Harvest

This volume contains a variety of chapters about the demonstrated and suspected effects of natural and human-related agents on biodiversity. The effects of human-related agents may be indirect (such as habitat or climate change) or inadvertent—perhaps even the result of well-intentioned efforts to preserve biodiversity, such as the isolation of nature preserves or the potential for disturbance caused by ecotourism. Although nonconsumptive use of wild species has increasingly become a focus for exploitation by humans, this chapter explores the direct effects of consumptive exploitation—harvest—on biodiversity.

Humans have long harvested, for commerce and for sport, many kinds of wild species from many different environments. Yet, as some human societies rethink their relations with other animal species (Scheffer 1976), the potential effects of harvest have become an increasingly contentious issue in the late twentieth century.

Much has been written about the effects of harvest, though the distinction between ethical and scientific arguments is frequently blurred (Decker et al. 1991). This chapter deals with some of the principal scientific arguments about the effects of harvest on biodiversity and skirts the ethical ones, if only because science, as a way of learning and improving the reliability of knowledge, might indirectly inform ethics, values, and therefore policies (Clark 1992; H. R. Pulliam, statement by the director, National Biological Service, before the House Appropriations Subcommittee on Interior and Related Agencies, 1995).

Historically, the scientific arguments about the effects of harvest on biodiversity revolved around how harvest affected the abundance or persistence of populations of single species, issues that still dominate the scientific literature and the day-to-day activities of many agencies charged with the management of natural resources. It is widely acknowledged, however, that we have little reliable information about the effects of harvest on wild populations. To improve our knowledge, we need a fundamentally new relation between the science and management of natural resources—namely, adaptive management (Walters 1992; Ludwig et al. 1993; Williams and Johnson 1995; Williams et al. 1996). By definition, biodiversity is exceedingly more complex than the most complex single population, so it follows that the potential effects of harvest on biodiversity must be exceedingly more complex. Because such complex issues cannot be dealt with in their entirety in this chapter, I focus on a few examples across several levels of biological structure from genes to populations and to ecosystems. I show that harvest exploitation *necessarily* alters some aspects of biodiversity. Thus, by extension, even nonconsumptive exploitation that indirectly, yet effectively, "removes" or prevents organisms from normal interactions in populations must also alter biodiversity. At the end of the chapter, I discuss the much more contentious issue about whether such change actually matters, to whom or what it matters, and how we might go about understanding these issues.

Much of the contention about the effects of harvest on individual populations exists, at least in part, because arguments frequently are rife with undefined terms. To help avoid similar problems and to erect a framework for the remainder of this chapter, I briefly define biodiversity and its relation to individual species and to populations (the traditional foci for studies of the effects of harvest exploitation). I then quickly review the concepts of sustainable use and sustainable yield management and how


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harvest affects populations. Within this framework, I discuss the potential effects of harvest on biodiversity.

Biodiversity

Diversity is a state of variety, or variability, among objects in a collection; biodiversity refers to the state of variety among objects in collections of biological material. In popular and scientific literature, biodiversity frequently refers narrowly to the variety of species (sometimes called species richness) present at a particular place and time.

Species occupy just one of several levels in each of two intersecting hierarchies, or classification schemes, for biological structure: one taxonomic and the other functional (Fig. 1). Biodiversity refers to the entire variety that exists in biological material at the many levels of both the taxonomic and functional hierarchies (Trauger and Hall 1992).

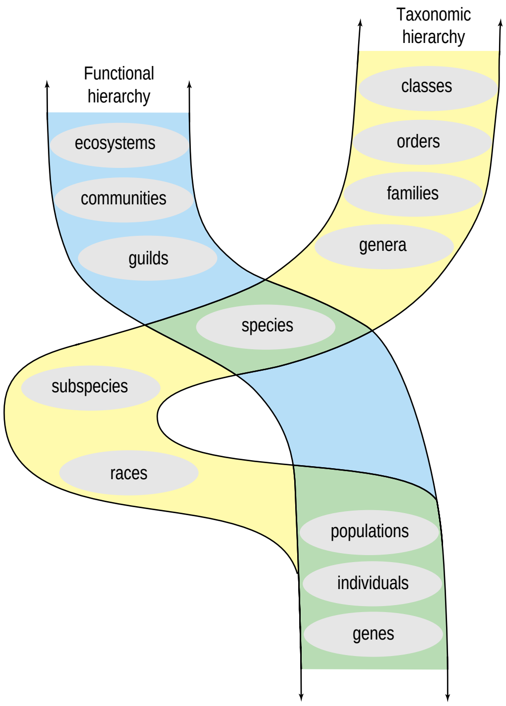

Fig. 1. Biological systems can be arranged in at least two nested hierarchies, one functional and the other taxonomic. The functional hierarchy reflects how researchers arrange biological material at various levels of interaction among the lower, component parts of a system. The taxonomic hierarchy provides a system for ordering and naming the diversity of life forms on Earth. To a great extent, it also reflects the suspected evolutionary relationships among the various taxa. The species concept is so important to biologists because species occur in both hierarchies. Thus, events that affect species have ramifications up and down both hierarchies.

Taxonomic Diversity

The state of variety in any collection (especially collections of species) is contingent on how many kinds of distinguishable objects are perceived. To varying degrees, in different circumstances and among different kinds of organisms (for example, insects versus birds), it is sometimes difficult to agree upon the diversity of a collection of species because exactly what defines a particular species is sometimes problematical, both for scientists (Dowling et al. 1992; Cronin 1993; Moritz 1994) and for policy makers (O'Brien and Mayr 1991; Geist 1992; Hill 1993). Unfortunately, the question of whether harvest affects diversity of species turns on the question of whether particular species exist as distinct entities and by whose definition.

Taxonomy provides a sort of great filing system to order the tremendous diversity of life forms for purposes of study, but it is not clear that the unique character and names assigned to individual species necessarily reflect anything unique about the particular functions of those species in ecosystems (Lawton 1991; Baskin 1994; Moffat 1996). Nor is it clear whether systematics and taxonomy as traditionally practiced are a necessary component of any agenda to conserve biodiversity (Renner and Ricklefs 1994a,b; Oliver and Beattie 1996), though it certainly seems so, given the amount of time and energy scientists spend arguing about the designation of species.

Major political and biological decisions often rest on the outcome of arguments about which names are preferred for groups of similar organisms. For example, the decision to further manage the harvest of American black ducks, a species that has declined over the past 30 years, depends, in one view (for example, Ankney et al. 1987), on whether black ducks will so freely hybridize with mallards that the species is doomed to extinction anyway. Similarly, because red wolves appear to be hybrids of gray wolves and coyotes, some researchers are concerned that the red wolf will be delisted from its endangered status (Brownlow 1996). Alabama sturgeon and shovelnose sturgeon present similar dilemmas.

The extreme difficulty is that, even though the term *species* has been used for centuries, there remains no standard, universally agreed-upon rule for delimiting each species (Fig. 2). There has been a flurry of recent attempts to deal with such criticisms and to delineate, objectively and fully, alternative groupings of similar organisms (such as evolutionarily significant units, recognizable taxonomic units, and morphospecies [for example, Moritz 1994]). These efforts correlated with the appearance of powerful molecular techniques for identifying fine differences in the genetic makeup of individual organisms (Brownlow 1996). Ultimately, all such classifications are still subjective, which causes further blurring between ethical and scientific judgments (Cronin 1993). Nevertheless, diversity clearly does exist at many levels in the taxonomic hierarchy, and the reasons for our concern about the state of biodiversity range from utilitarian (as-yet undiscovered drugs, genes, or other commercially viable products may exist in species residing in remnant natural ecosystems) to ethical (diversity has an intrinsic right to exist).

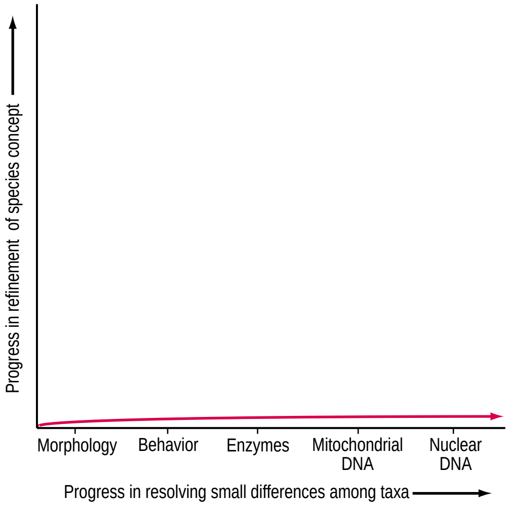

Fig. 2. Since the species concept appeared, scientists have greatly progressed in applying technologies to resolve finer and finer differences among organisms; this enables researchers to cluster organisms based on their degree of similarity. Because researchers have made much less progress in precisely defining a species, much argument exists about what the differences revealed at finer scales of resolution mean with respect to the designation of a species.

Functional Diversity

In this chapter, I emphasize the effects of harvest on diversity within and among levels of the functional, rather than the taxonomic, hierarchy. Within the functional hierarchy, variety is apparent at many levels—at the level of genes within and among individual organisms, of individuals within and among populations, of populations of different species within and among communities, and so forth. With the exception of individual organisms (except, perhaps, asexually reproducing species, for which even the identification of individuals may be difficult), scientists experience similar difficulties classifying within the functional hierarchy as in the taxonomic hierarchy. For instance, no universally agreed-upon boundaries exist for where one population ends and another begins nor where one community ends and another begins.

Within the very real constraint of the uncertainty associated with such classifications, I discuss the effects of harvesting—explicitly by humans, and, by extension, by other predators with whom humans share space in ecological food webs—on biodiversity at three levels of organization: genes within and among individuals, individuals within populations, and species within communities.

Harvest Effects on Populations

Sustainable Use and Sustainable Yield

Since the earliest references to sustainable harvest of renewable resources, some of which can be found in the Old Testament, the key idea has been to harvest in such a way that the removal of individuals from a population would not cause a decline in the ability of the population to replenish itself. Until fairly recently, though, the sciences of population ecology and those related to resource management evolved differently because they had fundamentally different questions and values about nature and populations of wildlife at their roots (Nudds 1979). Ecologists tended most often to focus on why populations fluctuate; wildlife, fisheries, and forestry scientists were concerned primarily with understanding how to sustain harvests from populations. To that extent, the science of resource management was rooted more firmly in agriculture than in ecology.

Indeed, utilitarianism, as fostered by Francis Bacon, gave rise in North America to a school of progressive agriculture, whose views then heavily influenced a school of progressive scientific conservation and a philosophy of “wise use” for forests and other wildlife, as espoused by Gifford Pinchot and Theodore Roosevelt (Worster 1977). In contrast, the environmental movement in North America (often linked more closely to ecology than to resource management) can be traced to the romantic tradition of Gilbert White and Henry David Thoreau, who strongly influenced John Muir and the protectionist school of conservation (Worster 1977). Wildlife biologist Aldo Leopold transcended these two schools during his career, first advocating Pinchot-like views for the scientific management of game resources and later espousing philosophies based on a broader appreciation of the ecology of natural systems (Kennedy 1984). Nevertheless, “barnyard management” philosophies still pervade many areas of natural resources management (Lavigne 1991; Dobb 1992) and, though the concept of sustainable use has a long history, the relatively new concept of sustainable development, when used in reference to harvests of renewable resources, actually has not evolved much from earlier notions of conservation as wise use (Lavigne et al. 1996).

By the mid-twentieth century, resource-management scientists had borrowed heavily from the science of population ecology,

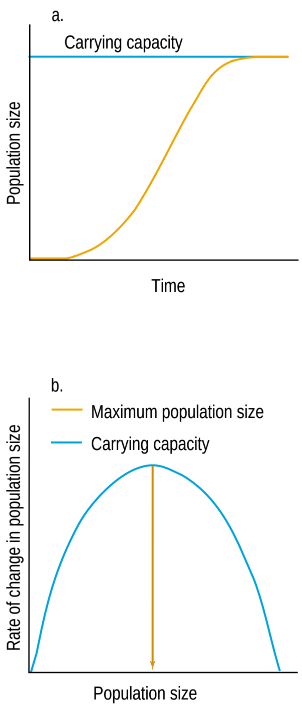

Fig. 3. Under a stringent set of conditions, which can probably only be approximated in nature, a) population size grows over time to its carrying capacity, which is when the rates of births and deaths exist in a dynamic equilibrium and the population grows no further. b) As a population grows, its rate of change in size increases, but at a decelerating rate. When the population size is half as large as the carrying capacity, the population's rate of change is at its maximum and declines thereafter, reaching zero when the population reaches carrying capacity. In theory, such a population could be continuously harvested to one-half of its carrying capacity, thereby producing a perpetual, maximum yield without compromising the ability of the population to be replenished. This is the kernel of the maximum sustained yield theory.

especially fisheries science. A specific and highly quantitative form of the sustainable use concept—maximum sustained yield theory (Fig. 3)—appeared, embued with the authority of mathematical equations of population dynamics developed many years earlier by theoretical ecologists (Hutchinson 1978). Unfortunately, the many simplifying assumptions of maximum sustained yield theory proved eventually to be its Achilles heel (Holt and Talbot 1978). This is especially true of the assumption that when harvesting the population of interest all other species in complex ecological food webs could be ignored, and of the assumption that nature is relatively constant and benign, enabling populations to persist at relatively constant sizes. In contrast, present-day natural resource management is evolving and becoming more firmly established on an ecological foundation as, indeed, is agriculture.

Compensation and Compensatory Mortality

To understand whether and how harvest exploitation might affect biodiversity, it is essential to understand how harvest might affect populations, particularly their size and composition, because effects at the level of populations can potentially range up and down the biological hierarchy (Fig. 1). The scientific literature on this subject is daunting, not only because of its sheer size (nothing generates discussion and analysis like controversies about the effects of hunting), but also because the terminology is inconsistent and confusing. For example, a harvest that removes even one individual from a population necessarily, but trivially, *limits* the population size, but it does not necessarily *regulate* it (Sinclair 1989). Regulating factors are a particular class of limiting factors that, depending on the biological characteristics of particular harvested species and the amount of time that passes after a harvest, may actually increase rather than decrease the number of individuals or the growth rate of the harvested population (Fig. 4).

Errington (1945) seems to have introduced the idea that if a harvest removed from a population the exact number of individuals that would die of natural causes anyway, the harvest (after a period of reproduction by the remaining individuals) would not change the population size from that which would occur in the absence of harvest. In other words, harvest mortality would merely be *compensatory* to, or substitute for, natural mortality. However, if the number of individuals that were harvested exceeded the number that would die naturally, then harvest mortality would be *additive*. This is different from *compensation* by the population for the removal of harvested individuals (Caughley 1985).

Whether a population exhibits compensation when it is harvested depends on whether and how the natural birth and death rates differ when population numbers change as a result of the harvest (Fig. 4). For many species, including many often assumed to respond positively to harvest, birth and death rates may be only weakly linked to population size, or at least lag behind changes in population size (Fryxell et al. 1991); these populations, then, only partially compensate (Caughley 1985) for the removal of harvested individuals.

The responses to harvest for many other species may be entirely independent of population size or may vary with changing environmental conditions (Berryman 1991). In these cases, long-term fluctuations of harvested populations may be chaotic, increasing the possibilities for population collapse (Fig. 4). Such a scenario may be true even for populations that have the potential for some kind of compensation, especially if harvest holds a population to a size where its birth and death rates are largely independent of the number of individuals in the population (Fig. 4).

I do not consider these complicated phenomena further, but this brief discussion illustrates a point I made earlier: that because the complexities involved in studying the effects of harvest on just a single population are numerous, so, too, must be any consideration of harvest effects on biodiversity. If compensatory harvest mortality is taken to mean *that which substitutes for natural mortality*, then unless we can somehow predict and exact a harvest that precisely mimics the mortalities that a population would experience through natural mortality, harvest will necessarily affect biodiversity. Consequently, we should be skeptical of claims that assert the feasibility of sustainable harvests that do not alter biodiversity. The critical issue is, however, whether altered biodiversity necessarily matters—and, if so, why it matters—at the genetic, individual, population, and community levels.

Much has been written about the importance of biodiversity and the need to conserve it, but from a scientific perspective many of these articles consist of hypotheses that need to be critically evaluated. Instead of concentrating here on the intrinsic ethical reasons to conserve biodiversity, I focus on what we think we know and do not know about whether changes in diversity that result from harvest actually matter with respect to the persistence of individuals, populations, and the higher-order systems (communities and ecosystems) in which individuals and populations live.

Harvest Effects at Three Levels of Biodiversity

Harvest and Genetic Diversity

Most biologists believe that populations are composed of individuals whose genetic makeup is suited, or adapted, to the particular environments they inhabit. Genes, sometimes in interaction with environmental factors, determine how individuals will grow and respond to environments. A diversity of genetic material exists within individual organisms and among individuals in populations. Biologists are concerned with the amount and distribution of this genetic diversity and how it changes when population size changes (Soulé 1987; Pimm 1991). Although biologists believe that small populations are particularly susceptible to extinction for many reasons, a great deal of their attention has focused on the fates of species with small populations and low levels of genetic diversity (Nunney and Campbell 1993). Too little genetic diversity, as might result from the inbreeding that occurs among close relatives in small populations, may disrupt the potential for a species or population to adapt to changing environments over the long-term, or it can lead directly to reduced ability for the population to survive and reproduce in the short term.

Historically, populations of many species were reduced substantially—some to extinction—by harvesting that was conducted primarily for commerce (Shaw 1985; Lavigne et al. 1996). When populations are severely reduced, a kind of genetic bottleneck occurs, the result of which is reduced genetic diversity in the population in subsequent generations. Even a population that recovers in size after a short time at a reduced size may be largely composed of genetically similar individuals. For example, even though present-day populations of northern elephant seals are substantially larger than they were after harvesting severely reduced their numbers in the last century, the populations still display a remarkably low level of genetic diversity compared with their counterparts in the Southern Hemisphere whose numbers were not as severely depleted.

The relation between population persistence and genetic diversity is, however, complicated and not well understood. For example, the population of northern elephant seals did grow despite low levels of genetic diversity, so if the viability of a population is assessed by its ability to grow, then the low level of genetic diversity presumed to have resulted from harvest did not affect viability. Similarly, natural populations on islands frequently start from few individuals and potentially suffer from founder effects (that is, a lot of inbreeding necessarily occurs, resulting in low levels of genetic diversity), yet grow and may persist. Also, populations of many introduced or invasive species begin from a few individuals. On the other hand, scientists believe that the reason the North Atlantic population of black right whales may not be growing, even though the population is protected, is because its reproductive success has been impaired by low genetic diversity caused by a severe reduction in population size from harvest.

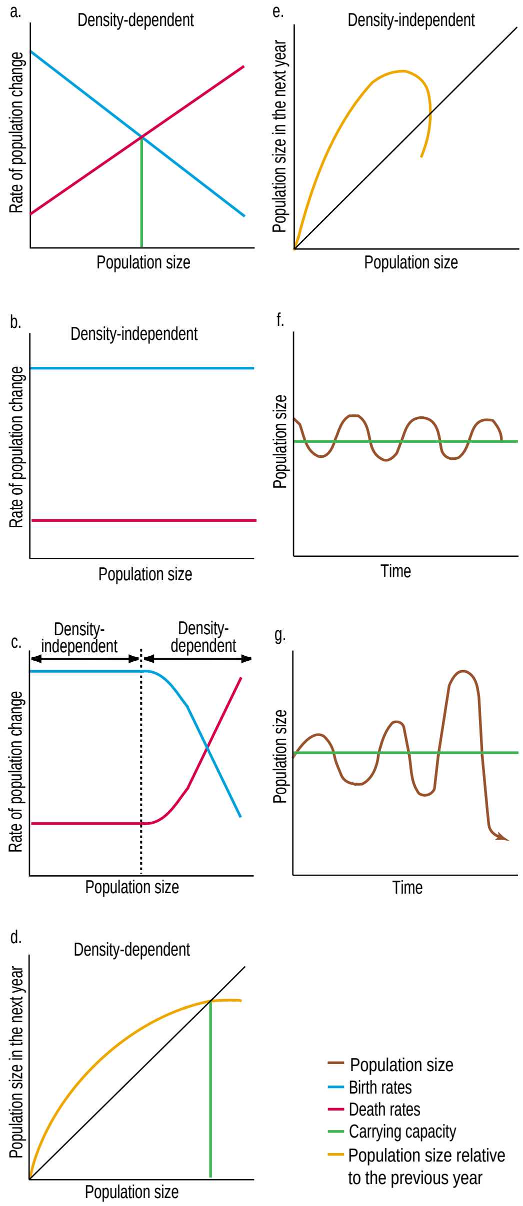

Fig. 4. a) The type of population growth to equilibrium (as shown in Figure 3) is obtained when rates of birth and death change linearly with an increase in population size. Specifically, the birth rate declines and the death rate increases until they are balanced at the population's carrying capacity; that is, the change in the rates *depends* on the size, or density, of the population. Another scenario b) is when the birth and death rates do *not depend* on density, but instead remain constant over a range of population sizes. In this instance, populations theoretically should continue to grow quickly and not show any deceleration of growth even at high numbers. More realistically, c) unbounded growth is not the rule in nature because environments are not limitless, although small populations may grow at rates not influenced by their density until the populations grow quite large, at which point effects of density on growth may suddenly appear. Real data from the kinds of large-bodied, long-lived species that humans frequently harvest (such as large mammals) often show this kind of relation between birth and death rates as population size changes. Harvesting can lower population sizes of such a mammal species to where the population might respond according to the approximations of maximum sustained yield and into a region where the assumptions of maximum sustained yield are violated. The relationship between the size of a population at one time (N_t) and its size at some later time after a harvest (N_{t+1}) is very different when birth and death rates are d) density-dependent or e) density-independent. The diagonal line connects values of N_t and N_{t+1} that are equal. The population's compensation for density reduction can cause an increase in population size at a later time, but the response is very different for a population at a size where the birth and death rates are not influenced by density. If birth and death rates are influenced by density, the population trajectory over time may f) fluctuate around an equilibrium size. If birth and death rates are density-independent, the fluctuations may g) be of increasing amplitude, suggestive of chaotic behavior. The fluctuations of increasing amplitude seen in g) increase the probability that the population could, by chance, become reduced to zero, which means, of course, extinction. Such cycles are observed in long-term data sets from marine fisheries and white-tailed deer.

Harvest may also result in genetic problems for natural populations in another, less direct way. For example, in areas where fisheries stocks have been depleted by harvest or other factors, it is common to augment stocks with individuals selected and reared in fish hatcheries. In some fisheries, continued harvest may only be possible with the continual addition of hatchery-reared individuals (an aquatic analog to *put-and-take* hunting). Considerable debate exists about how the release of large numbers of genetically similar individuals affects the persistence of remnant wild populations (Ryman and Laikre 1991).

Harvest and the Diversity of Individuals

Organisms harvested by humans typically reproduce sexually, are long-lived, and are large-bodied when compared with almost all organisms in the animal and plant kingdoms. Within populations there is a diversity of individual organisms of different sexes and ages. The reason scientists and managers have spent so much time developing techniques to identify the sex and age of individuals (Bookhout 1994) is that, in theory and in practice, variability in sex and age composition of individuals affects the growth rate and size of the populations they compose (Beasom and Roberson 1985; Getz and Haight 1989). In fact, resource managers have long tried to manipulate population size by directing harvest mortality to individuals of particular ages or sexes (Giles 1978). For example, to decrease the size of a large population, a general guideline might be to reduce the proportion of females of reproductive age. To allow a small population to increase, mortality might be directed to males (particularly for species in which a few males mate with many females), thereby reducing competition for food with females and their offspring.

It follows, then, that harvest and the diversity of individuals of different sexes and ages within populations are inextricably linked. The fact that the diversity of individuals with respect to sex and age is another kind of biodiversity is less obvious and seldom appreciated. It is unclear, however, whether changes in sex and age diversity generally have beneficial or detrimental effects on populations. For instance, sex-selective harvests of male deer may, or may not, produce more "high-quality" males (Beasom and Roberson 1985). Harvests of males only have been reported to produce desired results for some populations, sometimes with unanticipated side effects such as increases in abundance of antlerless individuals, which can increase competition for food and reduce body condition and reproductive performance (Beasom and Roberson 1985). Similarly, a harvest intended to change the preponderance of one sex sometimes may result merely in compensatory, biased production of the rarer sex. Female white-tailed deer that do not conceive until late in estrous, as would occur when encounters with rare males are infrequent, more often produce sons than daughters (Verme and Ozoga 1981), leaving deer population managers no further ahead in their attempt to adjust the sex ratio of the population.

Scientists long assumed that the removal of nonbreeding individuals among species where the ratio of breeding males to females is skewed was beneficial and would not affect the population's reproductive potential (Giles 1978). Such species, though, usually possess highly organized, if not readily apparent, social systems that may undermine a sustainable harvest if disrupted by mortality directed to certain age and sex classes of individuals. For example, the selective removal of individuals from populations for trophy hunting or for obtaining breeding stock for game ranches often causes significant differences from natural mortality patterns (Fig. 5); these differences could potentially greatly reduce reproductive success and actually lead to population collapse (Ginsberg and Milner-Gulland 1994).

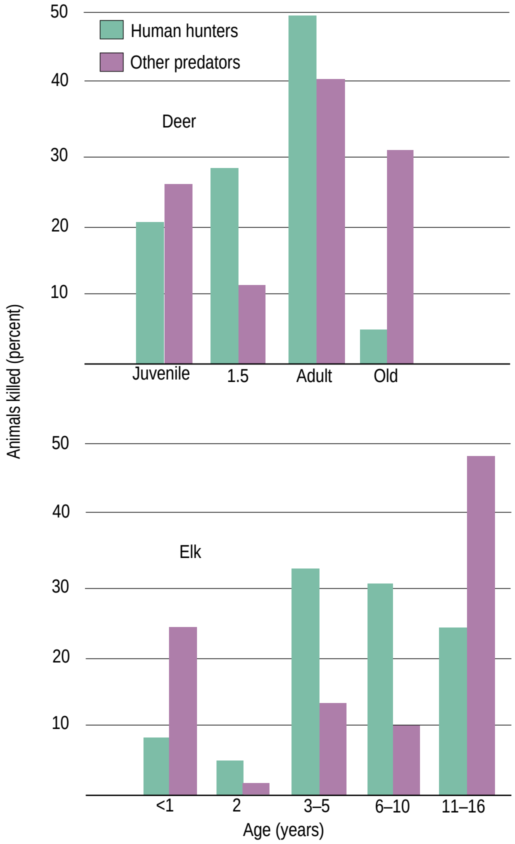

Fig. 5. Mountain lions in Idaho tended to kill more young and old deer, and wolves in Manitoba tended to kill more young and old elk, than they killed prey of prime breeding age. In contrast, humans hunting deer and elk nearby and at the same time tended to kill middle-aged individuals. Consequently, humans usually did not exact a harvest in which the mortality merely substituted for that which might occur naturally. Instead, humans altered the diversity of individuals of different ages within the prey populations differently than did the other predators.

Harvest and Species Diversity

Because harvest affects biodiversity at lower levels in biological hierarchies (Fig. 1), it follows that it must affect diversity at higher levels of organization, such as communities. A community, which is sometimes thought of as synonymous with a food web (Yodzis 1993), is the set of all species living together and interacting at a particular place and time. Interacting means, for example, that the species compete with one another, or one eats the other, but there is considerable ambiguity in actually measuring interaction (especially interactions less obvious and overt than predation) and its strength (Yodzis 1993). Nevertheless, how much interaction occurs among species has important theoretical implications for assessing the effects of disturbances such as harvest on the persistence and stability of communities (May et al. 1979; Yodzis 1994a,b). Space does not permit a thorough review of these ideas, though I will further discuss the general question about whether the persistence of a community is affected if the diversity of its constituent species is affected by harvesting some of those species.

Measurement of Species Diversity

The diversity of species in a community can be indexed quantitatively in many ways. The simplest index, and one frequently employed, is a count of the number of species, which is called species richness. As a measure of diversity, however, richness is heavily influenced by the presence of rare species in the community (Fig. 6). Consider, for example, two communities consisting of two species each and a total of 100 individuals. In one, the number of individuals is divided among the species in the ratio 99:1, and in the other, 50:50. Though species richness is equal, it is hard to be comfortable with the conclusion that the diversity of the two communities is the same. Clearly, were it not for the presence of just one individual in the one community, it would have just one species—only half the richness of the latter community.

Scientists have proposed alternative measures of species diversity that weigh the importance of each species in the calculation by its abundance relative to other species in the community. These various indexes, though, all convey essentially the same information about the variety in any collection of species and only differ in their sensitivity to the inclusion of rare species in the community on the calculated value of diversity (Hill 1973). But it is this very sensitivity to the inclusion of rare species that makes the use of different indexes problematical for assessing the effects of harvest on the diversity of species in a community: the answer might depend on the index used to quantify diversity.

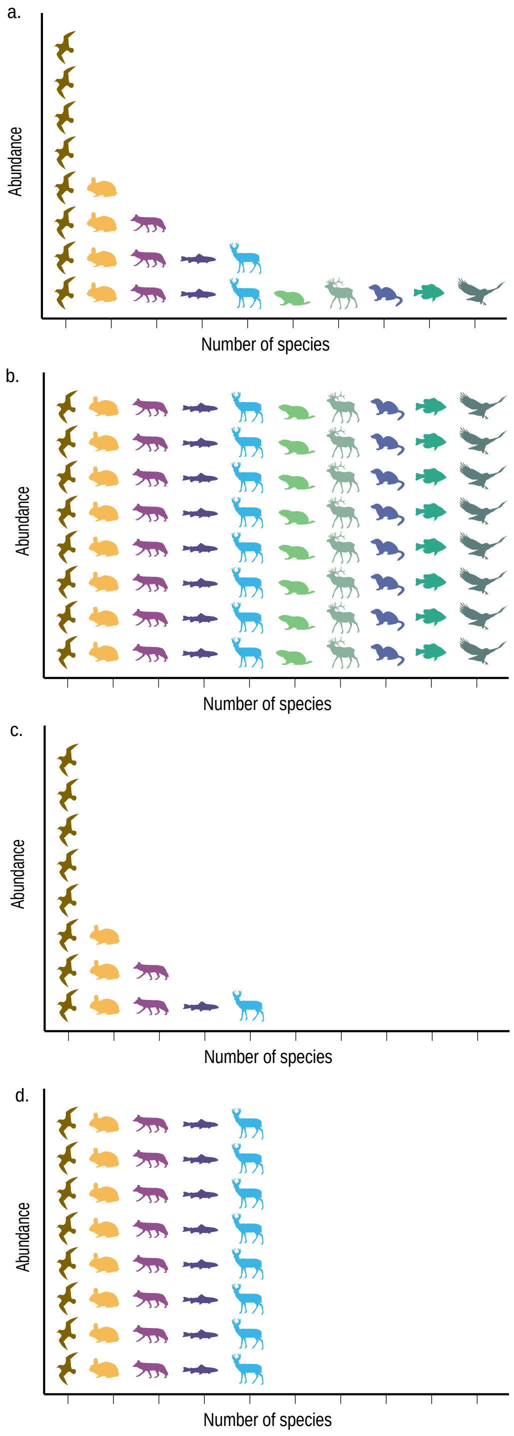

Fig. 6. As a measure of species diversity in a community, a species richness index is extremely influenced by the presence of rare species, as shown here in species-abundance diagrams for four hypothetical communities, two in which species richness (the actual number of species in a community) is 10 (a,b) and two in which species richness is five (c,d). Each community set has one community in which the relative abundances of species (or the evenness of the distribution) are equal (b,d) and one in which they are not (a,c). By the criterion of species richness, a) and b) have equal diversity and c) and d) have equal diversity, although b) and d) have much higher diversity by any index that takes into account the relative abundances of the species. A harvest that alters the abundance of a species must therefore alter diversity measured by any of those indices, but a similar harvest would not produce detectable change in diversity if diversity is measured simply as species richness.

Paradoxically, although richness is the index of diversity most sensitive to variation in the number of rare species, it will not detect changes in diversity brought about by a harvest of one or more species in the community unless the harvest is responsible for the complete eradication of one or more species. Conversely, any of the alternative diversity indexes that are less sensitive to variation in the number of rare species will necessarily detect a change in diversity caused by a harvest that alters the abundance of one or more species relative to the others.

Harvest Effects on Relative Abundance of Species

Whether harvest changes diversity of a community is clearly contingent on the kind of analysis performed, but what of the biological effects of altering the relative abundance of species? Assume, for example, that a harvest of a particular population of a species in a community affects the size of that population. This seems reasonable because, as noted previously, the stringent conditions under which a harvest would have no effect on population size hardly ever occur in the real world (Holt and Talbot 1978). Depending on whether the removal of individuals has a limiting or regulating (Sinclair 1989) effect on the population, the long-term effect of harvest might be either to increase or to decrease the population relative to the size it would be without harvest. By itself, this does not necessarily translate into a biological effect on the entire community in which the species population occurs, because changing the abundance of a particular species may not have far-reaching consequences for other species in the community, especially if the harvested species interacts only weakly with the other species in the community. Further, if harvest mortality substitutes for some kind of natural mortality, then to the extent that harvested organisms are not food for some other organisms in the community, it might be argued that harvest doesn't affect the population or the entire community. However, because it is difficult to imagine any organism in nature that is not food for some other (if not during its lifetime, then certainly after), it must follow that sooner or later a harvest necessarily alters the variety of species, with consequences for something somewhere in complex food webs.

Keystone Species

The logic and implications of various qualitative and quantitative definitions of diversity aside, ample evidence exists that harvests which alter the abundance of some species can directly and indirectly affect species diversity in the rest of the community, particularly if a harvest alters the abundance of a *keystone* species, which is an *organizing* species that has such particularly strong interactions with other species in a community that changes in its abundance cause significant changes in the abundances of other species. Paine (1966), who developed this concept based on a series of experiments in marine intertidal systems, removed the top predator, a sea star, from some areas and noticed that diversity of other intertidal species decreased. In addition, the removal of the starfish caused an increase in the populations of a few species that were able to outcompete others. Lubchenco (1978) extended this idea by showing that predator removal could decrease or increase species diversity of a community, depending on the kind of habitat from which the predators were removed and on whether the preferred prey of the predators were strong or weak competitors with other species. Today, examples of keystone species are recognized from a wide variety of systems: sea otters in coastal kelp beds, moose and beaver in boreal forests, and gopher tortoises in southeastern sandhills, among many others.

Humans are also keystone predators that can significantly alter the diversity of communities by harvest (or culls) of particular species, a fact long recognized, especially in fisheries literature (May et al. 1979). Some elegant new analyses of the effects of harvest by humans on multispecies fisheries (Yodzis 1994a), and the effects of a cull of South African fur seals (ostensibly to reduce competition with humans for fish) in the Benguela ecosystem (Yodzis 1994b), suggest complex and far-reaching effects of such harvests on the species composition (diversity) and the stability of entire communities.

Harvest and Habitat Fragmentation

Finally, harvest by humans can less directly affect the diversity of species by altering the habitats in which they live. Worldwide, habitat change through forest harvesting, as well as agricultural development and urbanization, may leave small, remnant patches of undisturbed habitat, but such residual natural areas (even some set aside to preserve the diversity of species in them, such as national parks) contain a much lower diversity of species than they would otherwise contain if they were still part of large, contiguous landscapes (Glenn and Nudds 1989; Nudds 1993).

Conclusion

I have argued that there are necessarily and obviously effects of harvest at each of several levels of a nested hierarchy of biological organization: at the level of genes within and among individuals, among individuals of different sexes and ages within populations, and among populations of different species within communities. My intent is not to insult by the simplicity of the arguments, but to take the opportunity afforded by this otherwise scant introduction to the topic of harvest effects to infuse a cautionary note into a literature becoming all too cluttered with ill-defined terms, illogical arguments, and glaring contradictions. None of this, of course, will stop some claims that sustainable use of renewable resources does not affect biodiversity. However, to point out *only* that such statements are necessarily, at some level, false is about as helpful as trying to argue that they are true. Consequently, I want to make some general comments about whether the changes that occur as a result of harvest *matter*, and to whom or what. I conclude with some suggestions about how we might find out what changes matter, given that the ecological and evolutionary consequences of harvest are not well-understood.

Conservation of Biodiversity: What's the Goal?

What has been absent from discussions about conserving biodiversity is a clear definition and agreement about precisely what ought to be the objective for the management of biodiversity. This problem particularly plagues discussions about ecosystem health (Suter 1993; Steedman 1994) and integrity. The U.S. Environmental Protection Agency, however, borrowing from Karr's (1991:69) Index of Biological Integrity, defined ecosystem integrity as "diversity, composition and functional organization that is representative of natural habitats within a geographic region." It is important that this definition makes it explicit that integrity must be defined relative to a standard; in scientific terms, this means in relation to control areas (Solbrig 1991). Finally, Article 7 of The Convention on Biodiversity (Johnson 1993:85) charges the signatories to "identify… activities…likely to have significant adverse effects on the conservation…of biodiversity and monitor their effects…" Thus, it is important that sufficiently large natural areas be protected as baselines or controls (Sinclair 1983) against which to compare the diversity, composition, and function in ecosystems altered by humans, including those altered directly and indirectly by harvesting. Where typical scientific controls are not feasible, alternative means to assess the effects of harvest on biodiversity are possible. This approach, called adaptive management, explicitly links management actions, such as setting the sizes and timing of harvest quotas, to scientific analysis of the effects of harvest (for example, see Walters 1992; Williams and Johnson 1995; Williams et al. 1996).

Significant new information about the role of biodiversity, at least at the level of species in communities, suggests that its *purpose*, so to speak, may be to provide *redundancy*, which has a stabilizing effect on whole communities and ecosystems (Pimm 1993; Moffat 1996). In other words, in the face of significant environmental change, diversity may buffer ecosystems against collapse of ecological function. Experimental evidence suggests that some functions of ecosystems, such as trapping atmospheric gases, production, respiration, and water retention, decline when diversity declines (Naeem et al. 1994). Bethke (1993) and Bethke and Nudds (1993) showed that even though the abundances of individual species of waterfowl fluctuate widely in climatically variable environments, waterfowl communities are actually more persistent through time the more variable the environment—stability of the whole comes at the expense of the stability of the parts (Pimm 1993). Thus, biological integrity defined by function, as opposed to species composition or diversity per se, may be a more important policy objective (Angermeier and Karr 1994) for the management of harvest.

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