trivial. Even more dramatic (but not wetland) examples, such as the spatial translocation of nutrients by hundreds of millions of passenger pigeons, must surely be relevant to issues such as forest patch dynamics and the long-term reduction in forest productivity that has been recorded for several regions (e.g., Sheffield and others 1985).

Natural area reserves, such as Everglades National Park, rarely constitute more than a token vignette of the original functioning landscape system. In this case, Everglades Park constitutes only 6% of the original Everglades system. Wading birds such as the wood stork (*Mycteria americana*) forage throughout the landscape as far as 80 km from the nest colony and are dependent upon the frequency, amplitude, and seasonal timing of water levels that concentrate the fish prey in drying pools of surface water (Kushlan 1987, Ogden and others 1987). Virtually no degree of management of the habitat within the park can compensate for poor management of the landscape outside the park (Kushlan 1979, Harris 1984, Schonewald-Cox and Bayless 1986). The one to three million wading birds that inhabited south Florida 100 years ago have been reduced to perhaps 16,000 breeding birds (1%) by 1987 (Figure 5) (M. Collopy, personal communication). This drastic reduction reflects the cumulative impact of plume hunting at the turn of the century, habitat loss and degradation in this century, and, most importantly, water management decisions that are still debated today (Robertson and Kushlan 1974, Kushlan 1987, Ogden and others 1987). Park authorization in 1934 and dedication of Everglades National Park in 1947 have not abated the decline, because the biota within the park are critically linked to water management in the landscape surrounding the park.

In the words of one authority: "... while ecosystem management in reserves can provide habitats for colonial water birds, this, alone may not protect populations. Such reserves maintain only a residuum of the support system and population, usually for only part of the year. A regional strategy is imperative" (Kushlan 1983).

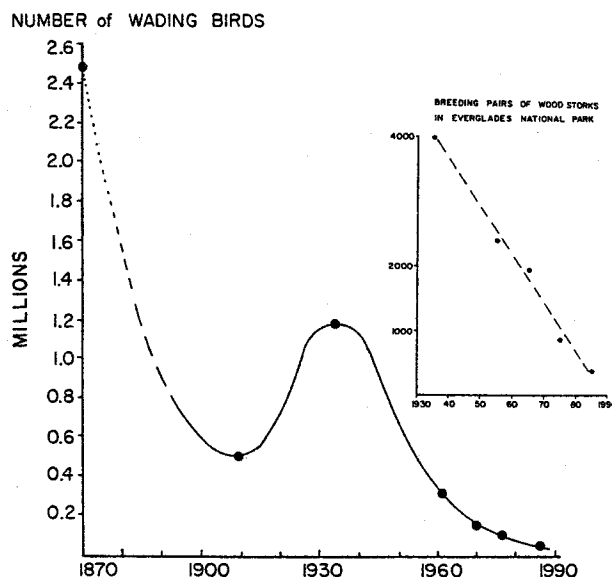


Figure 5. Long-term decrease in the wading bird populations of south Florida and in the wood stork population (insert) within Everglades National Park since its creation in 1947. Data from Robertson and Kushlan 1974, Kushlan and White 1977, Ogden and others 1987.

Food Chain Support and Loss of Habitat

Food chain support may interact with loss of nesting habitat either to cause or at least contribute to the demise of species and groups of species. The swallow-tailed kite (*Elanoides forficatus*) is one of many species of North American neotropical migrant birds whose population levels show long-term decline (Figure 6). Like several other species on the decline (see Briggs and Criswell 1979, Robbins 1979, 1980, Robbins and others 1986), the kite is classified as an "area-sensitive" species because its occurrence and reproductive success is dependent on extensive tracts of habitat (Hamel and others 1982), in this case riparian forest interspersed with open wetland foraging areas. Not only is the total acreage of riparian forest declining rapidly (MacDonald and others 1979, Frayer and others 1983, Abernethy and Turner 1987, Harris and Gosselink 1988), but fragmentation into smaller and more isolated tracts (Figure 7) may lead to equal or even more serious indirect effects (e.g., Whitcomb and others 1981, Harris 1984, Harris and Wallace 1984, Wilcove and others 1986). The destruction and fragmentation of riparian forest as well as selective logging of large, emergent trees that serve as preferred nest sites are surely factors in the decline of swallow-tailed kites (Cely 1979).

Like most other kites, the swallow-tailed kite is morphologically and behaviorally adapted to forage as an aerial predator, in this case on wetland macroinverte-

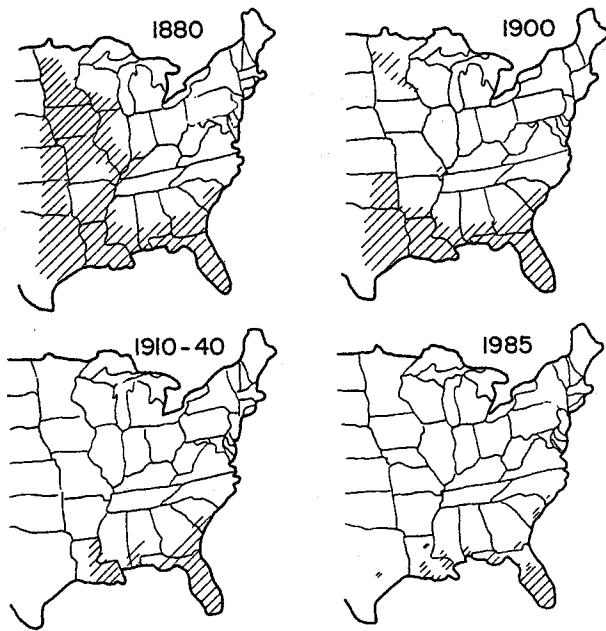


Figure 6. Distribution of swallow-tailed kite in the United States, 1880–1985. The swallow-tailed kite is one of many North American neotropical migrant bird species that have been greatly reduced in number and breeding range during recent decades. The reduction no doubt represents the cumulative effect of several land use and wetland management factors. Modified from Cely 1979.

brates, such as dragonflies, and cold-blooded vertebrates, such as amphibians and reptiles (e.g., Snyder and Wiley 1976). Concurrent with the reduction of riparian forest nesting habitat, large proportions of open wetland that produced the food base and served as kite foraging areas were also lost. The effects of stream, river, and wetland pollution have probably reduced production of macroinvertebrates such as dragonflies (Franz 1982) to the detriment of swallow-tailed kites. Perhaps pesticide residues are also implicated.

This example illustrates not only the interrelation of habitat and food chain support necessary to maintain area-sensitive or wide-ranging species, but also how dramatic the portrayal of cumulative impacts can be in the face of almost total ignorance of causality. While experimental research directed toward isolating and verifying causal, proximal, single-factor mechanisms is no doubt called for, the level of ongoing research is so low that it does not even document the bird's declining status (this species is not listed in the breeding bird status report). Thus, while the cumulative impact seems clear, and the ultimate causes (wetland fragmentation and area loss and prey base reduction) seem clear, establishment of specific causal mechanisms seems unlikely in this century.

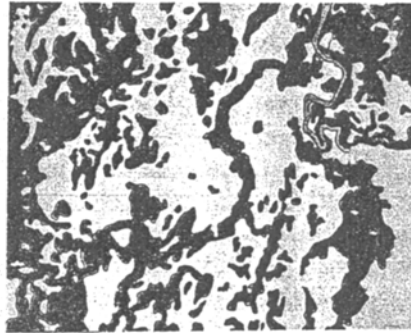
Interactions of Land Use, Habitat Fragmentation, Alien Species, and Native Vertebrates

Interactions of land use, habitat fragmentation, alien species, and native vertebrates frequently accumulate to levels that are catastrophic for native species. Although intensity of competition, parasitism, and predation have frequently been analyzed at the population and community levels, only rarely have the concepts been applied at the level of the ecosystem (Esch and others 1975). Yet, Odum (1985) proposes that increased levels of parasitism and species loss might be anticipated as an ecosystem response to stress.

Early explorers of the Great Plains described a flocking bird (*Molothrus ater*) in close association with American bison (*Bison bison*). The advantages of remaining close to the nomadic bison apparently provided sufficient selective advantage to cause the buffalo bird to become North America's only obligate nest parasite (Friedmann 1929). Simultaneous with the near extirpation of the bison, cattle were introduced, and the greatly opened and fragmented forest of the eastern states provided the bird with a substitute large ungulate in a greatly modified environment (the bird's name was conveniently changed to brown-headed cowbird). Brittingham and Temple (1983) have charted the frequency of occurrence of cowbirds on eastern bird counts from 0% late in the last century to 100% by the 1980s. Because of the cowbird's evolution on the Great Plains and prairies of the Midwest, the females are largely restricted to open lands associated with fields, homesteads, powerlines, and forest clearings. Whereas nest parasitism by female cowbirds is essentially nonexistent in the interior of large forest stands, nearly all open nests near clearings or forest edges may be parasitized (Brittingham and Temple 1983). Effects of cowbird parasitism on species such as Kirtland's warbler (*Dendroica kirtlandii*) are so severe that, in addition to habitat management, an active cowbird-trapping program has been implemented and the specific details of a captive-breeding program for Kirtland's warbler are being explored.

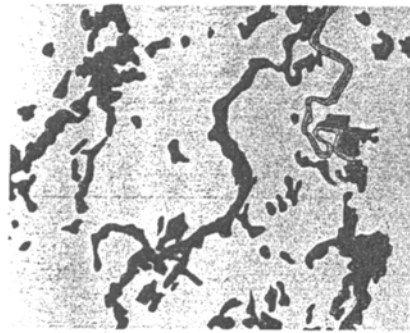
Throughout the 19th century Bachman's warbler (*Vermivora bachmani*) nested in gaps in the pristine forest of the Southeastern Coastal Plain (Hamel 1986). Because the wetter of these forested openings were commonly invaded and dominated by canebrake (*Arundinaria* spp.), they are frequently referred to as canebrakes. Cane becomes very dense after several years without burning, and because it is intolerant of its own shade, its vigor, reproduction, and perpetuation are dependent upon the natural occurrence of fire (Shepherd and others 1951, Hughes 1966). Cane is also vulnerable to heavy, sustained grazing, and re-

HABITAT FRAGMENTATION IN



1941

JACKSON COUNTY, AR



1967



1962

NORTH CAROLINA'S POCOSINS



1979

Figure 7. Examples of habitat fragmentation over time. Fragmentation of formerly expansive tracts of wetland habitat into isolated patches causes change in many aspects of habitat structure and ecological function. Upper panel: Jackson County, Arkansas. From US Fish and Wildlife Service, n.d. Lower panel: Pocosins, North Carolina. Modified from Richardson 1981.

quires periodic respite from intense grazing in order to maintain vigor (Hughes and others 1960). Thus, for somewhat different reasons, both cane and Bachman's warbler occurred as gap-phase species on wet sites in the pre-Columbian coastal plain.

Bachman's warbler has not been observed in 10 years and is now presumed extinct (P. Hamel, personal communication). The combination of relentless and/or intense grazing since the introduction of cattle, overly protective fire exclusion programs throughout the first half of this century, and active forestation programs seems to have greatly reduced the occurrence of canebrakes and their suitability as habitat for species such as Bachman's warbler. The combination of a generally open landscape with ubiquitous cattle facilitated range expansion of the parasitic brown-headed cow-

bird and increased densities of other potential nest predators and competitors such that Bachman's warbler was apparently forced to extinction.

No single factor, or combination of factors, is demonstrably responsible for this extinction. Yet the combination of direct and indirect factors definitely accumulated to levels beyond the ability either of scientists to predict extinction or of conservationists to prevent it.

Loss of genetic integrity may result from accumulated impacts that affect population distribution and demography. Concurrent with increased human density and land use intensity, both of the large mammal carnivores native to the southeastern United States—the red wolf and the Florida panther—became increasingly limited to isolated wetlands and seem to

have accumulated severe demographic and genetic effects as a consequence. The following have been suggested as probable causes for decline: (1) loss of habitat and increasing fragmentation and isolation of remaining wetland areas, (2) amplified man-induced mortality beginning with active predator control and ultimately involving accidental death from hunters and automobile traffic, (3) depreciated prey base within the wetlands and decreased access to prey outside the wetland, (4) invasion of the habitat by alien species, and (5) amplified disease and parasite impacts.

The red wolf (*Canis rufus*) formerly inhabited the Mississippi River Valley and the Gulf coastal plain westward to east Texas and east through Florida and Georgia. Consistent with Gloger's rule, the red wolf is characterized by dark pelage, and totally black specimens were not uncommon. Because the isolated swamps and marshes in the Mississippi Valley and along the Gulf coast constituted the last wilderness areas of the South, remnant populations of red wolves remained in these wetlands until the 1960s (Nowak 1972, Lowery 1974). Under conditions of widespread distribution and viable population levels, wolf breeding and demography were governed by strong behavioral mechanisms. The pack is the social unit, social dominance governs breeding, females mate for life, and population level relative to available food resources influences survivorship and productivity. Related species or subspecies maintain genetic distinctiveness by a combination of geographical and ecological separation and species-specific behavioral patterns. When excessive levels of hunting, trapping, and other human-induced mortality impinge, populations are reduced and fragmented, and the social system is seriously disrupted or may collapse altogether.

With increased land clearing, agricultural development, and a general "opening-up" of the Eastern forest landscape, the coyote (*Canis latrans*) expanded its range eastward and gradually increased in abundance throughout the southeastern US. Because it is more of a habitat and food-habits generalist (Gipson 1974), the same forces that militated against the red wolf served to benefit the smaller, more omnivorous coyote. The combination of reduced and disrupted wolf populations that were behaviorally and demographically stressed, and increasingly abundant coyotes that were no longer geographically or ecologically separated from the wolf, led to interbreeding between wolves and coyotes. The consequent genetic "swamping" of the wolf led to a virtual elimination of the native red wolf genome (Shaw and Jordan 1977, USFWS 1979b, Truett and Lay 1984).

Both hookworms and mosquito-borne heartworms

are more prevalent and pathogenic in warm moist environments with wet soil than they are in more arid upland environments (D. Forrester, University of Florida Veterinary College, personal communication). Thus, as the red wolf became more restricted to wetlands, the incidence and pathogenicity of these parasites may well have increased. The introduction of free-ranging domestic dogs and the invasion of the landscape by coyotes provided a much higher canid population for heartworms to parasitize, and it is possible that this combination of factors accumulated to critical levels. The few remaining red wolves thought to represent the original genetic stock were removed from the wild beginning in 1973 and were used to initiate a captive breeding and reintroduction program (USFWS 1979b).

The environmental circumstances described for the red wolf apply equally to the Florida panther (*Felis concolor coryi*). In this case the release of western cougars into Florida panther range allowed some interbreeding and perhaps some loss of genetic integrity, but this is not the principal issue. The last remnant Florida panther population became isolated in the Everglades and Big Cypress areas of extreme south Florida. Because of Florida's rapid population growth throughout the state (4% per year for 100 years) and the long and increasingly narrow form of the peninsula (because of sea-level rise), the south Florida cats have probably been reproductively isolated for a considerable length of time. Distinct genetic maladies, possibly the result of inbreeding, are now being documented. For example, all adult males from which data have been obtained manifest nearly 95% infertile spermatozoa (Roelke 1986, USFWS 1987). The extent to which this malady affects the demography and population dynamics of panthers in the wild is yet unknown. Nonetheless, because animals of the higher trophic levels are rare under the best of circumstances, they seem particularly vulnerable to isolation, demographic variations, and inbreeding. Thus the loss of genetic diversity from within the species of wide-ranging top carnivores may translate directly to loss and/or diminished function (e.g., predation and competition) of those carnivores in the landscape-level system and a subsequent loss of species diversity at the community level.

The home-range size of Florida panthers is very large (adult males, 500 km²), and the males can be lethally territorial. Thus, little ecological compression can occur, and the relation between viable population and viable area may be deterministic. No single refuge of even a single tract of a few million km² will maintain a viable population in perpetuity. Only by maintaining

core populations within large tracts of public land and facilitating movement throughout the intervening landscape matrix will we be able to maintain these important elements of native biotic diversity (MacClintock and others 1977, Harris 1985, Branan 1986).

Conclusion

The above examples of cumulative impacts on vertebrate biotic diversity demonstrate the breadth of the issue. Loss of genetic diversity within species may, in the long run, be as serious as loss of the species themselves. Similarly, loss of diversity at the landscape level may well lead directly to loss of species and genetic diversity from within species. Land-use managers and decision makers, faced with the need to consider maintenance of species diversity among their goals, are in a difficult position. At present, because of the complexity of trophic interactions, we do not have the ability to predict the results of three or more different perturbations, although we can recognize those results retrospectively. Realistically, until much more information and understanding are developed, the best managers and decision makers can do may simply be to be aware of the history of impacts of varied land-use actions and alert to parallels with them in their own activities. At the same time, establishing biotic reserves must be accomplished. However, maintenance of biotic diversity cannot be achieved by simply setting aside reserves and disregarding the landscape-level processes occurring around them. Only by establishing a system of replicate wetland reserves and allowing each to function in an interactive landscape context can the maintenance of wetland biodiversity be assured.

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