8

Overexploitation

John D. Reynolds and Carlos A. Peres

There's enough on this planet for everyone's needs, but not enough for everyone's greed.

Gandhi

Exploitation involves living off the land or seas, such that wild animals, plants, and their products are taken for purposes ranging from food to medicines, shelter, and fiber. The term **harvesting** is often used synonymously with **exploitation**, though harvesting is more appropriate for farming and aquaculture, where we reap what we sow.

In a world that seems intent on liquidating natural resources, overexploitation has become the second most important threat to the survival of the world's birds, mammals, and plants (see Figure 3.8). Many of these species are threatened by subsistence hunting in tropical regions, though others are also threatened in temperate and arctic regions by hunting, fishing, and other forms of exploitation. Exploitation is also the third most important driver of freshwater fish extinction events, behind the effects of habitat loss and introduced species (Harrison and Stiassny 1999). Thus, while problems stemming from habitat loss and degradation quite rightly receive a great deal of attention in this book, conservationists must also contend with the specter of the "empty forest" and the "empty sea."

We begin this chapter with a brief historical context of exploitation, which also provides an overview of some of the diverse reasons people have for using wild populations of plants and animals. This is followed by reviews of recent impacts of exploitation on both target and nontarget species in a variety of habitats. To understand the responses of populations, we then review the theory behind sustainability. The chapter ends with a consideration of the culture clash that exists between people who are concerned with resource management and people who worry about extinction risk.

History of, and Motivations for, Exploitation

Humans have exploited wild plants and animals since the earliest times, and most contemporary aboriginal societies remain primarily extractive in their daily quest for food, medicines, fiber, and other biotic sources of raw materials to produce a wide range of utilitarian and ornamental artifacts. Modern hunter-gatherers in tropical ecosystems, at varying stages of transition to agriculture, still exploit a large number of plant and animal populations. By definition, these species have been able to coexist with some background level of human exploitation. However, the archaeological and paleontological evidence suggests that premodern peoples have been driving other species to extinction since long before the emergence of recorded history. Human colonization into previously unexploited islands and continents has often coincided with a rapid wave of extinction pulses resulting from overexploitation by novel consumers. Mass extinction events of large-bodied vertebrates in Europe, parts of Asia, North and South America, Madagascar, and several archipelagos have all been attributed to post-Pleistocene human overkill (Martin 1984; McKinney 1997). These are relatively well documented in the fossil and subfossil record, but many more obscure target species extirpated by human exploitation will remain undetected.

In more recent times, extinction events induced by exploitation have also been common as European settlers wielding superior technology expanded their territorial frontiers and introduced market and sport hunting. The death of the last Passenger Pigeon (*Ecopistes migratorius*) in the Cincinnati Zoo in 1914 provided a notorious example of the impact that humans can have on habitats and species. The Passenger Pigeon probably was the most numerous bird in the world, with estimates of 1–5 billion individuals (Schorger 1995). Hunting for sport and markets, combined with clearance of their nesting forests (Bucher 1992), had significant impacts on their numbers by the mid-1800s, and the last known wild birds were shot in the Great Lakes region of the U.S. at the end of the century. After that, it was simply a question of which of the birds in captivity would survive the longest, and "Martha" in Cincinnati "won."

The decimation of the vast bison herds in North America followed a similar time-line, but here hunting for meat, skins, or merely recreation, was the sole cause. In the 1850s, tens of millions of these animals roamed the Great Plains in herds exceeding those ever known for any other mega-herbivore, but by the century's close, the bison was all but extinct (Dary 1974). Following an expensive population recovery program, both the plains (*Bison bison bison*) and wood bison (*Bison bison athabascae*) are currently classified by the 2003 IUCN Red List as Lower Risk/Conservation Dependent, although the wood bison is listed as endangered by the U.S. Endangered Species Act and Appendix II of CITES.

An example that is lesser known is the extirpation of monodominant stands of Pau-Brasil trees (*Caesalpinia echinata*) from eastern Brazil, a source of red dye and hardwood for carving that gave Brazil its name. Pau-Brasil once formed dense clusters along 3,000 km of the Brazilian Atlantic forest, and the species sustained the first major trade cycle between the new Portuguese colony and European markets. It was exploited relentlessly from 1500 to 1875, when it finally became economically extinct. Since the advent of synthetic dyes, the species has been used primarily for the manufacture of high-quality violin bows, and Pau-Brasil specimens are currently largely confined to herbaria, arboretums, and a few small protected areas (Dean 1996). These examples suggest that even some of the most abundant populations can be driven to extinction in the wild by exploitation. Exploitation of both locally common and rare species thus needs to be adequately managed if populations are to remain demographically viable in the long term.

People exploit wild plants and animals for a variety of reasons, which need to be understood if management is to be effective. There may be more than food and money involved. The recreational importance of hunting and fishing in developed countries is well known. For example, hunting creates more than 700,000 jobs in the U.S. and a nationwide economic impact of about $61 billion per year, supporting nearly 1% of the entire civilian labor force in all sectors of the U.S. economy (LaBarbera 2003). Over 20 million hunters in the U.S. spend nearly half a billion days afield in pursuit of game, and fees levied to game hunters finance a vast acreage of conservation areas in North America (Warren 1997).

The importance of exploitation as a recreational activity is not restricted to wealthy countries. For example, in reef fisheries in Fiji, capture rates are highest with spears or nets, and while these techniques are used when fish are in short supply, the rest of the time people adopt a more leisurely pace with less efficient hand-lines, using the extended time for social and recreational purposes (Jennings and Polunin 1995). Cultural and religious practices are often important. For example, feeding taboos switch on or off among hunters in tropical forests according to availability of alternative prey species (Ross 1978; Hames and Vickers 1982). The fate of some endangered species is closely bound to religious practices, as in the case of the babirusa wild pig, *Babyrousa babyrousa*, in Sulawesi. This species is consumed heavily in the Christian-dominated eastern tip of Sulawesi, but rarely consumed over the Muslim-dominated remainder of the island (Clayton et al. 1997).

Impacts of Exploitation on Target Species

Many of the best-known impacts of exploitation on populations involve cases of direct targeting, whereby hunting, fishing, logging, and related activities are selective, aimed at a particular species. In this section we present examples from major ecosystems in both temperate and tropical areas.

Tropical terrestrial ecosystems

TIMBER EXTRACTION Tropical deforestation is driven primarily by frontier expansion of subsistence agriculture and large-scale development programs involving improved infrastructure and access. However, animal and plant population declines are typically preceded by hunting and logging activity well before the coup de grâce of complete deforestation is delivered. Approximately 5.8 million ha of tropical forests are logged each year (Food and Agriculture Organization 1999; Achard et al. 2002). Tropical forests account for about 25% of the global industrial wood production, worth U.S.$400 billion or about 2% of the global gross domestic product (World Commission of Forests and Sustainable Development 1998). Much of this logging activity opens up new frontiers to wildlife and nontimber resource exploitation, and catalyzes the transition into a landscape dominated by slash-and-burn and large-scale agriculture.

Few studies have examined the impacts of selective logging on commercially valuable timber species, and comparisons among studies are limited because they often fail to employ comparable methods that are reported adequately. The best case studies come from the most valuable timber species that have already declined in much of their natural geographic distributions. For instance, the highly selective logging of broadleaf mahogany (*Swietenia macrophylla*) is driven by the extraordinarily high value of this species on international markets. These conditions make it lucrative for loggers to pay royalty payments as well as high transportation costs of reaching remote wilderness areas. Selective logging of mahogany and other prime timber species affects the forest by creating canopy gaps and causing severe collateral damage due to construction of roads and skid trails, particularly in the case of mechanized operations.

One of the major obstacles to implementing a sustainable forestry sector in tropical countries is the lack of financial incentives for producers to limit offtakes to sustainable levels and invest in regeneration (see Essay 8.1 by Steve Ball for an example involving East African blackwood). Economic logic dictates that trees should be felled whenever their rate of timber volume increment drops below the prevailing interest rate (Pearce 1990). Postponing exploitation beyond this point would incur an opportunity cost because profits from logging could be reinvested at a higher rate elsewhere (see Chapter 5 for a full discussion of economic discounting). This is particularly the case where land tenure systems are unstable, and where there are no disincentives against mining the resource capital at one site and moving elsewhere once this is depleted. This is clearly shown in a mahogany study in Bolivia where the smallest trees felled are about 40 cm in diameter, well below the legal minimum size (Gullison 1998). At this size, trees are increasing in volume at about 4% per year, whereas real mahogany price increases have averaged only 1%, so that a 40-cm mahogany tree increases in value at about 5% annually, slowing down as the tree becomes larger (Figure 8.1). In contrast, real interest rates in Bolivia in the mid-1990s averaged 17%, creating a strong economic incentive to liquidate all trees with any value regardless of resource ownership. The challenges and prospects of sustainable forestry in the Tropics are discussed in more detail in a case study by Pinard and colleagues in Case Study 6.2

SUBSISTENCE HUNTING Humans have been hunting wildlife in tropical forests for more than 100,000 years, but consumption has greatly increased over the last few decades. Exploitation of bushmeat (the meat from wild animals) by tropical forest dwellers has increased due to larger numbers of consumers, changes in hunting technology, scarcity of alternative sources of protein, and because it is often a preferred food. Recent estimates of annual hunting rates are 25,850 tons of wild meat in Sarawak (Bennett 2002), 73,890–181,161 tons in the Brazilian Amazon (Peres 2000a), and 1–3.7 million tons in Central Africa (Fa et al. 2001).

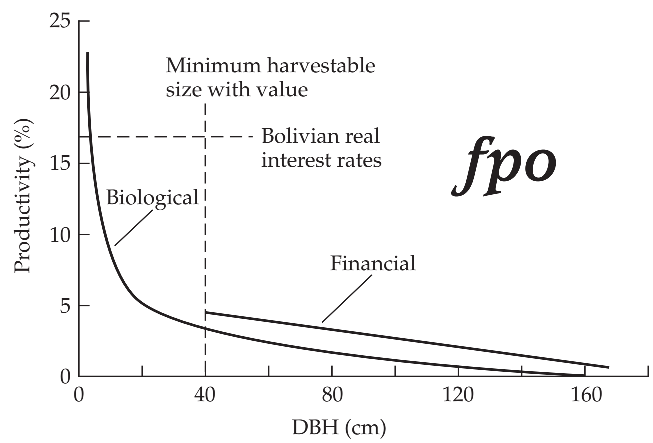


Figure 8.1 Productivity of Bolivian mahogany trees as a function of size expressed as tree diameter at breast height (DBH). Financial productivity is equivalent to size increments combined with a 1% real increase in price. Trees equal to or smaller than 40 cm in DBH have no commercial value, but at this size they increase at 5% in value per year. To maximize their profits, loggers should fell trees at a size when the financial productivity drops below the prevailing interest rate, which in Bolivia was 17% in 1989–1994. The discrepancy between the interest rates and tree growth rate provides a strong incentive to overexploit. (Modified from Gullison 1998.)

ESSAY 8.1

East African Blackwood Exploitation

Steve M. Ball, *Mpingo Conservation Project*

The Miombo woodlands, which cover a large swath of southern Africa, are a highly species-diverse ecosystem and the mammalian fauna requires large ranges. Thus, large contiguous areas of land must be protected for conservation of biodiversity to be effective. Even if the protected area system were well maintained, fragmentation would have a significant impact on the integrity of the conserved areas. Community-based conservation could fill the gap, providing buffer zones and corridors between reserves, but the communities need adequate incentive. The East African blackwood (*Dalbergia melanoxylon*) has the potential to do this.

The tree gets its name from its beautiful dark heartwood, which is inky black in the best-quality timber. The wood is used in the West to make woodwind instruments, especially clarinets and oboes, and locally it is a prime choice for wood carvers. It is the most valuable timber growing in the Miombo woodlands of southern Tanzania (Figure A). Both the species and its habitat are under threat from commercial exploitation and inward migration of people as a result of recent road improvements. The blackwood's high economic value, its status as Tanzania's national tree, and its cultural significance both in the West and in Tanzania make it an ideal flagship species to justify conservation of the habitat (Ball 2004).

Figure A A mpingo, an African blackwood tree. (Photograph courtesy of Steve M. Ball.)

Current exploitation levels are probably unsustainable, with at least 50% of trees being felled illegally without a license. Local forestry officials who depend on logging companies for transport into the field do not have sufficient resources to enforce existing regulations. Villagers generally know when illegal logging is taking place and could apprehend suspects, but they have no incentive to do so because all hardwood timbers remain the exclusive property of the government. Intentional fires are also thought to prevent regeneration and facilitate heart-rot in adult trees. Plantations are not an option because of their high costs, uncertain return, and long rotation time (blackwood is estimated to take 70–100 years to reach timber size).

Community-based forest management is now a major theme of conservation and rural development activities in Tanzania. In largely deforested areas these can succeed by focusing on firewood and water-catchment issues, but this approach is unlikely to succeed in southeastern Tanzania where forest cover currently exceeds 70%. However new laws allow for villages to take ownership of local forest resources if they can produce a viable management plan for the forest. This includes tenure rights over even high-value timber trees, such as East African blackwood, which were previously government-reserved species. License fees for felling timber could significantly increase village income, giving local people an incentive to look after their natural resource assets. Once schemes are well established, rural communities could use the promise of future income as collateral against micro-finance loans to increase the up-front benefits.

Simple economic analysis suggests that sustainable, community-based management of East African blackwood offers a powerful argument to justify conservation of the forest on public lands and to complement the protected areas system, providing income in buffer zones and corridors between reserves. However, it will be important to work with the suppliers of musical instrument manufacturers, and avoid a significant increase to their costs. If these challenges can be met, blackwood could be used as an economic key to conserve—as managed areas—large tracts of Miombo woodland. This would not happen through a system of forest reserves, but rather with a more inclusive strategy of sustainable exploitation of the region's natural resources.

Hunting rates are already unsustainably high across large tracts of tropical forests, averaging six times the maximum sustainable rate in Central Africa, for example (Figure 8.2). Consumption by both rural and urban communities is often at the end of supply chains that are hundreds of kilometers long, and that extend into many previously inaccessible areas (Milner-Gulland and Bennett 2003). The rapid acceleration in tropical forest defaunation due to unsustainable hunting occurred initially in Asia, is now sweeping through Africa, and is likely to move to even the remotest parts of the Neotropics. This pattern reflects human demographics in different continents: There are 522 people per km^2 of remaining forest in South and Southeast Asia, 99 in Central-West Africa, and 46 in Latin America.

Subsistence game hunting affects the structure of tropical forest mammal assemblages, as revealed by vil-

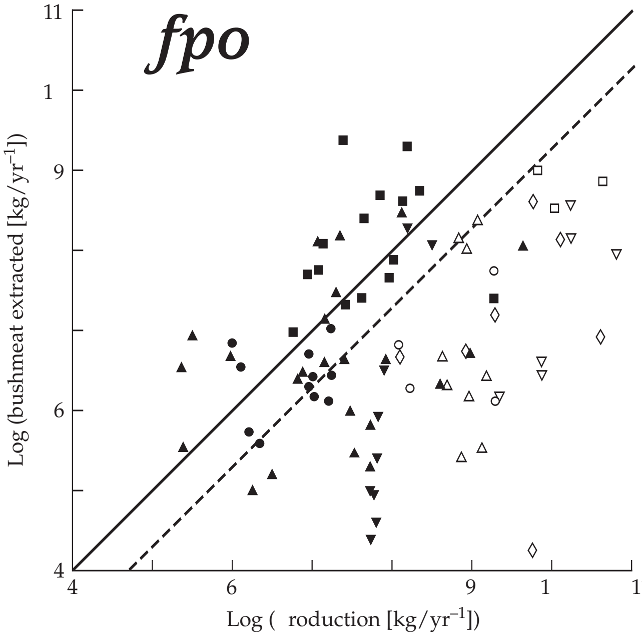


Figure 8.2 Hunting rates are unsustainably high across large tracts of tropical forests as seen in the relationship between total extraction and total production of game meat throughout the Congo and Amazon basin (solid and open symbols, respectively) by mammalian taxa. The solid line indicates where extraction equals production; the dashed line indicates exploitation levels at 20% of production, considered to be sustainable for long-lived taxa. Taxon symbols are as follows: ungulates (squares), primates (triangles), carnivores (circles), rodents (inverse triangles), and other taxa (diamonds). (Modified from Fa et al. 2002.)

lage-based kill profiles in Neotropical (Jerozolimski and Peres 2003) and African forests (Fa and Peres 2001). This can be seen in the composition of residual game stocks at forest sites subjected to varying degrees of hunting pressure where overhunting often results in faunal biomass collapses, mainly through declines and local extinctions of large-bodied mammals (Bodmer 1995; Peres 2000a).

NONTIMBER FOREST PRODUCTS Nontimber forest products (NTFP) are biological resources other than timber that are taken from either natural or managed forests (Peters 1994). Examples of exploited products (of whole plants or plant parts) include fruits, nuts, oil seeds, latexes, resins, gums, medicinal plants, spices, dyes, ornamental plants, and raw materials and fiber such as Desmoncus climbing palms, bamboo, and rattan. Forest wildlife and bushmeat can also be considered as a prime NTFP, but for a number of reasons they will be treated as a distinct category.

The socio-economic importance of NTFP extraction to indigenous peoples cannot be underestimated. Many ethnobotanical studies have catalogued the wide variety of useful plants or plant parts used by different aborigine groups throughout the Tropics. For example, the Waimiri-Atroari Indians of central Brazilian Amazonia make use of 79% of the tree species occurring in a single 1-ha terra firme (upland) forest plot (Milliken et al. 1992), and out of the ≥16,000 species of angiosperms in India, 6000 are used for Ayurvedic or other traditional medicine, and over 3000 are officially recognized by the government for their medicinal uses.

Exploitation of NTFPs often involves the systematic removal of reproductive units from the population, but the level of mortality in the exploited population depends on the method of extraction and whether vital parts are removed. Traditional NTFP extractive practices, for either subsistence or commercial purposes, are often considered to comprise a desirable, low-impact economic activity in tropical forests compared to alternative forms of land use involving structural disturbance, such as selective logging and shifting agriculture (Plotkin and Famalore 1992). As such, the exploitation of NTFPs is usually assumed to be sustainable and is viewed as a promising compromise between the requirements of biodiversity conservation and those of extractive communities under varying degrees of market integration.

A recent study of Brazil nuts (*Bertholletia excelsa*) questions the standard assumptions about sustainability of NTFPs (Peres et al. 2003). Brazil nuts are the base of a major extractive industry supporting over half of the tribal and nontribal rural population in many parts of the Brazilian, Peruvian, and Bolivian Amazonia, either for their direct subsistence value or as a source of income. This wild seed crop is firmly established in domestic and export markets, has a history of over 150 years of commercial exploitation, and is one of the most valuable nontimber extractive industries in tropical forests anywhere. Brazil nuts have been widely held as a prime example of a sustainably extracted NTFP, yet the persistent collection of *B. excelsa* seeds has severely undermined the patterns of seedling recruitment of Brazil nut trees. This has drastically affected the age structure of many natural populations to the point where persistently overexploited stands will succumb to a process of senescence and demographic collapse, threatening this cornerstone of the Amazonian extractive economy (Peres et al. 2003; Figure 8.3). Nevertheless, the concept of sustainable NTFP extraction is now so deeply entrenched into national resource use policy that extractive reserves (or their functional analogues) have become one of the fastest growing categories of protected areas in tropical forests (Fagan et al. 2005). The implicit assumption is that traditional methods of NTFP exploitation have little or no impact on forest ecosystems and tend to be sustainable because they have been practiced over many generations. However, virtually any type of NTFP exploitation in tropical forests

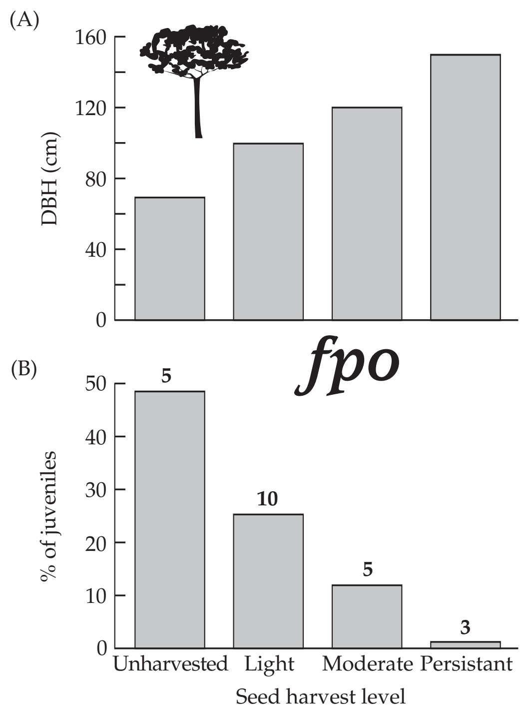


Figure 8.3 Relationships between historical levels of Brazil nut collection and mean tree size, expressed in terms of DBH, cm (A); and percentage of juvenile trees (B) in different populations. Numbers above bars indicate the number of populations studied throughout the Brazilian, Bolivian, and Peruvian Amazon. (Modified from Peres et al. 2003.)

will have an ecological impact. The exact extent and magnitude of this impact depends on the accessibility of the resource stock, the floristic composition of the forest, the nature and intensity of extraction, and the particular species or plant part under exploitation (Peres and Lake 2003).

Few studies have quantitatively assessed the demographic viability of nontimber plant products. A boom in the use of homeopathic remedies sustained by over-collection of therapeutic and aromatic plants is threatening at least 150 species of European wild plants and driving many populations to extinction (TRAFFIC 1998). Commercial exploitation of the pau-rosa or rosewood tree (*Aniba rosaeodora*), which contains linalol, a key ingredient in fine perfumes, involves a destructive technique that almost invariably kills the tree. This species has consequently been extirpated from virtually its entire geographic range in Brazilian Amazonia (Mitja and Lescure 2000). Chanel N°5® and other perfumes made with pau-rosa fragrance gained an enormous international market decades ago after being popularized by Hollywood stars like Marilyn Monroe, but the number of processing plants in Brazil fell from 103 in 1966 to fewer than 20 in 1986, due to the dwindling resource base. Yet French perfume connoisseurs have been reluctant to replace the natural pau-rosa fragrance by synthetic substitutes, and the last unexploited populations of pau-rosa remain threatened. The same could be argued for a number of NTFPs for which the exploitation by destructive practices involves a lethal insult to whole reproductive individuals, such as the extraction of fruits and palm-hearts in many arborescent palms. For example, in the Iquitos region of Peru, the fruits of *Mauritia flexuosa* palm trees, a long-lived forest emergent, are often collected only once by felling whole reproductive adults (Vasquez and Gentry 1998).

Enthusiasm for NTFPs in community development and conservation partly results from unrealistic studies reporting their high economic value. For example, Peters et al. (1989) reported that the net present value of fruit and latex extraction in the Rio Nanay of the Peruvian Amazon was $6,330/ha, assuming a 5% discount rate and that 25% of the crop was not taken. This is in sharp contrast with a 30-month study in Honduras that measured the local value of foods, construction and craft materials, and medicines extracted from the forest by 32 Indian households (Godoy et al. 2000). The combined value of consumption and sale of forest goods ranged from U.S.$18 to U.S.$24 per hectare per year, at the lower end of previous estimates (between U.S.$49 and U.S.$1,089 per hectare per year). NTFP extraction thus cannot be seen as a solution for rural development and in many studies the potential value of NTFPs is exaggerated by the assumption of unrealistically high discount rates, unlimited market demands, availability of transportation facilities, and absence of product substitution.

What, then, is the impact of NTFP extraction on the dynamics of natural populations? How does the impact vary with the life history of plants and animals? Are current extraction rates truly sustainable? These are all questions that could steer a future research agenda but the demographic viability of NTFP populations will depend on the species' ability to recruit new adults either continuously or in sporadic pulses while being subjected to repeated exploitation.

Temperate terrestrial ecosystems

FORESTRY According to one assessment, only 22% of the world's original forest cover remains in large, relatively natural ecosystems, or so-called "frontier forests" (Bryant et al. 1997). These remaining frontier forests are predominantly classed as either boreal (48%) or tropical (44%), with only a small fraction (3%) remaining in the temperate zone. However, much like tropical forests, most of the frontier forests in mid to high latitude regions are also increasingly threatened by logging and agricultural clearing (World Resources Institute 1998).

The overall impact of different sources of structural disturbance generated by modern forestry in the temperate and boreal zones may depend on the spatial scale and intensity of disturbance, the history of analogous forms of natural disturbance, the groups of organisms considered, and whether forest ecosystems are left to recover over sufficiently long intervals following a disturbance event such as commercial thinning or clearcutting. The patterns of landscape-scale human disturbance in these forests can be widely variable in intensity, duration, and periodicity, and are often mediated by economic incentives to cut timber from high-biomass old-growth forests, rather than natural regrowth or fast-growing tree plantations on a long rotation cycle.

The expanding frontier of commercial forestry into hitherto remote, roadless wildlands often results in high levels of forest conversion and fragmentation of remaining stands, with significant impacts to forest wildlife. A review of 50 studies in Canadian boreal forests on the effects of postlogging silviculture on vertebrate wildlife concluded that large impacts are universal when native forests are replaced by even-aged stands of rapidly-growing nonnative tree species (Thompson et al. 2003). Loss of special structures, such as snags containing nest cavities and large decaying woody debris, is particularly important in the decline of forest species depending on those structures (McComb and Lindenmeyer 1999). Unlogged boreal coniferous forests within protected areas in Finland, where population trends of land birds have been exceptionally well documented, are extremely important to the native old-growth avifauna, such as the Siberian Jay (*Perisoreus infaustus*) and the hole-nesting Three-toed Woodpecker (*Picoides tridactylus*), which have declined in areas under timber extraction (Virkkala et al. 1994). Indeed, logging is often considered to be the most important threat to species in boreal forests (Hansen et al. 1991; Imbeau et al. 2001). Some 50% of the red-listed Fennoscandian species are threatened because of forestry (Berg et al. 1994). Forests actively managed for biodiversity could support 100% of the species occurring in Washington state, whereas timber management on a 50-year rotation at the landscape level could support a maximum of 87% and a mode of 64% of the species potentially occurring in forests (Carey et al. 1996).

In summary, many of the detrimental impacts of forest management on biodiversity are associated with the large-scale structural simplification of the ecosystem at all forest levels, age-class truncation, and other consequences of intensive forest management intended to increase the yield of the desired forest component.

A reduction of this impact often involves modern principles of ecological forestry (Seymour and Hunter 1999), which may include a partial removal of the stand, often in a patch mosaic using relatively small clear-cut sizes so that each stage of forest development is represented somewhere in the landscape. As long as most stages are present at any one time, the requirements of nearly all species can be met somewhere (although see examples in Chapter 7 on the negative effects of habitat fragmentation). Furthermore, clear-cutting may only be used when and where absolutely necessary. Other exploitation methods include thinning and partial cutting, each with different effects on wildlife habitat. Landscape-level decisions to maximize the biodiversity value of the forest may include allocating different portions of the total area to successively longer rotations, ranging from 50 years for short-lived species up to 300 years for late-successional habitat.

HUNTING Large mammals, small game, and waterfowl are also major targets in temperate countries, where recreational hunting can be a popular sport across a large section of the constituents. Annual culls of large ungulates have been rather successful in North America, as shown by population trends, in both controlling populations and stocking the freezer of the average hunter. White-tailed deer (*Odocoileus virginianus*), the most common and widespread of wild ungulates in the U.S., increased from fewer than 500,000 around the turn of last century, to about 30 million today. Deer are among the most heavily hunted species in the U.S., with some 5 million killed by over 10 million hunters every year, generating about 20 billion dollars in hunting-related revenue in 2001 (U.S. Fish and Wildlife Service 2002). In Texas alone, it is estimated that the white-tailed deer population numbered more than 3.1 million in 1991 in spite of heavy hunting pressure, and approximately 474,000 animals were shot by hunters in that year. Resident birds and small to mid sized mammals frequently hunted or trapped for sport are often referred to as "small game." These may include game birds such as quail, pheasant, partridge and grouse, rodents and lagomorphs such as squirrels, rabbits, and hares, and even carnivores such as coyotes and raccoons. The effects of different hunting strategies upon populations of the most popular game bird in the U.S., the bobwhite quail, have been simulated showing that maximum yields can be sustained from annual capture rates of about 55% (Roseberry 1979). Hunting at such high rates, however, leaves little room for error in calculated bag quotas because it depresses the following spring populations by 53% below unexploited levels.

Ducks, geese, and swans are gregarious and often migratory species that also attract enormous attention from game hunters. As such, the establishment of annual waterfowl hunting regulations is a complex procedure shared by various governmental levels and private organizations, involving thousands of wildlife biologists and habitat managers under the jurisdiction of wildlife agencies. For example, retrieved duck and goose harvests during 2001 were 19.4 million in the U.S. and Canada, down by 6.6% on the total numbers bagged in the previous year (Martin and Padding 2002). In the U.S. alone, in 2001, this involved annual sales of 1.66 million federal duck stamps to 1.59 million hunters who collectively spent nearly 15 million hunter-days in pursuit of waterfowl. Needless to say, seasonal hunting license fees and leases of private hunting areas generate welcome cash used for both population management and for protection of habitats against other forms of land use.

The relatively orderly use of wildlife in North America is not necessarily the rule for all temperate regions. Illegal use and commercialization of wildlife continue to generate a substantial clandestine traffic—even for species that are fully protected on paper—in several mid- to high-latitude countries ranging from Chile to Russia. The problem usually lies not in the regulations, which are often already extensive and strict, but rather in lack of law enforcement that is often attributed to weak institutional capacity.

Aquatic ecosystems

MARINE ECOSYSTEMS The impacts of marine fisheries on target species are well known. Roughly three-quarters of the world's fish stocks are considered to be fully fished or overexploited (Food and Agriculture Organization 2002). Since the 1990s global catches have leveled off for the first time in human history, despite continuing advances in capture technology (Figure 8.4). Exploitation of aquatic animals now seems to be following the pattern that occurred in many terrestrial ecosystems long ago, with reliance on hunting of wild animals being supplemented by the captive rearing of domestic stock, through aquaculture (see Figure 8.4). No one should delude themselves into thinking that the move toward fish farming will save wild stocks, as many of the fish that are reared, such as salmon and trout, are fed with meal derived from wild fish! Indeed, stocks of many wild fishes have continued to decline. Recent surveys of 232 stocks showed a median decline of 83% over the past 25 years (Hutchings 2000, 2001; Hutchings and Reynolds 2004). A stock of Atlantic cod (*Gadus morhua*) off eastern Canada, which once seemed absolutely limitless, has undergone a decline of 99.9%, since the 1960s, leading to a designation of "endangered" under the Canadian Species at Risk Act (Committee on the Status of Endangered Wildlife in Canada 2003). This decision is not an isolated case; several other species of commercially exploited fishes have been listed recently as threatened with extinction (Musick et al. 2000; IUCN 2003). These developments show that some fisheries concerns are moving from the traditional focus on sustainability into the realm of extinction risk (Reynolds et al. 2002; Dulvy et al. 2003).

Concerns about extinction risk in the sea are most acute for those targeted species that have combinations of traits that make them most susceptible to capture, and biologically least productive (Reynolds et al. 2002; Dulvy et al. 2003). For example, the marine species that are most likely to be targeted are those that occupy shallow waters accessible to fishing gear, those that form dense shoals in predictable places, or those that are most valuable. If a species has one or more of these characteristics in combination with long generation times, the results can be hazardous to the health of the population. The Chinese bahaba (*Bahaba taipingensis*) is a fish that meets many of these criteria (Sadovy and Cheung 2003). It is a huge species of croaker (family Scienidae), which may exceed 2 m in length (Figure 8.5). It has traditionally been caught along its coastal range from Shanghai to Hong Kong. This species has been

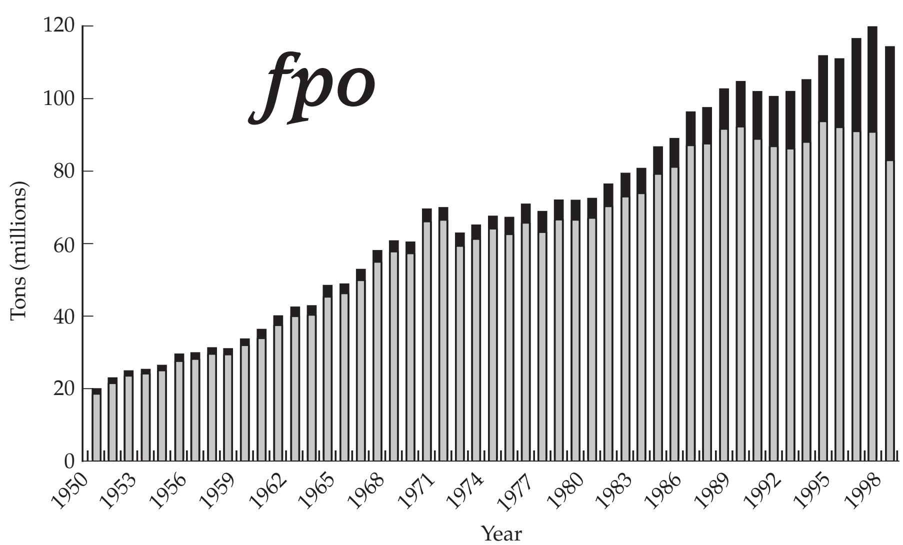


Figure 8.4 Trends in global fisheries. The gray portion of the bars indicate capture fisheries and the black portion of the bars indicate aquaculture. (From Hart and Reynolds 2002, based on data from FAO 2000; corrected for misreporting of capture fisheries of China by Watson and Pauly 2001.)

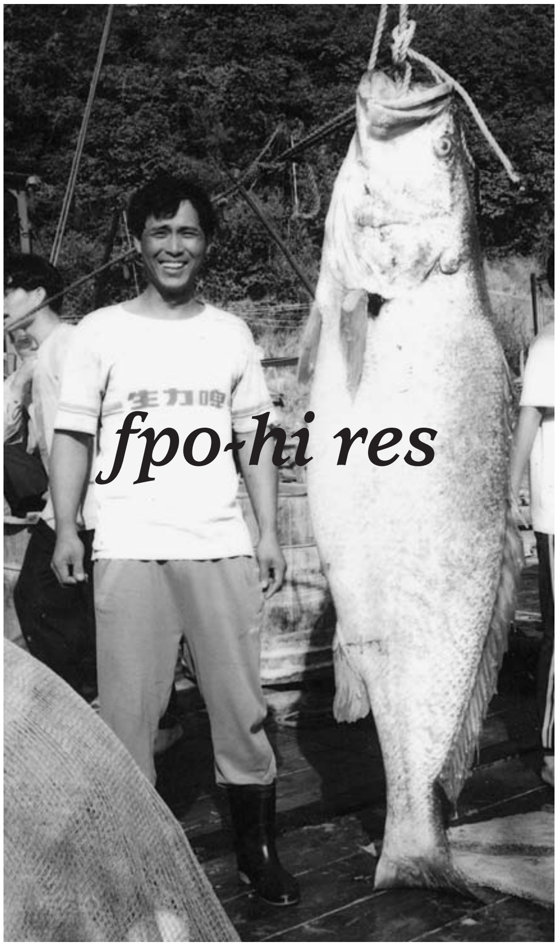


Figure 8.5 Chinese bahaba (*Bahaba taipingensis)* caught as an incidental by-catch by a trawler west of Hong Kong. (Photo courtesy of Cheng Tai-sing.)

popular for the medicinal properties of its swim bladder. Its numbers have declined to 1% of its abundance in the 1960s. During this time its price skyrocketed to the point where swim bladders in 2001 were worth seven times the price of gold (Sadovy and Cheung 2003). Scientists do not have enough information to say much about its population demography, but its large size invariably implies that it will take many years to reach maturity. This biological feature, combined with such strong economic incentives for people to catch it, have conspired to push the species to the edge of extinction.

The same basic rules of vulnerability for fish species apply to other taxa. For example, species of abalone along the Pacific coast of North America often occur in shallow waters, where they are readily accessible to divers (Figure 8.6). There has been serial depletion of these species, beginning with the most valuable and then moving on to less valuable ones (Tegner et al. 1996). This is reminiscent of the pattern that occurred with the great whales before the International Whaling Commission's moratorium on commercial whaling in 1986. The white abalone (*Haliotus sorenseni*) has been hit particularly hard. Ranging from California to Baja California, white abalone densities in some locations during the early 1970s were estimated at 1,000–5,000 per acre (Lafferty 2003). Commercial and recreational capture reduced its numbers to less than one per acre by the 1990s. In May 2001 this species became the first marine mollusc to come under the U.S. Endangered Species Act, with an estimated population in the wild of only about 3,000 individuals. Most remaining animals are restricted to deep waters beyond the reach of fishing (Lafferty et al. 2003). While the abalones' value and accessibility provided the motive and the means for overexploitation, it has also suffered from an additional problem: the Allee effect. This is the phenomenon whereby per capita fitness declines as a population becomes smaller (see Chapter 12). The ensuing feedback can cause populations to become more vulnerable as they become increasingly rare, potentially spiraling to extinction. In the case of abalone, the Allee effect arises through the need for individuals to be within 1 m of each other for a male's sperm to reach a female. Biologists have had some success with artificial fertilization in captivity, with the intention of rearing abalones for release into the wild.

FRESHWATER ECOSYSTEMS Many freshwater taxa are subject to exploitation for food and a variety of additional products. In 2000, the global estimate for all inland capture fisheries was estimated at 8.8 million tons (FAO

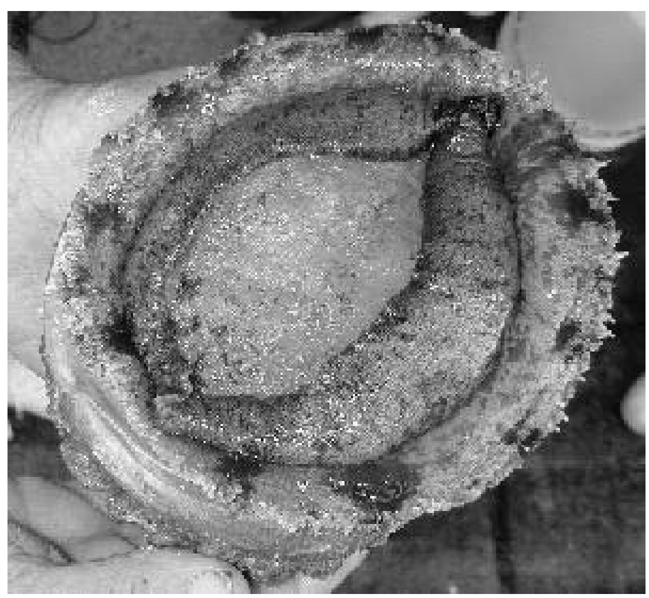


Figure 8.6 White abalone (*Haliotis sorenseni*) underside. (Photograph courtesy of K. D. Lafferty.)

fpo-lo res

2002). This figure is considerably less than the estimate for inland aquaculture (22.4 million tons). In many temperate countries, recreational fishing in fresh waters is a major past-time, yielding an estimated 2 million tons of fish (Cowx 2002). In 1996 it was estimated that 35 million people in the U.S. spent 514 million angler-days fishing, spending U.S. $38 billion in the process (U.S. Fish and Wildlife Service 1997). Among 22 European countries, the number of anglers was estimated at 21.3 million (Cowx 1998).

The world's salmon species illustrate the vulnerability of fish species that spend all or part of their life cycle in freshwater. Populations of four of the seven species of eastern Pacific salmon and trout in the genus *Oncorhyncus* are currently listed under the U.S. Endangered Species Act. Over-fishing has contributed to severe declines in many populations, often in combination with habitat loss through construction of dams that block their migrations, as well as degradation of spawning streams due to forest clearance and water abstraction (Lynch et al. 2002). The plight of salmon species is particularly sobering when one considers the enormous amount of attention that has been paid to these populations by scientists and conservationists, as well as their high economic and cultural significance. The most recent response of the U.S. government at the time of writing (May 2004) has been the announcement of the intention to count hatchery-released fish as "wild" (Kaiser 2004). Thus, the hundreds of millions of fish that are reared in captivity each year will elevate the population counts of many of the 27 populations of Pacific salmon and cutthroat trout that are endangered. This can lead to their removal from protection under the Endangered Species Act and presumably, the discontinuation of many habitat restoration programs. The decision ignores the fact that hatchery fish become domesticated rapidly, showing genetic and phenotypic divergence from wild stocks (e.g., Fleming et al. 1994; Heath et al. 2003). Furthermore, there is little evidence that hatcheries enhance the viability of wild stocks (Myers et al. 2004). Yet the regional director of the National Marine Fisheries Service, which has jurisdiction over salmon management, has declared that "Just as natural habitat provides a place for fish to spawn and to rear, also hatcheries can do that..." Presumably, zoos can also be considered natural habitats.

Fish are not the only taxa exploited from fresh waters. During the late 1800s and early 1900s millions of freshwater mussels (family Unionidae and Margaritiferae) were collected from freshwaters of Canada and the U.S., primarily to make buttons from their shells (Williams et al. 1993; Helfrich et al. 2003; Williams and Neves 2004). This exploitation was rarely sustainable, due to the slow generation times of these species. Mussels were saved from major impacts of exploitation by the switch to plastics for manufacturing buttons during the 1940s. However, today several million kilograms of mussels are still exported annually to Asia, where small beads are made from their shells and inserted into other bivalves for the production of pearls. Unfortunately, mussels now face much more critical threats from the "usual suspects" in freshwater conservation: pollution, damming, dredging, channelization, siltation, and competition with nonnative bivalves such as the Asian clam (*Corbicula fluminea*) and the zebra mussel (*Dreissina polymorpha*) (Strayer et al. 2004). These problems have led to 72% of the 297 species that occur in the U.S. being considered endangered, threatened, or of special concern, including 21 species that are extinct (Williams and Neves 2004).

Impacts of Exploitation on Nontarget Species and Ecosystems

Most hunting, fishing, and collecting activities affect not only the species that are the primary targets, but also those that are taken accidentally or opportunistically. Furthermore, exploitation may cause physical damage to the environment, and also may have ramifications for other species through cascading interactions, phase shifts in the structure of the ecosystem, and changes in food webs. Here we discuss a few examples of how extractive activities targeted to one or a few species can drastically affect the structure and functioning of terrestrial and aquatic ecosystems.

Tropical terrestrial ecosystems

LOGGING AND FOREST FLAMMABILITY Even logging targeted to a single timber species can puncture the forest canopy and increase the density of treefall gaps. This increase can trigger major ecological changes by increasing light and creating a warmer and drier microclimate in the understory, which thereby affects the dynamics of plant regeneration, and increases forest susceptibility to fire disturbance. In fact, even highly selective logging operations with modest levels of incidental damage to nontarget trees can generate enough structural disturbance to greatly augment understory desiccation and dry fuel loads, thereby breaching the forest flammability threshold (Holdsworth and Uhl 1999; Nepstad et al. 1999). Any source of ignition during subsequent severe droughts can initiate extensive ground fires that will dramatically reduce the functional and biodiversity value of previously unburned tropical forests (Barlow and Peres 2004). Surface wildfires that are at least partly induced by logging disturbance currently threaten millions of hectares of Amazonian, Mesoamerican, and Southeast Asian forests (Cochrane 2001; Siegert et al. 2001). Despite these undesirable direct and indirect effects, large-scale mechanized logging operations continue unchecked in many seasonally dry tropical forest regions.

HUNTING AND LOSS OF SEED DISPERSAL SERVICES Successful seedling recruitment in many flowering plants depends on seed dispersal services provided by large-bodied frugivores (Howe 1984). In tropical forests, the proportion of plant species with an endozoochorous dispersal mode (bearing seeds dispersed by an animal's digestive tract) is often more than 90% (Peres and Roosmalen 2002). Undispersed seeds simply fall to the ground underneath the parent's canopy and have a low survival probability (Augspurger 1984; Chapman and Chapman 1996). For example, 99.96% of *Virola surinamensis* seeds that drop under the parent are killed within 12 weeks (Howe et al. 1985). Many studies have shown lower seed mortality rates caused by fungal attack or vertebrate and invertebrate seed predators are lower at greater distances from parents. However, there have been only a few studies that have examined the effects of removing seed dispersers are lower on the demography of gut-dispersed plants. Wright et al. (2000) explored how hunting alters seed dispersal, seed predation, and seedling recruitment for two palms (*Attalea butyraceae* and *Astrocaryum standleyanum*) in Panama. They found that where hunters had not reduced mammal numbers, most seeds were dispersed away from the parent palms, but were subsequently eaten by rodents. Where hunters had reduced mammal abundance, few seeds were dispersed, but these tended to escape rodent predation. Thus, seedling density increased by 3–5-fold at heavily hunted sites compared to unhunted sites. In contrast, Asquith et al. (1999) demonstrated that recruitment of *Hymenaea courbaril* required scatterhoarding of their large seeds by agoutis (*Dasyprocta* sp.), and recruitment rates of many plant species that produce very large seeds cached by rodents is likely to be very low in heavily hunted areas.

Studies examining seedling recruitment under different levels of hunting pressure (or abundance of large-bodied seed dispersers) reveal very different outcomes. At the community level, seedling density in overhunted forests can be indistinguishable, greater, or less than that in the undisturbed forests (Dirzo and Miranda 1991; Chapman and Onderdonk 1998; Wright et al. 2000), but the consequences of increased hunting pressure to plant regeneration is likely to depend on the target species. In persistently hunted Amazonian forests, where large primates are either driven to local extinction or severely reduced in numbers, the probability of effective dispersal of large-seeded plants ingested primarily by these frugivores can decline by more than 60% compared to nonhunted forests (Peres and Roosmalen 2002). However, more conclusive evidence is required before the importance of the loss or reduction of effective animal dispersal services can be properly understood for different plant species.

Temperate ecosystems

Higher order interactions resulting from selective extinction or severe population declines of large mammals that play an important role as landscapers at the ecosystem scale have been documented in the temperate zone. Beavers (*Castor canadensis*) and their Eurasian congener (*Castor fiber*) are prime examples of ecosystem engineers, which can be defined as organisms that have the potential to dramatically alter the structure and function of ecosystems at large spatial scales. Large ponds created by the labor-intensive stream-damming activity of beaver colonies create large-scale semi-permanent flood disturbance that drastically changes the structure and patch dynamics of wetlands (Naiman et al. 1986; Wright et al. 2002). Beavers were once locally abundant in many parts of North America and Eurasia but their populations plummeted due to the pelt trade and habitat conversion in the nineteenth and early twentieth century, radically changing wetland ecosystems. No one knows the precise extent of these changes but it is clear that beaver damming activity has profound effects on the biogeochemistry of wetland systems (Naiman et al. 1994), the dynamics of shifting successional mosaics of aquatic patches (Johnston and Naiman 1990), and ultimately the population dynamics of other wetland species including waterfowl (McCall et al. 1996). Beavers are now making a gradual comeback in many parts of North America (although they were exterminated by 1700 and are yet to be reintroduced in many parts of Europe including Britain) but they often continue to be perceived as a nuisance requiring controversial measures of population control.

In temperate terrestrial ecosystems, large mammals that once had profound large-scale effects on the structure of plant communities but have been hunted to near extinction in historic times include bison, bears, and wolves. Joel Berger and colleagues (2001) demonstrated a cascade of ecological events that were triggered by the local extinction of grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) from the Yellowstone ecosystem. These include large increases in the population of a riparian-dependent herbivore, the moose (*Alces alces*), the subsequent alteration of riparian vegetation structure and density by ungulate herbivory, and the coincident reduction of Neotropical migrant birds in the affected willow communities, including riparian specialists such as Gray Catbirds (*Dumetella carolinensis*) and MacGillivray's Warblers (*Oporornis tolmiei*).

Where large predators (wolves, bears) have been removed through predator control programs, or other forms of direct persecution, ungulate populations can greatly increase in size, with subsequent impacts on plant communities. White-tailed deer in the U.S. and reindeer in Europe were once controlled by wolves and bear, and despite annual harvests, their numbers are larger than they were when controlled by native predators. The result is that their larger populations may overbrowse forests, which can cause extensive damage in some places (e.g., Väre et al. 1996 and Horsley et al. 2003). Particularly in areas where hunting is prohibited, deer populations can become so large that most tree and herb seedlings are consumed, which may lead to a change in patterns of forest succession (e.g., Horsley et al. 2003 and Pedersen and Wallis 2004), or to decline of rare species (e.g., Gregg 2004). Plant populations can be slow to recover from episodes of excessive herbivory. For example, a population of the rare orchid showy lady slipper (*Cypripedium reginae)* in West Virginia lost up to 95% of all stems during a 3-year period of excessive deer browsing, from which the population took 11–12 years to recover (Gregg 2004). Beyond effects on plants, uncontrolled herbivore populations can have indirect effects on decomposer (Wardle and Bardgett 2004) and spider communities (Miyashita et al. 2004).

Aquatic ecosystems

MARINE ECOSYSTEMS Marine fisheries are estimated to have a global by-catch of roughly 27 million tons annually, which is between one-third and one-fourth of the total marine landings (Alverson et al. 1994). This is probably a conservative estimate. Most of these by-catches were from trawl fisheries, followed by drift nets and gill nets. Shrimp trawls, with their small mesh sizes, account for roughly one-third of the total by-catch, with ratios of weight of discarded animals per weight of shrimp caught typically about 5:1. It has been estimated that shrimp trawlers in the Australian northern prawn fishery typically discard 70,000 individual organisms during each night of fishing.

Some by-catches are threatening species with extinction. All but two of the world's 21 species of albatross are considered threatened with extinction, and most of these have been severely affected by longline fisheries in the Southern Ocean (IUCN 2003). Albatrosses, as well as other seabirds such as petrels, drown when they take baited hooks as the lines are being set in fisheries aimed at species such as the Patagonian toothfish (*Dissostichus eleginoides*). While the rate of accidental capture per hook is very low, the potential risks are enormous when scaled up by the total fishing effort, with individual vessels often setting many thousands of hooks each day, and a total of over 250 million hooks being set each year since the 1990s south of 30º South (Tuck et al. 2003). Long-lived species such as seabirds have extremely low resilience against elevated adult mortality, due to their very long generation times and low rates of productivity. Recent reassessments by the IUCN (2003) have led to six species of albatross recently being "upgraded" toward more severely threatened status, with fisheries by-catch playing a significant role in each case. These problems are not confined to the Southern Ocean. For example, it has been estimated that 10,000 Black-footed Albatrosses (*Phoebastria nigripes*) may be killed each year in the central North Pacific (Lewison and Crowder 2003). Measures adopted to reduce mortality on seabirds include bird-scaring devices, the release of baited lines from below the water surface (where albatrosses cannot reach them), use of heavy lines that sink immediately, and use of fish oil on the surface, which dissuades seabirds from landing on the water.

Sea turtles are caught incidentally by longlines and trawlers. For example, it has been estimated that 20,000 turtles have been killed each year in the Mediterranean in longlines set for swordfish. Turtle excluder devices are now in widespread use in trawl fisheries, and these reduce turtle mortality by providing an exit flap that turtles can push through, while retaining the fish. Turtles are not the only reptiles taken as by-catch. It has been estimated that 120,000 sea snakes are taken annually by prawn trawlers in the Gulf of Carpentaria, Australia.

There are mounting concerns about the impacts of by-catches on populations of many fish species as well. The best-known cases involve sharks, skates, and rays (see Case Study 8.1 by Julia Baum). These fishes are toward the seabird–turtle end of the life-history continuum. For example, the European common skate (*Raja batis*) does not reach maturity until it is 11 years old. They used to be taken by the thousands as by-catch in prawn trawls in the Irish Sea (Brander 1981), but only six individuals were captured by extensive government bottom fish surveys between 1989 and 1997 (Dulvy et al. 2000). In this same region, there is evidence for complete local extinction of one and possibly two more species.

FRESHWATER ECOSYSTEMS In fisheries, it is easy to find freshwater equivalents of the kinds of difficulties that face many marine fish species. An example of nontarget fishes is the Mekong giant catfish (*Pangasianodon gigas*) (Figure 8.7), a species that is in a similar situation to the Chinese bahaba discussed earlier. This fish is restricted to the Mekong River Basin in Thailand (where no individuals have been caught since 2001), Laos, and Cambodia. Studies by Zeb Hogan and colleagues (2004) have shown that individuals can reach 3 m in length and weigh 300 kg, and are therefore extremely valuable to fishers. Furthermore, they are migratory, thereby running a gauntlet of nets set for other species. Finally, their only spawning grounds, in whirlpools and rapids in the Chiang Khong-Chiang Saen region of the Thai–Laos border, are being

Figure 8.7 Mekong giant catfish, *Pangasianodon gigas*, from the Mekong River. (Photograph courtesy of Zeb Hogan.)

dynamited as part of a plan to enhance river navigation. Conservation biologists have set up a scheme whereby fishers telephone them day or night if they catch a Mekong giant catfish, which the biologists then purchase at market price, tag, and release away from the nets. This is a stop-gap measure, being used to save a small number of fish while working on longer-term conservation measures. The prospects for this species do not look good, and its threat status has now been raised to "critically endangered" by the IUCN (2003).

Overexploitation can also have unforeseen effects on biodiversity through trophic interactions among species in an ecosystem. A freshwater example that is currently receiving a great deal of attention involves the effects of reduced numbers of Pacific salmon on productivity of streams and their riparian vegetation in northwestern North America (e.g., Cederholm et al. 1999). All native Pacific salmon species die after they spawn, and their decomposing bodies provide a large proportion of the nutrients received by streams in their range. These nutrients have been acquired when the fish were growing during the marine phase of their life cycle. Experimental studies have shown a variety of effects of nutrients from salmon carcasses. For example, carcass enrichment of artificial streams has led to an eight-fold increase in densities of macroinvertebrates, which also increased twenty-five-fold in artificially enhanced natural streams (Wipfli et al. 1998). These effects have been shown to have important feedback to productivity of the streams for salmonids themselves, because juvenile salmon prey on many of these insects (Wipfli et al. 2003). Studies have also shown higher growth of riparian trees such as white spruce, *Picea glauca* (Helfield and Naiman 2002). Indeed, there has been preliminary success in matching records of the sizes of salmon runs in southeastern Alaska from 1924 to 1994 with tree-ring growth in Pacific coastal rainforests (Drake et al. 2002). All of these examples imply that stream ecosystems, as well as associated terrestrial components, will have been affected strongly by the many extinctions and depletions of salmon populations that have occurred in recent decades.

Biological Theory of Sustainable Exploitation

The examples in the preceding sections give a flavor of the great diversity of forms of exploitation and impacts on species and ecosystems. Some of these forms of exploitation, such as fisheries, hunting, and forestry in temperate countries, have been occurring under scientifically informed management. Because this is a chapter on "overexploitation," most of the examples that we have chosen have not been very encouraging. In fact, species and ecosystems show a wide variety of responses to exploitation. In this section we review the theory that has been advanced to explain how populations and ecosystems respond to exploitation, and tie this to management options.

Biological populations are by definition renewable, but why should we ever expect plant and animal populations to be able to withstand the elevated mortality that occurs with most forms of exploitation? The key is the ability of birth or death rates to compensate when we remove individuals from the population. As populations are reduced by exploitation, there may be reduced competition for food, territories, shelter, and a lower transmission rate of diseases. This can lead to greater birth rates or enhanced survival. The tendency for such components of fitness to limit populations at high density is known as density dependence (Figure 8.8). This does not mean that populations do not experience episodes of density-independent growth, as would occur after sudden environmental changes, for example. But the tendency of populations to fluctuate around some sort of mean value, rather than growing indefinitely, can be attributed to density dependence.

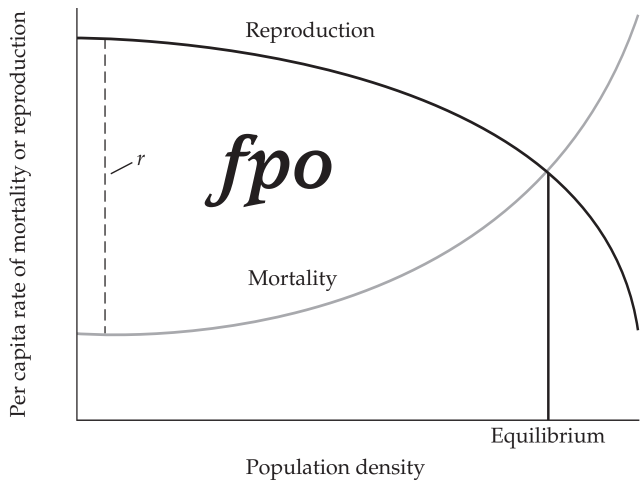


Figure 8.8 Density dependence stems from relationships between population density and per capita rates of birth and death. The difference between these at a small population size is the intrinsic rate of natural increase, r, and the density at which these rates are balanced is the equilibrium population size.

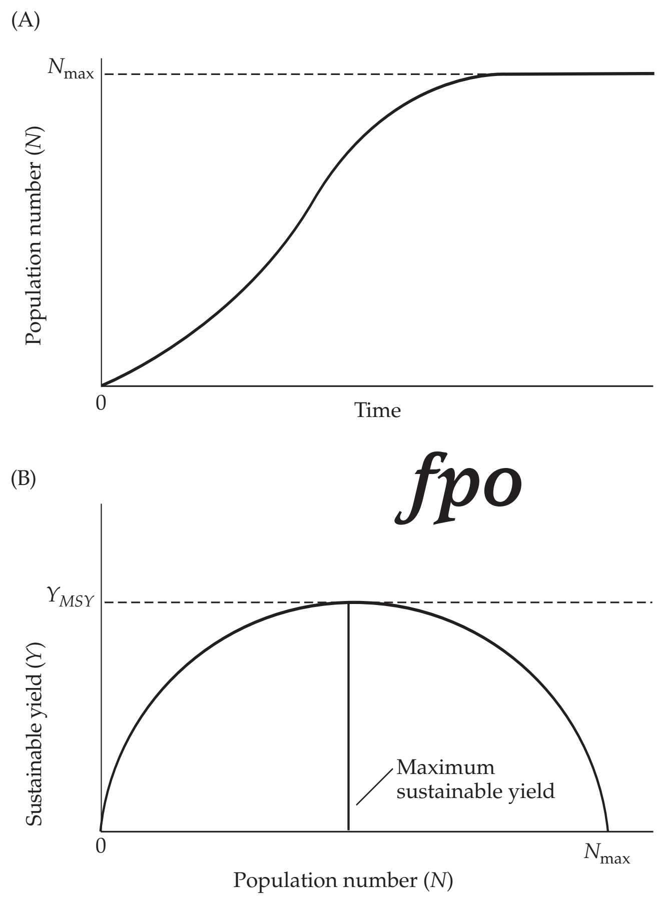


Figure 8.9 (A) Logistic population growth of a population up to a maximum population size, N_{max}. (B) Sustainable yield, Y (surplus production) against population size for the logistic case shown in (A). The maximum sustainable yield (Y_{MSY}) occurs at 50% of the maximum population size.

To understand sustainable and unsustainable levels of exploitation, we need to ask whether removal of individuals is equivalent to "thinning" the population, thereby allowing the survivors to grow more quickly or survive better, or is the removal occurring too rapidly for populations to compensate.

The simplest way to ask about the ability of a population to compensate for elevated mortality is to start with the logistic model, which gives the number of individuals at time t as:

$$N_t = \frac{N_{max}}{1+\left(\frac{N_{max}}{N_0}-1\right)e^{-rt}} \qquad [8.1]$$

Here N_{max} is the maximum population size (Figure 8.9A). This is often called the "carrying capacity," or equilibrium population size. None of these terms is meant to imply that populations remain stable, but they convey the idea of some sort of average size over a given period of time. N_0 is the initial number of individuals. The parameter r is the intrinsic rate of natural increase, that is, the difference between per capita birth and death rates at small population sizes where there is no density dependence. For many species we may want to substitute biomass for number of individuals, as in the case of fisheries, in which case we often see the terms B substituted for N.

Figure 8.9A shows the classical population growth rate that matches the logistic equation. This is the sort of trajectory that we would expect, for example, if we put a few *Daphnia* into a tank of water with phytoplankton as food. The population grows slowly at first, because there are few individuals producing offspring, but growth accelerates up to a point where the animals start running out of food, whereupon growth stops. In the real world, populations will be buffeted by changing environmental conditions, interactions with their predators, and so on. These can cause population fluctuations, cycles, or crashes. But the logistic is still a reasonable "default" option, conveying the essence of the potential for density-dependence. Specific details of the biology of species will determine whether the initial upward slope and final decline due to density dependence are steeper, shallower, or occur sooner or later than shown here.

The growth rate of this population before exploitation can be considered its surplus production, $g(N)$, and is given as:

$$g(N) = rN\left(1-\frac{N}{N_{max}}\right) \qquad [8.2]$$

This indicates, sensibly, that as the number of individuals, N, approaches the maximum population size, N_{max}, there is no growth, and even more sensibly, that growth stops when the population size is zero.

If the population in Figure 8.9A is being exploited at a steady rate, then its rate of change per unit time, dN/dt will be the difference between its surplus production and the yield, Y, for a given level of exploitation:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{N_{max}}\right) - Y \qquad [8.3]$$

The population's surplus production is the yield that can be removed sustainably. We can plot this property against different population sizes (Figure 8.9B). This gives us the classic dome-shaped yield curve that underpins all models of exploitation. This shows that the maximum sustainable yield (Y_{MSY}) occurs at an intermediate population size, which coincides with the inflection point in the logistic curve shown in Figure 8.9A. This makes intuitive sense: We can take the most from a population when it is at the size where it can grow most quickly. The dome does not have to be symmetric; a failure of the logistic assumption can cause it to lean to the left or to the right. For example, density-dependent processes such as cannibalism, competition, predation, or disease may occur at smaller or larger population sizes than depicted in Figure 8.9A (Sutherland and Gill 2001). If the curve leans to the right, we should allow the population to remain at higher numbers.

Stability of exploitation

In theory, we have discovered how many individuals we can take from the population to maximize the yield. But in practice, we will have a very difficult time taking exactly that number. For one thing, people rarely do what they are told, and common experience suggests that we have to assume that the population will probably be exploited at a higher rate than we recommend. Even the best-controlled fisheries and hunts are subject to the vagaries of uncertainty in the population estimates, or unforeseen circumstances such as weather conditions causing populations to behave in unpredictable ways. The question is, what happens when (not if) the population is exploited at a rate that differs from the one that theory suggests should be maximally sustainable? The answer depends on how the exploitation rate is managed.

Constant quota exploitation

Our formulation implies a system of exploitation in which the number of individuals removed is independent of the population size. That is, in Equation 8.3 we have subtracted Y from the surplus yield, rather than making Y proportional to N. This case is typically known as constant quota because the numbers removed are "constant" in the sense of being independent of the population size. Examples include fisheries that set quotas on numbers of fish that are caught, regardless of subsequent changes in the number of fish in the sea, or hunters who are given fixed limits that do not vary as the number of target animals goes up or down over time. This may sound extreme, because common sense suggests that quotas should be adjusted according to such changes in the quarry. And it is extreme. And so was the collapse of Peruvian anchovy in the 1970s, which occurred in part because people did not fully appreciate the implications of this assumption (see the discussion later in this chapter).

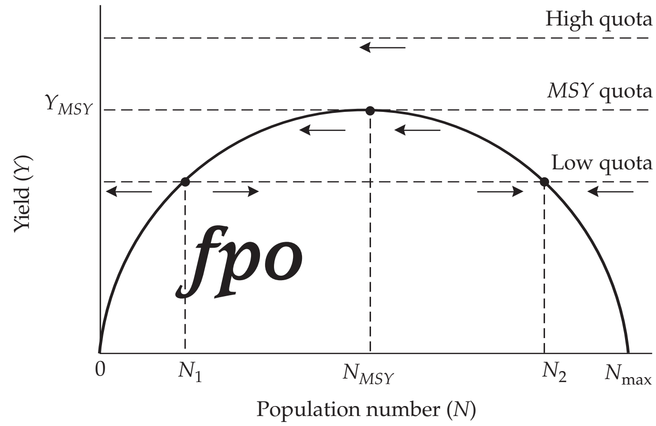


Figure 8.10 Equilibria and population stability under constant quota exploitation. The arrows indicate the directions of change in population size for each quota.

The constant quota situation is depicted in Figure 8.10, where each of three potential quotas runs horizontally across the graph, implying no relationship with population size. First, consider the high-quota line. Here, the yield exceeds the population's surplus production capability, perhaps because of illegal hunting activity, or because the population's resilience had been over estimated. The arrow beneath this line shows that with constant exploitation at this rate, the population will become extinct. Year after year the quota exceeds the population's ability to keep up with the elevated mortality. An alternative that seems more sensible is the MSY quota. However, this is a very risky target because it is impossible to get precise measurements of either the surplus production curve, or N. Furthermore, as we have argued, even if this were possible, there is still a good chance that we will be unable to set quotas sufficiently accurately to score a bulls eye when we shoot for the MSY point. If the population is at or smaller than N_{MSY}, the quota will exceed its surplus production and it will decline to zero. On the other hand, the N_{MSY} point will be stable if the population is initially higher, because although the MSY quota is initially higher than surplus production, as the population declines it will benefit from reduced density dependence. Still, given the difficulty of estimating MSY with precision, such a quota is dangerous. Finally, consider the low quota example. If the population is initially below N_1 it will still crash. However, if it is between N_1 and N_2, then its production will exceed the quota, and it will grow to N_2. If it is initially higher than N_2, it will be driven down to N_2 by the quota exceeding its surplus production. So N_1 is an unstable equilibrium and exploitation in that region should be avoided. In contrast, as long as we are sure the population is well above N_1, exploiting it with the low quota indicated would allow it to grow to a stable equilibrium at N_2. Here, finally, we have sustainable exploitation.

Proportional (constant effort) exploitation

A much more sensible way to set exploitation targets is to tie them directly to the size of the population. In practice, this is always bound to happen to some extent, because as plants and animals become scarce, people tend to switch to alternative species or other activities, even if no one is forcing them to do so. For example, local demand for game species in tropical forests tends to increase sharply when catches in the marine fishing sector fair poorly (Brashares et al. unpublished data), and tropical forest hunters become heavily reliant on smaller-bodied game species once large-bodied species are depleted (Jerozolimski and Peres 2003). Conservationists and resource managers amplify this kind of common sense by encouraging or forcing people to reduce pressures on populations that reach low abundance. So, unlike the case of constant quota above, we have exploitation effort that is proportional to the population size.

In this scenario the size of the yield, Y, will be equal to the exploitation rate, E, multiplied by the population size, N:

$$Y = EN \qquad [8.4]$$

From Equations 8.2 and 8.3 we know that a steady state will occur between the yield and the surplus production when $g(N) = Y$. This means that $g(N) = EN$. Therefore,

$$rN\left(1-\frac{N}{N_{\max}}\right)= EN \qquad [8.5]$$

We can rearrange this equation to find the equilibrium population size for any rate of exploitation, as long as E is below r:

$$N = N_{\max}\left(1-\frac{E}{r}\right) \qquad [8.6]$$

These equilibria are shown in Figure 8.11. The advantage of this form of management is that as long as the exploitation rate is below the intrinsic rate of natural increase, r, then all equilibria are stable. For example, whereas the high quota crashed the population under the constant quota scenario in Figure 8.10, here we find that if the population is initially below this removal rate, it will increase to N_1, and if it is above this point, it will decrease to N_1. The MSY is also stable, and it still occurs at half of the maximum population size.

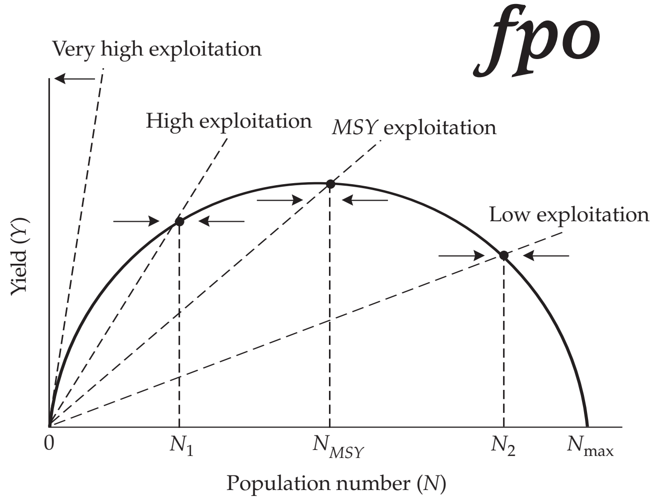


Figure 8.11 Equilibria and population stability under proportional exploitation (also called "constant effort exploitation"). Here, a constant fraction of the population is removed. The dashed lines have slopes E corresponding to different rates of exploitation. The arrows indicate the directions of change in population size for each scenario.

Figure 8.12 compares the risk of extinction from exploitation based on either constant quotas or proportional rates for a study of the American marten (*Martes americana*) in southern Ontario, Canada (Fryxell et al. 2001). The marten is a member of the weasel family (Mustelidae) found primarily in coniferous forests where it preys on a wide variety of small vertebrates as well as some invertebrates. Marten are trapped for their fur and trappers are granted licenses for exclusive access to trapping grounds. Fryxell et al. (2001) use a simulation model of data from commercial trapping from 1972 to 1991 to evaluate effects of different types of harvest. This analysis showed that whereas exploitation in proportion to the population size has a negligible chance of causing local extinction, this risk becomes quite high for moderate levels of exploitation under a constant quota system that does not track the population.

Threshold exploitation

The final class of exploitation strategies involves the use of population size thresholds to determine not only the rate of exploitation but also whether exploitation should take place at all (Lande et al. 1997, 2001). All populations are subject to random (stochastic) variations, for exam-

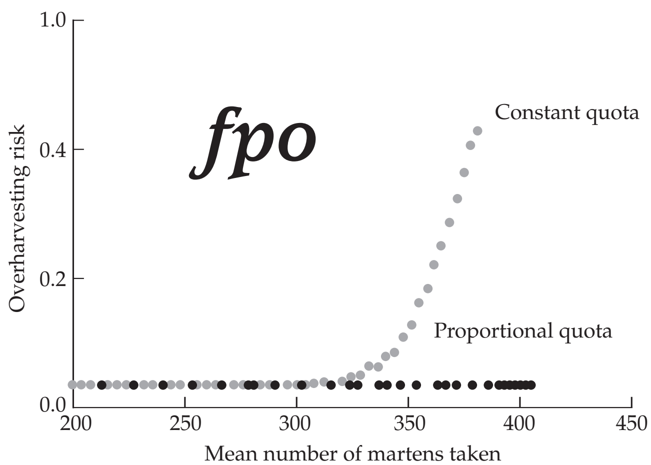


Figure 8.12 Probability of overexploitation (local extinction) in relation to mean yield of marten in commercial trapping in southern Ontario, Canada. The proportional quota line (black) refers to yields that track annual changes in the population whereas the constant quota line (gray) is based on the same absolute number of individuals being trapped each year regardless of population size.

ple, due to environmental variation. In the absence of exploitation, they will sometimes exceed their carrying capacities temporarily. We can take advantage of this by taking the entire "surplus" whenever the population is above its carrying capacity, but otherwise ceasing exploitation completely. This would maximize the cumulative yield while minimizing the chances of collapse. A more precautionary variant on this is to remove only a proportion of the surplus. This is an even safer version of the proportional exploitation method outlined above because it maintains the population near its carrying capacity. However, while such low rates of exploitation are excellent for conservation, it is difficult to convince people to accept such severe restrictions.

Bioeconomics

Understanding biological constraints is necessary to achieving a sustainable level of exploitation. But as we saw earlier in the chapter, we also need to understand the hunters' incentives and disincentives if we are to understand their impacts on the hunted, and provide management advice to mitigate such impacts. Bioeconomic models incorporate the costs and benefits of exploitation. Even in societies where exploitation is a necessity rather than a source of revenue, as in subsistence hunting, a cost–benefit framework can be very useful for understanding peoples' behavior (see Essay 8.2 for an example).

Open access and the tragedy of the commons

The "**tragedy of the commons**" (Hardin 1968) provides a powerful explanation for a lot of the damage that people are doing to the environment and to each other. Imagine you have sole access to the trout in a lake on your property. You will probably manage these trout quite carefully, because if you take too many, you will be the one who suffers in future. But if the pond straddles the boundary with your neighbor, then each of you should only take half the number you would take if you had exclusive access. Will you both be so prudent? Unless you get along very well with each other, probably not, because each person's self-restraint can be exploited by the other one. Imagine the outcome if we scale this example up to the North Sea, bordered by many countries, each with thousands of fishers, all competing for the same fish. The sea is a "common" fishing ground, and indeed, the massive over-fishing of the past century has been tragic for both fishers and their prey.

We can incorporate the tragedy of the commons into the scheme developed in the previous sections by assuming that the benefits from exploitation are directly proportional to the yield. So the dome in Figure 8.13 represents the benefits. Assume that the costs of exploitation are proportional to the effort necessary to obtain that yield. For example, in a fishery the more days spent at sea, the greater the costs of fuel and labor. This is depicted by the straight line rising from the origin. If we ignore the costs, the maximum benefits will be found at E_{MSY}, or the effort that provides the maximum sustainable yield. However, if the goal is to maximize profits, this would lead to a lower exploitation rate corresponding to the effort at which the difference between benefits and costs is maximized, at E_P. But the most important fundamental truth of

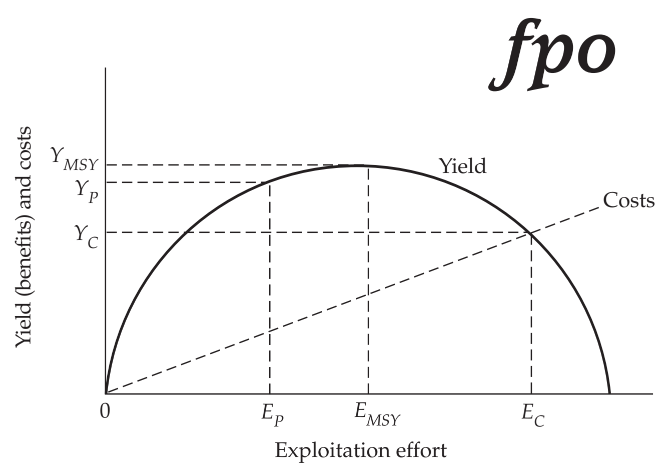


Figure 8.13 The economics of exploitation, represented by costs that are proportional to effort, and benefits proportional to yields. At E_P the profits are maximized, at E_{MSY} the maximum sustainable yield is obtained, and at E_C the costs are equal to the benefits. Note that unlike Figures 8.10 and 8.11, the x-axis here represents fishing effort (which increases from left to right, corresponding to population number decreasing from left to right).

ESSAY 8.2

Using Economic Analysis to Bolster Conservation Efforts
Marine Aquaria and Coral Reefs

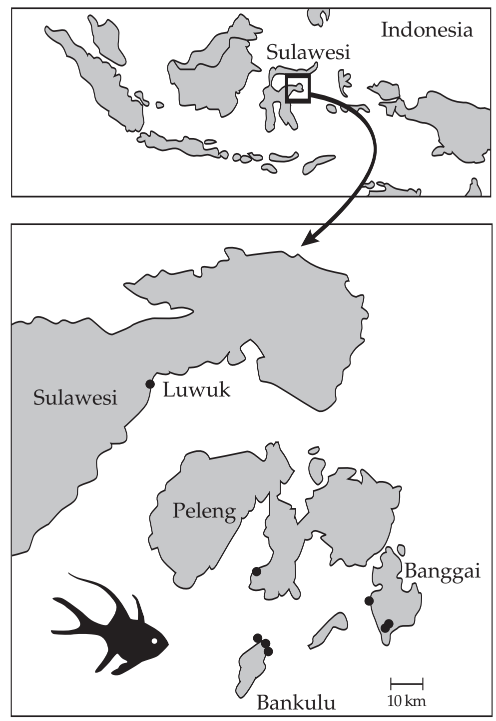
Gareth-Edwards Jones, *University of Wales, Bangor*

Advances in technology combined with increased interest in marine systems have contributed to a large increase in American households keeping marine aquaria. As part of the large global business associated with establishing and maintaining these aquaria, approximately 350 million fish are harvested annually from the wild and sold worldwide with a value of $963 million (Young 1997). This continued wild harvest is necessary as some species of aquarium fish do not breed well in captivity. Some of the more popular aquarium species are associated with coral reefs, and 85% of aquarium fishes are caught from coral reefs around the Philippines and Indonesia. Catching these fishes can be an important source of income for some communities, but it is increasingly happening on a large scale and there are 4000 aquarium fish collectors in the Philippines alone.

A network of traders are involved in the marketing of the fish; the fishermen themselves may sell to local traders who then sell to exporters and so on. There are significant financial gains at each step in the marketing chain. For example, an orange and white striped clownfish costs 10 cents when bought from a Filipino collector, but sells for $25 or more in an American pet store (Simpson 2001). Thus, traders in developed countries typically make the largest gains, while collectors or even the first traders make pennies. Because the returns to collectors are so low, there is room for conservation alternatives to be attractive; it does not take as much return to exceed the earnings of the people supplying the fish.

The impacts of collecting these fishes from the wild are quite varied. When using traditional netting techniques for catching the fish the most direct impact is a reduction in the population density of the harvested species, as shown for the Banggai cardinalfish (*Pterapoggon kauderni*) in Sulawesi, Indonesia (Kolm and Berglund 2003) (Figure A).

(I)



(II)

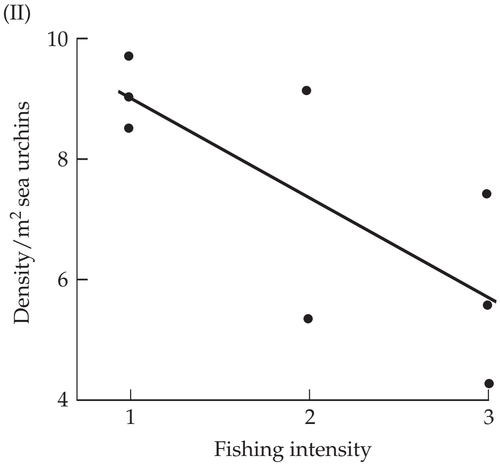


Figure A (I) Map of the Banggai Archipelago of Indonesia, showing study sites as black circles. The Banggai cardinalfish is pictured in the lower left corner. (II) Correlation between Banggai cardinalfish density and the intensity of fishing at eight separate sites in the Banggai Archipelago near Sulawesi, Indonesia. Because the cardinalfish is associated with sea urchins, their density is expressed per m^2 of sea urchins on the sea bed. Intensity of fishing was estimated from interviews with local people. Banggai cardinalfish are caught by nets only, so reductions in density are solely related to fishing pressure, not to reef destruction (Modified from Kolm and Berglund 2003.)

While traditional forms of harvesting can reduce species densities, an issue of greater concern is the use of cyanide to catch the fish. Fishermen typically crush hydrogen cyanide tablets in a squeeze bottle and squirt the resulting liquid into the crevices where the reef fish hide. The cyanide triggers asphyxiation or muscle spasm in fish, stuns them, and makes them easier to catch. These methods have been used since the 1950s and are believed to have quite a large impact on fishes and the coral reefs themselves. Experiments have tested the response of 10 species of coral to concentrations of hydrogen cyanide lower than those typically used by fishers. Eight of the coral species died immediately, and the other two died within three months. Death occurred because the cyanide disrupted the relationship between the coral and its symbiotic zooxanthellae. Doses as low of 50 mg/L cause death of the zooxanthellae, and one spray (approximately 20 cc) can kill the corals over an area of 5 m^2 within 3–6 months. These impacts are of concern as Southeast Asia has 30% of the world's coral reefs, and these have been declining in quality due to a variety of factors, of which cyanide fishing is but one. Now only 4.7% of Philippine and 6.7% of Indonesian reefs are in perfect condition and quite naturally these are the reefs targeted by collectors. The cyanide also affects fishes themselves. Half the poisoned fish die on the reef, and 40% of those caught alive die before reaching an aquarium (Simpson 2001).

Estimates of the economics of this practice suggest that the profitability of cyanide fishing to the fishermen is about $33,000 per km^2 over 25 years (10% discount rate). The direct losses to fisheries total $40,000 per km^2 and the tourism losses can range between $3,000 and $436,000 per km^2 depending on location (Cesar 1997). The nonuse costs of losing the coral reef are likely to be larger than these direct values.

Solutions?

This is an interesting situation where poor local people are seeking to harvest a local resource to sell it to richer Westerners, but a side effect of this harvest is the loss of another valuable resource. The marketed resource is nonessential to Westerners, (i.e., we could all live without a marine aquarium if we had to), but we like the aquariums, and many conservationists may argue that through keeping aquaria, people's interests in marine conservation could be heightened. So what should we do?

The solution seems to be to permit a sustainable harvest of fishes caught in a nondestructive manner. Attempts to achieve this can be legislative; for example the application of international law like CITES (Convention on the International Trade in Endangered Wild Fauna and Flora) to the relevant fish species could stop all trade in these species. Alternatively, tighter import controls could be implemented in the destination countries (e.g., in North America and Europe) whereby only fish harvested to approved standards would be permitted entry. While some legislative backing of this nature could be beneficial, in practice it will be very hard to police.

Alternatively, it may be possible to achieve more sustainable harvest by apportioning property rights to different sets of actors. Currently most marine fisheries are open access, and because of this are susceptible to the so-called "tragedy of the commons." In theory the solution to this is to allocate property rights to different groups of people. In the presence of property rights, the fishermen should seek to manage their resource with a long-term perspective, as opposed to the extreme short-term perspective that open access encourages (Ostrom and Schlager 1996). The allocation of property rights to fishermen is on-going around the world; for example, the Chilean government is offering the rights to harvest a benthic gastropod *Concholepas concholepa*, known locally as "loco" (Castilla and Fernandez 1998). This involves allocating certain areas of seabed to defined groups of local people from local communities who then manage them collectively.

While the theory of property rights is simple, recent work on the Chilean experience shows that the allocation of property rights is not a panacea and can lead to considerable social tension between different groups in a community. One important issue in all such efforts relates to policing the agreements, as it is difficult for hard-pressed officials to spot breaches of agreements at sea. In the absence of official policing, disagreements between groups about who can harvest where can become difficult, if not violent. These sorts of issues highlight the need for strong, functional institutions to help coordinate and manage any network of common property resources. While the need for such institutions is clear from theory and practice, their development can be a long and complex process requiring considerable effort from all involved (Ostrom 1990).

A third approach to dealing with these issues is being tested by the Marine Aquarium Council. They aim to set up a certification scheme whereby fish caught in traditional nets would be labeled in some way, which would enable consumers to buy these fish in preference to cyanide-caught individuals. If all consumers preferentially purchased certified fishes, then the advantage of using cyanide would disappear. To get such a certification scheme to work several issues have to be followed in parallel:

- There needs to be accurate identification of non-cyanide caught fishes near the point of capture. This can be done through testing samples of fishes in export warehouses for cyanide exposure.
- Fisherman need to be informed about the certification scheme and trained to use alternative collecting techniques, such as hand nets.
- Fishes caught without cyanide should be labeled so that fish buyers can choose to support practices that preserve reefs.
- Consumers should be educated about the environmental issues associated with the use of cyanide for catching fish.

Many such certification schemes are currently under development around the globe, particularly for food and forest products, and are easily linked to other management schemes such as the allocation of property rights. In most situations certified products will cost more than non-certified products. This is almost inevitable if, as in the case of aquarium fishes, the damaging fishing techniques are used because they are easier and cheaper than less-damaging techniques. But if consumers can be educated about the certification scheme, then the hope is that they would chose to buy the more expensive, certified products rather than the cheaper alternatives. In this way the combination of an efficient market economy and an educated consumer can bring real benefits to the environment. One of the most positive examples of this comes from Home Depot® stores in the U.S., patronized by millions of people each year. Home Depot® has begun selling and promoting certified forest products, thus vastly increasing their availability and visibility, and due to their enormous market share, reducing the costs.

Unfortunately, research done to date on food products suggests that ultimately price determines consumers' purchasing patterns. Generally only wealthier and more educated consumers are prepared to pay more for certified products. Thus if economic means are to be used to help conservation, there is a need to increase the general level of education and awareness in society—a continuing challenge to all conservation biologists. n exploitation revealed by this diagram is that in open access operations, we can expect people to join the exploitation until their individual costs become equal to their profits, at E_C. Exploitation will proceed to this risky break-even point because people are competing with each other.

The lesson from this analysis is that open-access exploitation leads to much greater rates of exploitation than are most profitable or safest for the long-term survival of the population. This is tragic both for the resource and for consumers, because each individual is catching less than they could if they had fewer competitors. Governments often respond by providing perverse subsidies (Myers 1998; Myers and Kent 2001), leading to lower apparent costs, and hence encouraging further overexploitation (Repetto and Gillis 1988). The capital invested in many activities such as commercial fisheries and logging operations cannot easily be converted to other uses, making it difficult for people to leave the business when times are hard. Naturally, this leads to resistance against restrictions on exploitation rates. In fact, exploitation can have a one-way ratchet effect, with governments providing aid to encourage overexploitation when populations are already low, as well as supporting investment in the activity when times are good, to increase profits. The consequent over-capitalization leads to a one-way trip toward overexploitation.

Discounting

Even when people have exclusive rights to exploit a resource, they may still be tempted to exploit it heavily now, rather than conserve it for the future. This is because we place a higher value on current than on future worth. This is due to economic discounting (see Chapter 5). Discounting can have serious implications for efforts to restrain overexploitation of renewable resources (Clark 1976). For example, suppose you could either let a forest grow for 100 years, when the larger trees will fetch twice their current value, or chop it down now. Which should you do? From a purely economic perspective the most sensible thing might be to cut it now and invest the money because the interest may accumulate faster than the growth rate of the standing timber.

This carries a rather sobering message for conservationists: Even with small discounting rates that are well within reasonable bounds for economics, it may be economically rational to exploit populations to extinction rather than leaving them to provide future returns. This may be especially true for slow-growing species such as whales and hardwood trees, which take a long time to accumulate value. This does not imply that conservationists should roll over in the face of economics, but merely that they will need to consider more than the economic investment value of renewable resources to formulate cogent argues for conservation. As many of the chapters of this book make clear, this is not difficult.

Comparison of Methods for Calculating Sustainable Yields

There are many ways of putting the theory of sustainable exploitation into practice, depending on what people need to know, and how much time and money they can spend getting the information. For example, the International Whaling Commission uses some of the most sophisticated population models in the world to calculate the impacts of hunting on whale populations. Their models need to be robust, in order to stand up to the tremendous pressures exerted by those who are "for" or "against" whaling. Yet, to be used effectively, these models often demand a lot of information about the biology of whales that is not yet available.

Methods for calculating sustainable yields have been reviewed by Hilborn and Walters (1992), Milner-Gulland and Mace (1998), Quinn and Deriso (1999), Jennings et al. (2001), among others. Here we give only the bare minimum needed to understand the logic of each method and the pros and cons of using them.

Surplus production

Surplus production models are also called surplus yield models or simply "production" models. They are most often used in fisheries. The simplest ones require very little data, thanks to an ingenious derivation by Schaefer (1954) who pointed out that if you know how yields have responded to different levels of exploitation effort over time, then you could estimate the dome-shaped yield curve shown in Figure 8.9B. Effort might be measured as number of fishing boats out each day of the year, but in non-fisheries contexts it could also be the number of days spent hunting by all hunters in a given area per season. The corresponding yields might be the thousands of tons of bluefin tuna (*Thunnus maccoyii*) caught by the fishery each year (or number of mallards, *Anas platyrhincos*, shot per year in an area).

While this is a helpful simplification, it has several pitfalls that have led to extremely dangerous outcomes when this method was first applied. First, it treats each year as an independent replicate, which it will not be, due to lags in the ability of the population to respond to different levels of mortality. For example, cod in the North Sea take about four years to reach maturity. Therefore, no matter how much you reduce density dependence by reducing the number of adults in any given year, it will take four years for the survivors to produce offspring that become old enough to be caught. So if you double the fishing effort from one year to the next, you may catch twice as many fish. But obviously this cannot be due to the survivors producing twice as many young, because in that second year, those young fish will only be one year old, and not big enough to be caught. What is really happening is that more fish are caught with a doubling of effort simply because you are scooping more adults out of the population. You are not learning much about the ability of populations to respond to lower densities, you are simply cutting more deeply into your original stock of fish. The population is decidedly not in equilibrium with the fishery. This dangerous assumption was the downfall of the original production models (Hilborn and Walters 1992). The biggest collapse in the history of fisheries happened to the Peruvian anchovy (*Engraulis ringens*) in the early 1970s when the fishery was operating at a level that a surplus production model suggested to be safe (Boerema and Gulland 1973).

A number of much more sophisticated surplus production models have been developed since the rise and fall in popularity of the original Schaefer version (Polacheck et al. 1993; Schnute and Richards 2001). While these require more information than the elegantly simple early version, they can get around the dangerous equilibrium assumption. In fact, in fisheries they have been shown to sometimes outperform more complex models.

Yield per recruit

Yield-per-recruit models were developed originally as part of the "dynamic pool" concept in the landmark fisheries book written by Beverton and Holt (1957). The dynamic pool refers to models that keep track of separate processes that add to a population, such as recruitment and growth, or that subtract from it, such as natural mortality and fishing mortality. The basic principle can be applied to many other forms of exploitation.

Imagine a species that becomes more valuable as it ages, due to increasing size. Older fish provide more meat and older trees provide more wood. If exploitation is weak, most of the fish or trees will be big when they are taken, which is good. But if we wait too long, natural mortality will have taken its toll and there won't be as many individuals available to us. Yield-per-recruit models search for the level of mortality that maximizes the yield under this tradeoff between numbers and value. Here, a "recruit" is defined as an individual that has become big enough to be captured, not in the demographic sense of an individual that has reached maturity. Once the level of mortality has been found that maximizes the yield per recruit, we can calculate the total yield that will be obtained from a given level of mortality, if we know how many recruits are coming each year. That is how fishing quotas are set in many countries today (Jennings et al. 2001). Yield in this context is measured in biomass (number of fish caught in each age cohort multiplied by that cohort's mean weight).

This method requires information about how the value (often size) of individuals increases with age, as well as an estimate of natural mortality rates, because natural mortality determines the rate at which individuals die before we have a chance to get them. While growth data are often available, natural mortality can be difficult to estimate because scientists are usually late on the scene, with exploitation well underway by the time they start collecting data. This makes it difficult to disentangle natural from human-induced mortality. Yield-per-recruit models are the standard approach used in many temperate fisheries, but developing countries in the Tropics rarely have the resources to collect the growth and recruitment data needed to use this technique as a management tool.

Full demography

For some species there has been sufficient economic value or conservation concern to lead to the production of full-blown population models. These models combine information on vital rates such as births, juvenile survival, age at maturity, and adult survival. These parameters are often analyzed with matrix models in which populations are divided into discrete classes based on their age or stage in the life cycle (reviewed by Caswell 2001, and Lande et al. 2003). The most comprehensive models incorporate stochastic variation in parameters, and quantify uncertainty in the outputs.

Assessment of population growth rates is a common practice to deduce whether populations are declining as a result of direct exploitation, or exploitation of their habitats. For example, Lande (1988) used a model to make a preliminary determination of whether the Northern Spotted Owl (*Strix occidentalis caurina*) was in decline in the northwestern United States. This species was suffering from overexploitation of old-growth forests, prompting potential listing under the U.S. Endangered Species Act. A significant population decline would be indicated by a population growth rate, λ, that is significantly less than 1.0. Lande's model was based on estimates of clutch size, fledgling survival probability, the probability of successful dispersal, and survival of subadults and adults. The estimated population growth rate was 0.961. However, this estimate had a high degree of uncertainty, due to uncertainty in the underlying parameter estimates. When these uncertainties were scaled up through the model, the estimate of λ had a confidence interval of ± 0.0562. Therefore, λ could not be distinguished statistically from a value of 1. Further field research ensued, yielding better parameter estimates, and worse news for the owls, with significant population declines detected in 10 of 11 sites (Forsman et al. 1996).

Other uses of demographic analyses are to diagnose the reasons for population declines, and also to suggest the likelihood of success of various management procedures (Caswell 2001). For example, many populations of sea turtles suffer from egg collecting, hunting of adults, and bycatch of juveniles and adults in fisheries. Should conservationists concentrate on protecting eggs, juveniles or adults? Crouse et al. (1987) examined the effects on population growth rates of enhancing survival of each of these and other life stages in loggerhead turtles (*Caretta caretta*). They found that protection of eggs was far less important to population demography than protection of older life stages. This and subsequent research (e.g., Crowder et al. 1994, Heppell et al. 1996) contributed strongly to changes in conservation tactics, most notably through the adoption of mandatory turtle excluder devices in trawlers in the United States. Spatial analyses also can improve understanding of what management interventions may be most effective. For example, analyses of the coincidence of turtle sightings and shrimp trawling activities allows specific recommendations for area closures that can reduce bycatch mortality by avoiding larger concentrations of sea turtles in areas of lower economic importance (McDaniel et al. 2000). Finally, continued monitoring coupled with population modeling allows evaluation of how well management efforts are doing, and suggestions for improvements (e.g., increased compliance; Lewison et al. 2003) (Figure 8.14).

The simplest structured population models often ignore density dependence. That is, the probability of surviving long enough to move from one age class (or stage) in the life cycle and eventually reproducing, is kept constant as the population changes in size. As we argued earlier, this assumption may be defendable in some situations, but because the concept of sustainability is founded on density-dependent compensation, some people would argue that it makes little sense to ignore density dependence in exploitation models. A study of the edible palm, *Euterpe edulis*, showed the value of incorporating density dependence explicitly (Freckleton et al. 2003). This edible palm is found in the Brazilian Atlantic forests. Edible "palm hearts" correspond to the apical meristem of this species. Extraction of the apical meristem kills the plant. Freckleton et al. (2003) modeled a population of edible palms divided into seven stages according to size of the plant and its reproductive state. Probabilities of surviving and growing from one stage to the next, as well as annual reproductive output, were calculated from field studies, which showed strong density dependence in these parameters. For example, seedlings (the first stage in the model), compete with each other for light and resources, and are also shaded out by high densities of adults (Silva Matos et al. 1999). Analyses showed that when the correct amount of density dependence in survival and growth from one stage to the next were incorporated, populations were predicted to be able to sustain considerably higher levels of exploitation before they become eradicated.

Adjustments based on recent results

If we can monitor either the population itself, or the numbers of individuals that are taken as a result of various management measures, then we can adjust the quotas each year to take account of new information. For example, in North America hunting licenses for waterfowl and mammals are allocated each year according to the health of the populations. So, if goose populations increase from one year to the next, the hunting season may be extended. Box 8.1 provides an example of this method applied to the setting of quotas for trapping marten in Canada.

Demographic rules of thumb

Parameter-hungry models are useless for the vast majority of the world's exploited species, because we usually lack even the most fundamental information about the biology of the organism and the activities of the people who exploit them (Johannes 1998). The cruel irony is that it is often the species that we know least about that are in most trouble from intentional or accidental exploitation. Most of the tropical vertebrates that are hunted for their meat fall into this category, as do most whales, sea turtles, sharks, and rays. Various demographic rules of thumb have been developed that seek to overcome this problem.

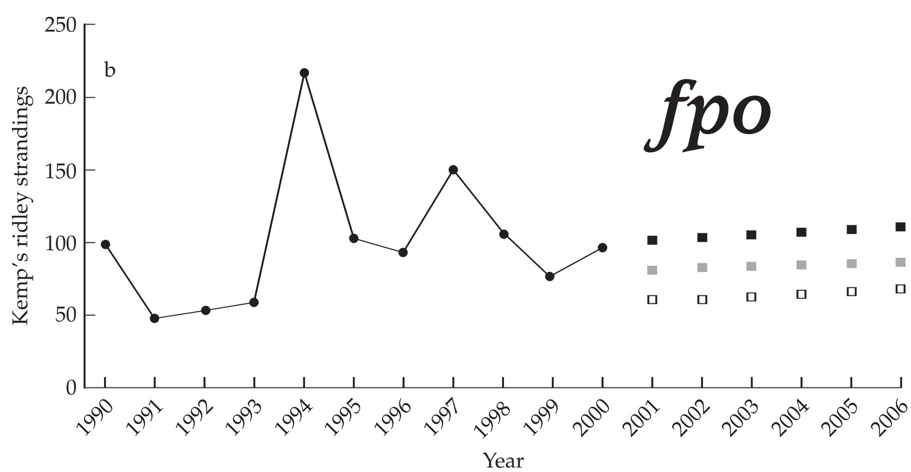


Figure 8.14 Projected annual strandings for Kemp's ridley sea turtles based on three potential levels of compliance by shrimpers in using turtle excluder devices in their nets. Black squares = compliance at 2000 levels, gray squares = 50% improved compliance over 2000 levels, and open squares = full compliance. Fluctuations in strandings reflects variation in compliance and sea turtle abundance in areas where shrimp fisheries are most active. (Modified from Lewison et al. 2003.)

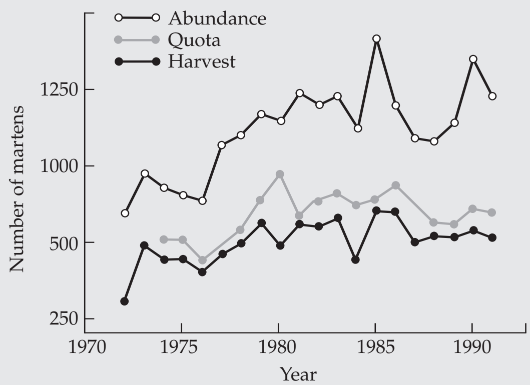
BOX 8.1 Adjustments of Quotas for the Marten (*Martes americana*) According to Previous Results

John Reynolds, *University of East Anglia*

Commercial trapping of martens in Ontario is regulated by trap-line quotas, which are issued by the Ontario Ministry of Natural Resources. Fryxell et al. (2001) analyzed data from a district in the southern part of the province where trappers were compelled to report how many animals they caught each year. Trappers had also been asked to submit carcasses voluntarily so that biologists could determine the age structure of the animals. Over the period of 1972–1991, 53% of the trapped animals were brought in for age determination. The numbers and ages of animals caught were the only information available to local managers, who used this information to adjust quotas upward or downward each year.

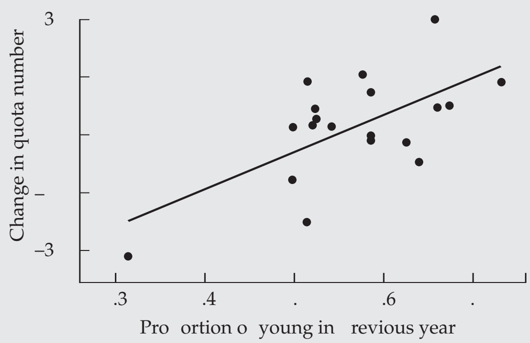
How successful were the local managers in guessing the right quotas according to recent trapping results? To answer that question, Fryxell et al. (2001) used an age-structured model to calculate population sizes and optimal quotas over the time period. They found that the marten population had varied three-fold over the 20 years, and that although the local managers did not have this clear information, they set quotas that matched this variation quite well (Figure A). The proportion of young animals in each year was correlated with the quotas that the managers set the following year (Figure B). This proved to be a very sensible strategy, because the proportion of young trapped was closely correlated with estimates of the annual rate of increase of the population (Figure C). Simulations by Fryxell et al. (2001) suggested that the highest average yield during this period would have been obtained if 36% of the animals had been trapped each year. This was remarkably similar to the average value of 34% that had been set by the local managers!

How did the local managers do so well? Close cooperation between managers and the trappers was essential, as were the strong links between the proportion of young animals trapped each year, the population growth rate, and the population size. This example shows that good cooperation combined with an ability to predict population growth rates can lead to effective conservation management, even in the absence of detailed information.



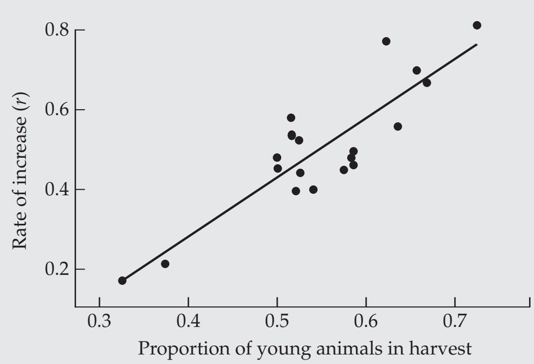
fpo

Figure A Data from commercial trapping of marten, *Martes americana*, in a district in southern Ontario, Canada. Estimated population sizes (open circles) were mirrored by quotas (gray circles) and number of martens harvested (black circles).



fpo

Figure B Changes made by local managers to quotas were related to the proportion of young that were trapped in the previous year.



fpo

Figure C The proportion of young trapped was a good predictor of estimates of annual population growth rates, calculated as $\ln(N_t / N_s)$, where N_t is the abundance at the start of the trapping season and N_s is the number of survivors from the previous year's trapping season.

One of the best-known rules of thumb has come to be known as the Robinson and Redford model, which was developed as a quick shortcut to assess whether exploitation of tropical mammals can be defined as sustainable (Robinson and Redford 1991). This model simply calculates the total annual sustainable production (population increments through births and immigration), assuming that the maximum potential production (P_{max}) occurs at about 60% of carrying capacity (K). This figure accounts for any density-dependent effects on population growth and is intermediate between the (MSY) at 50% of K, as used in classic logistic models of population growth, and models where MSY is reached at about 70% of K (McCullough 1982). The model is possibly more realistic for tropical forest vertebrates and is expressed as:

$$P_{max} = (0.6D \times \lambda_{max}) - 0.6D \qquad [8.7]$$

In this equation, D is an equilibrium population density estimate near K (or in a nonhunted area similar in structure and composition to the hunted area); and λ_{max} is the maximum finite rate of increase for a given species from time t to time $t + 1$ (measured in years), which depends primarily on the number of breeding females and the annual number of offspring produced per female. In addition, this method calculates maximum quotas for a species by assuming that the proportion of the maximum production that can be taken is 60% for very short-lived species, 40% for short-lived species, and only 20% for long-lived species. Estimates of maximum sustainable offtakes are then compared with hunting data (obtained from household interviews, counts of animal carcasses consumed at forest dwellings, and surveys of wildlife meat sold in urban markets) to determine whether the population production exceeds or is less than the demand within a given hunting catchment.

These data, however, cannot be easily translated into actual cull rates because the collateral mortality induced by hunters may be considerable or even exceed the number of kills that are actually retrieved and consumed. In the Brazilian Amazon, for example, the number of woolly monkeys (*Lagothrix lagotricha*) that are lethally wounded by shotgun pellets, but subsequently fail to be retrieved by hunters, can be far greater than those that actually reach consumer households (Peres 1991). Moreover, many studies are likely to overestimate production, and therefore sustainable hunting quotas, because reliable population density estimates are obtained from sites that are not comparable ecologically to the sites where hunting is taking place. Moreover, density estimates are often obtained from high-density sites, where field studies are most feasible, and then extrapolated to sites with much lower densities (Peres 2000b). Finally, λ_{max} can be highly variable, is rarely known for any given target species at the sites being evaluated, and can easily be overestimated if the only available data come from populations in captivity or long-term studies in high-quality habitats. Nevertheless, this model provides a preliminary measurement of hunting sustainability in poorly studied systems and has the advantage of simplicity and side-stepping more data-hungry approaches that could not be applied to most game hunting scenarios in tropical forests. There have been a number of applications (e.g., Fitzgibbon et al. 1995, Muchaal and Ngandjui 1999) and criticisms and extensions of the Robinson and Redford model (e.g., Slade et al. 1998, Peres 2000b, Milner-Gulland and Akcakaya 2001, Salas and Kim 2002), but it continues to be popular in tropical hunting studies.

Spatial and temporal comparisons

Most of the time, we have to settle for inferences about sustainability from simple evidence such as comparisons of densities of target species in locations that vary in the intensity of hunting, or interviews with hunters about changes in the abundance of their prey. Often these types of evidence can be combined to yield powerful conclusions about whether extractive activities are sustainable, but without being able to make precise quantifications of benchmarks such as maximum sustainable yields. For example, a study of hunting of Madagascar radiated tortoises, *Geochelone radiata*, used a combination of interviews with hunters, a comparison of changes in the species' range size over time, and comparisons of the tortoise's abundance in sites that differed in hunting pressure (O'Brien et al. 2003). The tortoises are collected for food and the pet trade. This study estimated that 45,000 tortoises are collected each year from southern Madagascar in the catchment of two cities. Hunters are traveling increasingly far to obtain their animals, and densities were highest in the most remote, unexploited sites. This activity is taking place in spite of the species being protected by law. This information, combined with documentation of range contraction, led the authors to conclude that the species is headed for extinction unless corrective measures are taken. Hunting rates could be reduced through education and awareness programs aimed at reducing demand, alternative income-generating schemes, and enhanced legal enforcement.

Sustainable Use Meets Biodiversity

This chapter has repeatedly run into contrasts between theory and practice, goals and implementation. A comparison between "north" and "south" illustrates the diversity of issues surrounding exploitation. In most temperate countries hunting, fishing, and forestry management protocols have been developed through a long history of trial and error based on biological principles. In most tropical countries, exploitation regulations are typically nonexistent or unenforceable. The concepts of game wardens, fisheries officers, bag limits, no-take areas, and hunting licenses are completely unfamiliar to the vast majority of tropical subsistence hunters and fishers who often rely heavily on wild animals as a critical protein component of their diet. In many tropical countries, wildlife is an "invisible" commodity and local offtakes are often not restrained until the stock is depleted. This is reflected in the contrast between carefully regulated and unregulated systems where large numbers of hunters may operate. For example, Minnesota hunters sustainably kill over 700,000 wild white-tailed deer every year, whereas Costa Rica can hardly sustain an annual hunt of a few thousand individuals without pushing the same cervid species, albeit in a very different food environment, to local extinction.

But even well-meaning management prescriptions can be completely misguided, bringing once highly abundant target species to the brink of extinction. The 97% decline of saiga antelopes (from >1 million to <30,000) in the steppes of Russia and Kazakhstan over a 10-year period has been partly attributed to conservationists actively promoting exports of saiga horn to the Chinese traditional medicine market as a substitute for the horn of endangered rhinos (Milner-Gulland et al. 2001). Saiga antelopes were finally placed on the Red List of Threatened Species in October 2002 following this population crash.

Even within cultures, there may be a diversity of perceptions about the objectives of management. For example, in countries that can afford to engage in fisheries management, the standard goal has been to achieve maximum sustainable yields of the target species. In the past 15 years, however, collapses of fish stocks and concerns about by-catches and damage to marine habitats have led to new objectives, such as obtaining sustainable yields while minimizing impacts on ecosystems (Reynolds et al. 2002). Not everyone agrees with these objectives, especially those who perceive that their traditional livelihoods are at risk from reduced quotas. Furthermore, there is also debate within the scientific community about what these objectives mean in practice, and how to implement them. In some sectors, such as forestry, managers are used to dealing with highly polarized debates between those who seek to preserve forests and those who seek to log them. Today, fisheries managers are facing similar scrutiny from many conservationists, who are asking new questions about impacts on habitats and ecosystems. Indeed, the past decade has seen the first listing by the IUCN of commercially exploited fishes as threatened with extinction (e.g., Atlantic cod), and the first cases of exploited marine fishes and mollusks being listed under the U.S. Endangered Species Act (e.g., smalltooth sawfish, *Pristis pectinata*, and white abalone).

In many instances failure to protect species from overexploitation has more to do with institutional short-comings than lack of scientific knowledge. European and North American fisheries scientists know a tremendous amount about the demography of the major commercially exploited fish species, yet this information has not prevented some species from reaching historically low population levels in the past decade. Of course it would help to know even more about the animals that we are trying to manage, such as impacts of low densities on reproductive behavior, trophic interactions in relation to habitat alterations, and links between environmental variability and recruitment. But translating this information into management action for the long-term benefit of fishers and fishes would still run into the age-old problem of lack of political strength in the face of criticism from those affected negatively by restrictions. In many developing countries, such problems are compounded by the dire lack of alternatives for food and employment. When combined with a lack of institutional structures to implement any policies that may be acceptable, it is easy to understand why exploitation often runs a course that is slowed only by accessibility of the resource.

As with most of the other conservation issues covered in this book, we feel that while the future holds some enormous challenges, it is by no means entirely bleak. For example, the adoption of precautionary principles in exploitation by many countries, combined with greater concern for impacts on ecosystems, is certainly a move in the right direction. We are also encouraged by the large number of imaginative programs in many countries that are aimed at giving local people incentive to make sustainable use of plant and animal populations and their habitats; Elizabeth Bennett et al. discuss some of these programs in Case Study 8.2 and Michelle Pinard et al. discuss them in Case Study 8.3 (see examples in Chapter 16, also see Case Studies 6.1 and 6.2). Indeed, there is a growing appreciation for the enormous economic and social value of ecosystem services from wild nature that far exceed the economic benefits of conversion to agriculture or other uses (Costanza et al. 1997; Balmford et al. 2003). For example, a forest can provide far more than just timber, including flood defense, carbon storage and sequestration, and pollination of adjacent crops. Many researchers are now working to find novel ways of rewarding local people for exploiting resources sustainably in return for benefits received by others. These are exciting times for integrating science with the policy of exploitation, and it is imperative that these efforts are successful if we are to meet the challenge of sustaining wild populations and their habitats.

CASE STUDY 8.1

Overexploitation of Highly Vulnerable Species

Rational Management and Restoration of Sharks

Julia Baum, Dalhousie University

"Sharks … may be considered as one of the richest 'strikes' in the only inexhaustible mine—the sea."
Barrett, 1928, *Scientific Monthly*

Anthropogenic impacts on natural ecosystems have almost always begun with the overexploitation of large vertebrates. Consequent species collapses or extinctions had markedly transformed terrestrial, freshwater, and coastal ecosystems by the early twentieth century, while oceanic species were still largely protected by their distant location and large geographic ranges. Oceans, it seemed, were too vast and their creatures too plentiful and widespread to be unduly impacted by humans. But in the past few decades, humans have come to dominate these ecosystems as well. Today, industrialized fishing fleets are ubiquitous throughout the world's oceans, reaching even the remotest locations and leaving few refuges for marine species. As a result, overexploitation now threatens the future of many large oceanic vertebrates, including whales, tunas, billfishes, and sea turtles. And sharks, rather than being one of the richest "strikes" in the ocean are one of the most vulnerable (Figure A).

Sharks are among Earth's oldest inhabitants, having evolved over 400 million years ago. Along with skates and rays, sharks comprise the subclass Elasmobranchii within the class Chondrichthyes, distinguished from bony fishes by their cartilaginous skeletons. The world's 350 shark species are a diverse group, ranging in size from dwarf sharks that reach less than 20 cm to the 12 m long whale shark, occupying habitats from freshwater lakes to entire ocean basins, and occurring in arctic and tropical waters from the surface to depths of a thousand meters. Our perception of sharks as ferocious predators belies the fragility of their populations. Sharks tend to grow slowly, mature at a late age, and give birth to few pups following a long gestation period—characteristics more reminiscent of marine mammals than fishes. These traits result in low intrinsic population growth rates, leaving sharks unable to withstand heavy fishing pressure, and with little compensatory ability to recover from over fishing.

Figure A Scalloped hammerhead sharks (Sphyrna lewini) swimming at Cocos Island, Costa Rica. (Photograph © Philip Colla www.oceanlight.com.)

fpo-hi-res-replace?

Localized shark fisheries that developed in the few decades following Barrett's description were characterized by "boom and bust" patterns. Fisheries for the soupfin shark in California and Australia, dogfish in Scotland, and porbeagle shark in the Northwest Atlantic all collapsed in under a decade.

Despite this history of population collapses and sharks' known vulnerability, their exploitation has intensified globally. Shark fisheries underwent a resurgence in the 1980s, driven both by the decline of traditional food fish species and by increased demand for shark products. Shark meat is increasingly consumed in Western societies, and the high demand for shark-fin soup in Asia has made shark fins one of the most highly valued marine products (Rose 1996). The practice of finning—removing the fins and returning the remaining carcass to the water—has now been made illegal in the Atlantic, but a worldwide ban is needed. Besides these directed fisheries, many sharks are caught incidentally, in fisheries targeting other species. In particular, pelagic longline fisheries, which target swordfish and tunas throughout temperate and tropical oceans, are the world's largest source of shark by-catch (Bonfil 1994).

Quantifying the impact of current exploitation levels on shark species has proven difficult. Sharks have typically been a low research and management priority because of their historically low economic value and because their catches are often incidental. As a result, basic population parameters such as age at maturity and longevity are unknown for many species, and shark catches have been poorly monitored. Fisheries observers usually monitor only a fraction of the overall fishing effort—perhaps 5% in domestic waters, and even less in international waters—and until recently most fisheries recorded shark by-catch in a generic "shark" category rather than identifying individual species. Thus, many shark assessments are done on aggregated species groups, obfuscating any variation in species' responses to exploitation. Compounding these problems are the wide ranges of many sharks, which commonly cross international boundaries, and even entire oceans, imposing serious constraints on our ability to monitor their populations.

New research provides strong evidence that coastal and oceanic shark populations have undergone rapid, large declines in the Northwest Atlantic (Baum et al. 2003). To demonstrate this, researchers analyzed the largest dataset sampling the Northwest Atlantic pelagic ecosystem, that of the U.S. pelagic longline fishery. This type of gear consists of mainlines tens of miles long suspended horizontally in pelagic waters (upper water column) by floatlines and buoys, with baited hooks attached on branchlines at set intervals. Thus it resembles a transect through the pelagic ecosystem. The fishery, which operates from Newfoundland into the Gulf of Mexico and south to Brazil, and includes both coastal and distant offshore waters, covers the entire range of Northwest Atlantic coastal shark populations and a substantial proportion of oceanic shark populations. Because fishers were required to record shark catches from each longline set and because their fishing effort was intense, researchers could estimate changes in abundance even for rare shark species: Between 1986, when fishers first started recording some sharks to species, and 2000, the dataset comprises over 200,000 longline sets and 117 million hooks! Researchers used statistical models to standardize catch rates for variations in the gear, location, and timing of sets. Estimated mean catch rates can then be compared across years as an index of a species' relative abundance.

All shark populations examined in the study are estimated to have declined by 40%–89% since the mid-1980s (Baum et al. 2003). Researchers estimate that since 1986 hammerhead sharks have declined by 89%, great white sharks by 79%, thresher sharks by 80%, and tiger sharks by 65% (Figure B). The remaining coastal sharks (CST), examined together because of the potential for misidentification in the logbooks of these similar looking congenerics, declined by 61% just since 1992. Blue and mako sharks are estimated to have declined by 60% and 40% respectively since 1986; oceanic whitetip sharks by 70% since 1992 (see Figure B). These latter species range across the entire Atlantic. Thus, while the data do not cover their entire populations, because other longline fisheries exert intense fishing pressure across the Atlantic, it is quite plausible that the pattern found in the Northwest Atlantic is representative of the entire region. Despite the enormity of documented declines, they are likely underestimates because they do not account for changes that occurred during the first three decades of offshore shark exploitation in the Northwest Atlantic (i.e., from 1957 to 1985).

Halting shark population declines is necessary if we are to avoid species extinctions; reversing them is essential if we are to restore populations to their former levels. Restoration requires that we understand the composition and abundance of natural shark assemblages, that is, that we have some knowledge of what it is we want to restore. Jackson (2001) notes that because most ecological studies began years, and sometimes

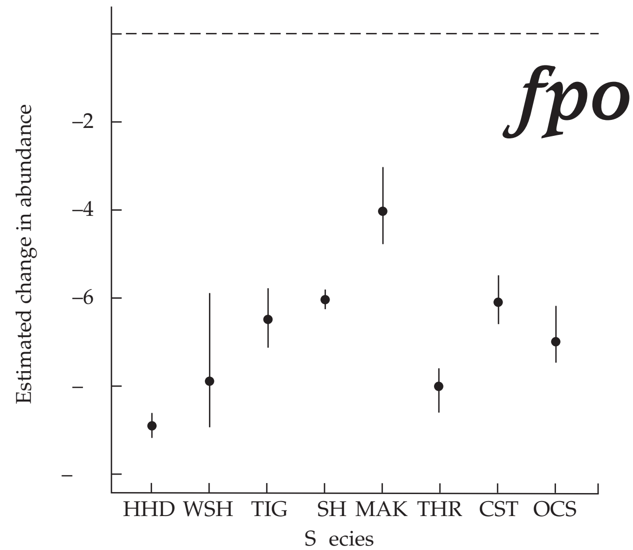


Figure B Total estimated change in relative abundance (± 95% confidence interval) for scalloped, great and smooth hammerhead (HHD), great white (WSH), tiger (TIG), blue (BSH), shortfin and longfin mako (MAK), common and bigeye thresher (THR) sharks between 1986 and 1999, and for bignose, blacktip, dusky, night, silky, and spinner (CST) and oceanic whitetip (OCS) sharks between 1992 and 1999.

centuries, after anthropogenic influences began, the former natural abundance of many large vertebrates in coastal ecosystems was fantastically greater than today. Assessments based on recent data alone obscure the original abundance of species, such that we may become complacent about species that are now rare. This lack of historical perspective on what is natural is coined the "shifting baseline" (Pauly 1995).

Estimating the baseline abundance of pelagic sharks in the Northwest Atlantic is possible because of the short history of disturbance in the open ocean compared to most other ecosystems: We need only look back to the early development of industrial offshore fisheries in the late 1950s. In the Gulf of Mexico, research surveys were conducted in the mid-1950s using pelagic longlines, to determine the potential for a commercial tuna fishery (Wathne 1959). These surveys provided some of the first biological information available on pelagic sharks, and on the region's offshore resources. Sharks were so abundant on these surveys that they damaged a high proportion of tuna on the longlines and were considered a serious problem. Researchers in the 1950s documented that between 2 and 25 oceanic whitetip sharks were usually seen around their vessel during gear retrieval (Wathne 1959). Oceanic whitetip and silky sharks were the second and fourth most commonly caught fishes overall on the pelagic longline sets, comprising almost 15% of the total catch, and 85% of all shark catches. Matching these data to comparable information from the current pelagic longline fishery reveals a very different picture. By the late 1990s these two species accounted for less than 0.5% of the total catch, and only 16% of shark catches, suggesting that substantial changes have occurred in the Gulf of Mexico's shark assemblage in less than half a century. Recent research papers on sharks have either not mentioned the oceanic whitetip shark or have dismissed it as a rare exception in the Gulf of Mexico, with no recognition of its former prevalence in the ecosystem. In contrast, a new analysis that incorporates these historic data estimates that oceanic whitetip sharks have declined by over 99% in 50 years, suggesting that this species is ecologically extinct in the Gulf of Mexico (Baum and Myers 2004).

Beyond the risk of species extirpations in the Northwest Atlantic, estimated shark declines may indicate broad ecosystem changes. Consumers such as sharks usually exert important controls on food web structure, diversity, and ecosystem functioning. The generality of the loss of pelagic consumers in the Northwest Atlantic is particularly worrisome: Most pelagic shark populations appear to be remnants of their natural abundance, and many other apex predators, including the swordfish and marlin, are drastically reduced. Although the ecosystem impacts of overexploitation in the open ocean remain largely unexplored, any changes are likely to be massive in scale given the vastness of these ecosystems, and are likely to be difficult to reverse given the life history of sharks.

The estimated loss of pelagic sharks in the Northwest Atlantic may also reflect a common global pattern of decline in shark species. Longlines and other pelagic fisheries are pervasive in all oceans, catching many of the same shark species as in the Northwest Atlantic, turning the risk of extirpation in that region into the risk of global extinction. Apart from the species discussed here, most other sharks face similar exploitation pressures and monitoring constraints. Around the world, most sharks are caught in multispecies fisheries, be it pelagic longlines, bottom trawls targeting other fishes, or directed shark fisheries that catch several species. This is problematic because the pursuit of productive target species will continue to drive the fishery, even after less-productive shark populations have collapsed. Finally, because of the difficulty in adequately sampling the large geographic ranges of shark populations, shark collapses and local extinctions may occur unnoticed. Local extinctions of two other elasmobranch species, the common skate (*Raja batis)* and the barndoor skate (*Dipturus laevis*), for example, were only documented after the fact (Brander 1981; Casey and Myers 1998).

Restoration of shark populations will require fundamental changes to their management. If we are to avoid extinctions of shark populations, fisheries need to be managed for the viability of the most vulnerable, rather than the most productive, species. This means that substantial reductions in fishing pressure in most fisheries that catch sharks are needed. Recovery targets that incorporate a historical perspective are needed, and management must work toward these. Effective international management plans need to be implemented and enforced to account for sharks' wide geographic ranges. Finally, as individuals we need to make responsible choices about the fish we consume by becoming informed about their status and the effect of fisheries on incidentally caught species.

Sharks have existed for over 400 million years, but have been threatened with extinction in less than 50. We may now be a critical juncture—where the decisions made today will decide the ultimate fate of these species.

CASE STUDY 8.2

The Bushmeat Crisis

Approaches for Conservation

Elizabeth L. Bennett, Wildlife Conservation Society, Richard G. Ruggiero, U.S. Fish and Wildlife Service, Heather E. Eves, Natalie D. Bailey, and Andrew Tobiason, Bushmeat Crisis Task Force

In Africa, forest is often referred to as "the bush," thus wildlife and the meat derived from it is referred to as "**bushmeat**." Bushmeat is eaten for subsistence, and is also traded in local and regional markets to supply protein to people in cities and towns.The bushmeat trade in Africa is a multi-billion dollar a year industry involving millions of animals from cane rats to elephants (Wilkie and Carpenter 1999; Fa et al. 2002), and millions of hunters, traders, market sellers, and consumers (Figure A, Mendelson et al. 2003). Scientific studies show that the majority of this unregulated, commercial hunting for wild meat is unsustainable and threatens biodiversity conservation goals (Robinson and Bennett 2000). Recent estimates of hunting rates in the Congo Basin show that a majority of species are hunted unsustainably (Fa et al. 2002). The expansion of bushmeat hunting poses a risk not only to the viability of wildlife species, but also to the livelihoods of the people who share the land with them (Figure B; Milner-Gulland et al. 2003), as well as to human, wildlife, and livestock health (Hardin and Auzel 2001; Wolfe et al. 2004).

Recommendations for promoting and regulating the bushmeat trade as a means to support rural livelihoods (Brown 2003) are generally not supported by current management ca-

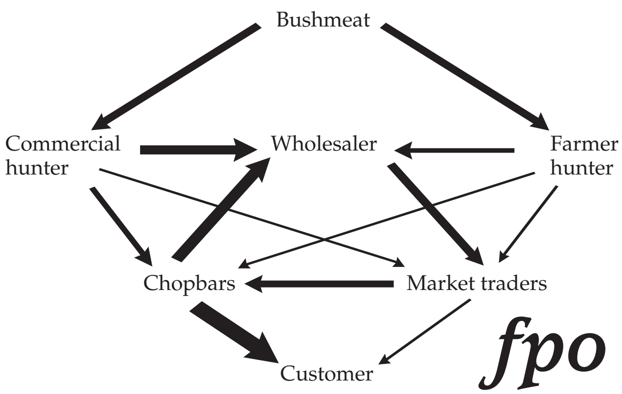


Figure A The cycle of the bushmeat trade.

pacity, policy, ecological, or economic realities (Fa et al. 2003; Wilkie et al. in press). While some suggest that a sustainable trade in wildlife for bushmeat can exist (Cowlishaw et al. 2005), these claims are generally based on species with high reproductive potential, such as rodents, in degraded habitats (Robinson and Bennett 2004). Such scenarios generally emerge after all the large-bodied mammals have already been hunted out (Bennett et al. 2002). Long-distance commercial trade in wildlife from tropical forests is almost inevitably unsustainable, and under the very limited circumstances in which it might be biologically feasible, strong management capacity must be in place. Such capacity is lacking across central Africa.

Robinson and Bennett (2000) document numerous root causes of the bushmeat crisis that must be addressed in efforts to conserve wildlife. Expanding human populations increase demand for bushmeat, while poverty and food insecurity create increased reliance on natural resources. Private companies in extractive industries usually do not engage in wildlife management planning, thereby facilitating increased access and unsustainable exploitation of wildlife resources. Governments and other land managers often have low capacity for monitoring and enforcement, or have poorly designed or implemented wildlife policies. Rural and urban human populations frequently have inaccurate perceptions of the limitlessness of wildlife and a general lack of awareness of wildlife use impacts. The poor, in particular, lack protein and income alternatives to bushmeat. These driving causes, compounded with the unsustainable commercial wildlife hunting levels impacting populations all across Africa have resulted in a crisis which threatens massive population declines; particularly vulnerable are the forest species which are an order of magnitude less productive than grassland species.

Solutions to the bushmeat crisis must simultaneously address these causes while supporting both undisturbed core areas and some regulated-use areas. Such plans may assure that wildlife and biodiversity are conserved for future generations and that the livelihoods of marginalized rural peoples are supported (Milner-Gulland et al. 2003). Protected areas are an essential component to any landscape management plan. Biodiversity conservation goals and alternatives for income must be coupled with appropriate wildlife regulations and enforcement to limit hunting to local areas and to nonendangered species with high reproductive rates (Eves and Ruggiero 2000).

Solutions include policy development, capacity building for education and enforcement personnel, development of both protein and income-generating alternatives, incorporating wildlife management planning into economic development and extractive industry activities (especially logging, mining, and road-building), and collaborative information sharing and management for development of best practices, adaptive management, and long-term monitoring. Such solutions necessitate the commitment and collaboration of government, nongovernmental organizations (NGOs), the private sector, and communities to support essential wildlife management planning activities that include governance, enforcement, and community participation to support biodiversity protection (Ruggiero 1998).

Progress in many of these areas is now being made. While the bushmeat issue was not well-known or understood before the late 1990s, it has since become a central issue for many conservation projects and international efforts (Bushmeat Crisis Task Force 2004). The Bushmeat Crisis Task Force (BCTF) was created in 1999 as the first coordinated effort by North American wildlife conservation groups and professionals from a range of disciplines to focus efforts on the growing unsustainable, illegal, and commercial trade in bushmeat in Africa and around the world. BCTF has prioritized four areas of engagement for this collaborative action: information management; engaging with key

Figure B Duikers on the back of a logging truck in Gabon. (Photograph by R. Ruggiero.)

decision-makers; formal education/training program development; and public awareness. Professionals from conservation, government, industry and development fields work with the BCTF staff and steering committee to identify and analyze available information, develop consensus on solutions, produce resources, and identify areas of collaboration potential. Major BCTF initiatives include working with key decision makers (KDM) in Africa and the U.S. toward policy development and mobilization of resources; the Bushmeat Education Resource Guide (BERG), which supports public education by zoological parks and other institutions; the Bushmeat Promise, a campaign designed to engage the public toward action; and the Bushmeat Information Management and Analysis Project (IMAP), which provides geo-referenced BCTF project and publication databases online, assembles bushmeat-relevant datasets from around the world, and gathers new data on relevant information in the Congo Basin. For more information about the bushmeat crisis and what is being done to address it, visit the Bushmeat Crisis Task Force website: www.bushmeat.org.

Since the establishment of BCTF and other bushmeat efforts, public awareness in the U.S. and Europe has been raised considerably. Only a handful of media articles were produced prior to 2000, but more than 750 were produced in the five years that followed (Bushmeat Crisis Task Force 2004). A number of awareness programs in urban and rural Africa communicate the impacts of the bushmeat trade on wildlife and human communities that enable consumers to make better-informed decisions (Obadia et al. 2002). Formal education and training tools are also developed in Africa and the U.S. to further educate key decision makers, field personnel, and the public (Bushmeat Crisis Task Force 2004; Bailey and Groff 2003).

At the international policy level, the World Conservation Union (IUCN) adopted an official bushmeat resolution in 2000, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) created a bushmeat working group in 2000, the Africa Law Enforcement and Governance (AFLEG) treaty signed in 2003 by both timber producer and consumer nations identified bushmeat as a priority concern, and the Convention on Biological Diversity (CBD) established a working group to review the issues related to nontimber forest products, including bushmeat.

Further evidence of an increased focus on addressing the unsustainable bushmeat trade is the Congo Basin Forest Partnership (CBFP). Officially established at the World Summit on Sustainable Development in September 2002, CBFP is an association of 29 governments and international NGOs collaborating to promote biodiversity conservation and improved livelihoods. CBFP partner organizations and their projects employ aspects of the bushmeat trade as indicators of the success of these landscape-level management efforts. Three leading success indicators are directly related to bushmeat: wildlife management planning and enforcement, protein and income-generating alternatives, and training and awareness to enable behavior change.

While numerous projects focus on one or two focal aspects of the bushmeat trade, there are a few that stand out as examples of the multi-stakeholder, multi-level effort that is essential to address the unsustainable bushmeat trade effectively, amidst a landscape of human development activities.

Wildlife Management in Logging Concessions

One example of such collaboration is the Project for Ecosystem Management of the Peripheral Zone of the Nouabalé-Ndoki National Park (PROGEPP), a wildlife management program based in the Kabo and Pokola logging concessions in the northern Republic of Congo. This project, initiated in 1999, is a joint effort of the Government of the Republic of Congo, the *Congolaise Industrielle des Bois* (CIB) logging company, the Wildlife Conservation Society (WCS), and the communities associated with the concessions. Aside from the government, the CIB logging company is the single largest employer in Congo and their logging concessions have acted as a magnet for immigration. The population of Pokola, the largest town near the concession, has more than doubled since 1999,from 7,200 to 16,000. Many would hunt bushmeat if not controlled and if other food options were unavailable. Instead, as a result of the project, wildlife populations are thriving, including gorillas, chimpanzees, elephants, and bongo, and people are maintaining a healthy mixed, protein-rich diet. The key to this success is conducting a complex of activities that include wildlife management planning, training, monitoring, education, and enforcement while simultaneously developing alternative sources of income and protein-rich foods.

Elkan and Elkan (2002) provide an overview of PROGEPP including three key rules adopted with regard to hunting in the concession—no snare hunting, no hunting of legally protected species, and no export of bushmeat outside the immediate community—a model established earlier with local communities associated with the adjacent Nouabalé-Ndoki National Park. The rules are made known to all workers and their families, especially truck drivers who often serve as intermediaries for illegal trade, as well as communities not affiliated with CIB, and are enforced by "eco-guards" at numerous checkpoints. In addition, conservation and land-use zoning was created according to traditional community zones and natural resource use. No-hunting areas, community hunting zones, and buffer zones around the Nouabalé-Ndoki National Park were adopted and established in the logging concessions.

CIB, like any large company working in an area of limited government capacity is in a position to dramatically influence how land and resources are being managed beyond their mandated exploitation, and fulfills many public services for its employees and nearby communities. As a complement to the social, health, and education programs CIB already provides, the wildlife management plan includes company provision of affordable livestock and protein-rich food alternatives.

Since the project's inception, snare rates are significantly reduced, endangered species are found even in areas where regulated hunting is taking place, and protein alternatives are being incorporated into the culture of the logging concession (Elkan and Elkan 2002). In addition, national policies regarding the provision and training of eco-guards within all logging concessions in Congo have been adopted.

Conservation is Good Business

The information emerging from PROGEPP identifies wildlife management planning and enforcement, partnership development, and provision of protein and income-generating alternatives as keys to bushmeat management success. Similarly, a project in Zambia involving an agricultural cooperative is showing signs of conservation success based on these same priority actions (Lewis 2004). The basic premise for this conservation program is that "food secure, farm-based communities with alternative sources of income to illegal use of wildlife can contribute positively to wildlife production" (Lewis 2004).. The Community Markets for Conservation and Rural Livelihoods (COMACO) efforts developed by WCS in collaboration with the Zambia Wildlife Authority (ZAWA) and the Ministry of Tourism, Environment and Natural Resources (MTENR) are designed to directly address the causes that drive overexploitation of wildlife for bushmeat in this region—food insecurity, need for income, poor land-use practices, and access to markets.

The COMACO project is innovative among conservation programs as it actively engages individuals and communities in a business cooperative and has been very effective in coordinating the support of the private sector. Producer depots supply a central trading post and households and communities can belong to the cooperative as long as they make a commitment to improving land-use practices and supporting conservation. That is, families must agree to a specific land-use management plan and producer-group conservation by-laws before being accepted in the program.

The COMACO project in 2003–2004 had over 750 conservation farming groups supplying depots with rice, chickens, groundnuts, and honey. The cooperative negotiates higher prices for these products, and in turn farming groups turn in hunting materials; over 30,000 snares and nearly 500 guns were collected during one three-year period. This model is most applicable to subsistence and cash-crop farmers who have enough food but not enough income, live at a medium density, and produce conservation-friendly products (Lewis 2004).

Critical to the entire initiative is the linked focus on wildlife protection. Experience across the entire tropical globe shows that providing protein and income alternatives alone do not reduce hunting. COMACO overcomes this by linking the cooperative with increased protection of wildlife; all cooperative members are also involved in wildlife enforcement, and their doing so is a prerequisite of their eligibility for the program. Hence, they are both benefiting from improved livelihoods while also protecting their local wildlife.

While these examples are promising it is important to note that such systems are site specific, require trained and committed experts in wildlife, community development, enforcement, and education and demand long-term commitment of personnel, financial resources, monitoring, and evaluation. Application of similar programs without such resources and capacity in place are unlikely to succeed. Caution should be used in responding to plans that support broad-scale policies of regulated trade in bushmeat as they are unlikely to lead to achieving either biodiversity conservation or development goals in the long, or even in the short-term. Quite the opposite, they are more likely to result in further impoverishment of rural communities and degradation of the natural resources upon which they depend. What is required is a global commitment and response that simultaneously and sufficiently supports nations that have identified the bushmeat problem as a threat to their natural and cultural heritage so that locally-designed efforts such as those described have the opportunity to succeed. This will include sufficient resources to enable training, enforcement, development of protein and economic alternatives, landscape-level management that includes protected area as well as multiple-use zones, and awareness programs for the public.

CASE STUDY 8.3

Managing Natural Tropical Forests for Timber

Experiences, Challenges, and Opportunities

Michelle A. Pinard, University of Aberdeen, Manuel R. Guariguata, Environmental Affairs, Convention on Biological Diversity, Francis E. Putz, University of Florida, and Diego Pérez-Salicrup, Universidad Nacional Autónoma de México

Applied forest ecologists, or silviculturalists, find managing the immense diversity of natural tropical forests for various goods and services a challenge, not only because of the complexity of these forests but because the requirements for sustainability are also diverse and complex. While the diversity may often seem overwhelming, natural forests in the moist tropics have many of the attributes that one might consider conducive to management. For example, they are productive in terms of the diversity of goods and services, and are known to be highly resilient; many areas that currently support old-growth tropical forest fpo-hi res

are the result of secondary forest succession after agricultural fields were abandoned hundreds of years ago (e.g., Darien, Panama; Bush and Colinvaux 1994). Despite the opportunities represented by these attributes, examples of good management are few. There is huge variation in forestry practices across the tropics, with some countries and forest owners moving toward more sustainable practices, while others continue to convert or degrade forest, often under the pretense of timber management.

Our aim is to explore some of the variation among forest management practices and to identify what seems to be working to improve management. We also discuss what we see as the main challenges and opportunities for sustainable management of natural tropical forests. Although we focus on the ecological, economic, and social bases of sustainable forest management for timber, our motivation is principally forest conservation. It may seem strange to be trying to save tropical forests with chainsaws and bulldozers, but the majority of the tropical forests that remain are only likely to be saved if they can be managed profitably for timber. In many cases, if people cannot make money from forests, then the forests will likely be destroyed in favor of some more lucrative land use, such as agriculture.

Figure A Selective logging typical involves cutting a few valuable species, and extracting them via skidders or draft animals. (Photograph by M. Pinard).

Background and Context for Tropical Forest Management

Because of the high diversity of tropical trees and the concomitant low population densities of marketable species, logging in natural forests in the tropics is typically selective; a relatively small number of trees above a threshold size (the minimum felling diameter) are felled and extracted. The logs are usually skidded out of the forest using bulldozers, rubber-tired skidders, farm tractors, or draft animals (Figure A). Where machines and draft animals are not available, large logs are often sawn into thick boards that are manually carried out of the forest.

Logging impacts on the residual forest vary with harvest intensity, level of pre-harvest planning and control, soil type and terrain, and forest stature and structure, among other factors (Figure B). Due to the selective nature of harvesting, forests are repeatedly logged after intervals of a few years to a few decades. Where logging is scheduled so as to achieve a sustained yield of timber, this approach to forest management is referred to as a polycyclic silvicultural system. Where properly designed, several harvesting episodes (or cuts) are scheduled within a rotation (nominally, the time it takes for a tree to grow to maturity). In theory, cutting cycle lengths and harvesting intensities are determined on the basis of the rate of commercial timber productivity. Harvesting also can be done more strategically, as a silvicultural treatment to promote the regeneration of ecologically similar groups of trees. For example, light-demanding tree species are favored by intensive stand interventions, whereas if less timber is harvested per unit area, more shade-tolerant species benefit. Unfortunately, the temptation of marketable standing timber often overwhelms efforts to secure sustained yields. As a result, timber-mining operations favor both slow-growing, shade-tolerant species, and fast-growing pioneers, not the species with marketable timber. Moreover, given the general lack of reliable data on forest productivity, managers establish cutting cycles by making educated guesses at how fast trees grow.

The deleterious environmental impacts of logging can be minimized if well trained and closely supervised crews fell and extract timber following a detailed harvest plan. In forests from Borneo to Brazil, loggers participating in research projects on "reduced-impact logging" have demonstrated that good logging practices are technically fea-

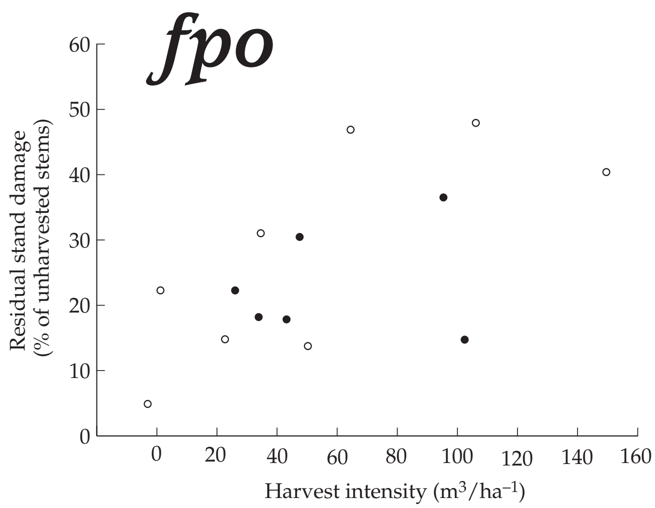


Figure B Variability in harvest intensities (m^3/ha^{-1}) and incidental damage to the residual stand (percentage of unharvested trees) across the tropics. Open symbols are areas in which harvesting was planned and controlled; closed symbols are areas in which harvesting was carried out in a conventional way (typical for the region, generally with little planning and control over operations). (Modified from Pinard et al. 2005.)

sible and that their application is financially viable (e.g., Holmes et al. 2002). Logging damage to the residual stand can be reduced by up to 50% when trees are felled in predetermined directions and logs are skidded out of the forest along pre-planned pathways (e.g., Pinard et al. 2000). Unfortunately, due to unsupportive forest policies, industry resistance to change, corruption, and the massive profits from exploitative logging, reduced-impact logging methods are seldom fully used (Putz et al. 2000).

The socioeconomic and political contexts in which forests are exploitatively logged or managed for the sustained yield of timber vary tremendously across the tropics. Most tropical forest-rich countries are poor in terms of most economic measures, many stagger under huge international debts to development banks, and some are poorly governed. The expertise needed to manage forests is often scarce even in countries with governments committed to maintaining a permanent forest estate. Furthermore, corruption can seriously impede the best-intended efforts at management. Making matters more complicated is the fact that forests may be owned by individuals, communities, corporations, or governments that grant concessions to industrial corporations and, all too often, claims of ownership overlap or are otherwise contested. Equally worrisome is the fact that although most of the large forest tracts that remain in the tropics are currently in remote locations far from markets, accessibility is rapidly increasing as major road-building efforts push back forest frontiers. It also should be noted that many forests planned for forest management are actually inhabited by people who are not involved in management planning and other decision-making processes. These social, economic, and political challenges are coupled with the biophysical challenges of managing little-known forests under what are often adverse environmental conditions.

High Financial Opportunity Costs of Maintaining Forests

Anyone promoting sustainable forest management must grapple with the high financial opportunity costs of managing forests relative to the profits from extracting all of the marketable trees and converting the forest to some more lucrative land use. By "opportunity costs," economists refer to the cost associated with giving up or postponing an opportunity, such as the chance to invest in alternative income-generating activities. This challenge is particularly powerful in many tropical countries where industrial agriculture, cattle ranching, and predatory logging pay so much better than maintaining forest under sustainable management (e.g., Pearce et al. 1999; Southgate 1998). Due to the "time value of money" (future profits and future costs are "discounted" in terms of current value, see Chapter 5), even unsustainable and eventually very costly practices can be financially very attractive. Market failures, particularly the serious undervaluing of forest goods and services, and policy failures, such as the provision of subsidies for unsustainable agricultural practices, further undermine efforts to promote sustainable forest management (Richards 1999).

Examples of how high opportunity costs interact with policy failures to promote deforestation in the tropics could be cited from almost anywhere, but the liquidation of forests in the 1980s in Costa Rica is especially illustrative. Costa Rican forest management is conducted on a strictly private basis. There are no government concessions, nor does the government directly manage production forests. Up until recently, the opportunity costs of managing forests for sustained timber production were apparently too high to make the option attractive (Kishor and Constantino 1993). In addition, Costa Rica's relatively young, volcanically-derived soils can support pasture for many more years than those established in less fertile locations such as in eastern Amazonia. Up until 1969, when the first modern forestry law was passed in Costa Rica, forests were legally considered impediments to land conversion for pasture, agriculture, and development activities. During the 1970s and 1980s, forest conversion was fuelled by government subsidies for cattle production, coupled with excessive regulation of private landowners that caused them to lose interest in managing forests on a sustainable basis. As a result, annual deforestation rates and consequent rates of forest fragmentation were very high (Sanchez-Azofeifa et al. 2001). The driving forces for forest conversion in Malaysia and Mexico were different from those in Costa Rica, but ended up with the same massive scale of deforestation.

Almost all Malaysian forests were claimed by the government and let out to logging concessionaires, but after logging, many were converted into oil palm plantations. Societal financial benefits from logging, while a great deal less than they might have been due to corruption and mismanagement, fuelled national development. In Malaysia today, slash-and-burn agriculture is rare and many people live in cities and work in high-tech industries but the biological costs of this development were immense.

In Mexico, the extensive deforestation that occurred in the 1960s and 1970s was an indirect result of the "green revolution," a global initiative to terminate hunger. The government implemented a "national deforestation plan" in which small-scale farmers were given the right to lands they converted to agriculture. The objectives of the program were to produce more agricultural goods and to relieve political pressure from landless farmers. Of course, the cost of such program was paid by society at large, as the value of tropical forests was simply ignored (Dirzo and García 1991; Masera et al. 1997; Turner et al. 2001).

Pressures to Overexploit

As countries rich in forests develop economically, the growth of capacity in wood-processing industries often exceeds the sustainable rate of supply of raw materials. Typically, where industries initially thrive on a large supply of timber from forest conversion and first cuts in heavily stocked, old-growth forests, with time, forests available for conversion decline and the industries need to rely on the more modest harvests from the permanent forest estate (Southgate 1998). This type of "boom and bust" cycle has occurred in many different parts of the tropics. For example, the government of Ghana is struggling to impose an annual allowable cut of only 1 million m^3, which is based on the best available growth and yield data but is far below the industry's capacity (Adam 2003). As in many other places, Ghana's timber-processing industry has great political power and is applying pressure on the government to increase the allowable annual cut beyond the maximum sustainable yield (Adam 2003). Any further increases in harvesting could only be achieved by reducing the lengths of cutting cycles or by increasing the intensity of each harvest by selecting more species or more trees of the favored species by reducing minimum felling diameters. Available data on standing volume, forest productivity, and ecological impacts suggest that these options are not ecologically viable in even the short term and are not economically viable in the long term.

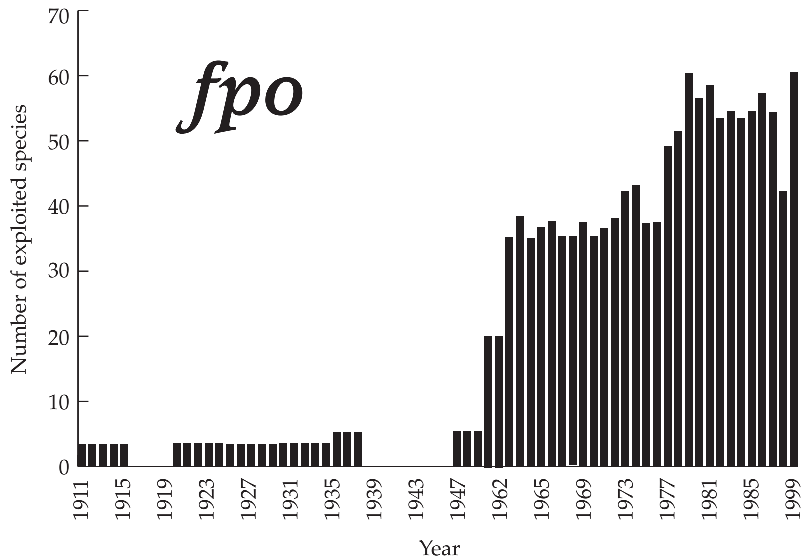


Figure C The number of tree species exploited for timber in Ghana between 1911 and 1989. Data compiled from annual reports of the Ghana Forestry Department. For those years without bars, no data were available. (Modified from Adam 2003.)

Insecurity of Land Tenure

Among the problems plaguing tropical countries, property rights issues figure prominently. Because forest management is a long-term endeavor, insecurity of land tenure, or at least guaranteed access to the resources the forest provides, is a necessary prerequisite for making investments in sustainable forestry. The failure of many tropical governments to assure landowners and forest concession holders that they will continue to control their property forever, or at least receive appropriate compensation if it is taken away from them, is a powerful justification for treating forests as if their natural resources are not renewable. But while security of tenure seems like an important prerequisite for sustainable management, it is not in itself sufficient to assure that forests will be treated as if the future matters. Under some conditions, providing secure tenure can promote deforestation if forest owners use their property as collateral for bank loans to buy cattle or chainsaws.

Marketing and Managing for More Species

Although technical challenges for tropical silviculture (e.g., timber harvesting and stand tending) tend to be secondary to socioeconomic and political problems, applied forest ecologists still have important roles to play. These roles are expanding as conservation and environmental service provisions are included more explicitly in management priorities. Furthermore, as markets begin to accept formerly noncommercial timber species, studies on the population biology and physiological ecology of these species become critical.

Tropical silviculture has its roots in the management of a few high value Asian and African species such as teak (*Tectona grandis*) and the African mahoganies (*Khaya* spp., *Entandophragma* spp.). In contrast to conditions in the first half of the twentieth century, forest managers in the moist tropics now can market dozens of species (Figure C). In Amazônas, for example, in the early 1990s, 90% of the state's timber production was based on four species, *Copaifera multijuga*, *Ceiba pentandra, Nacleosis caloneura,* and *Virola surinamensis*. With the exhaustion of the economically accessible stocks of these species, increased demand for sawn timber, and improvement of law enforcement, new industries have been established and the list of species used by industry has expanded considerably (e.g., to 70 species in one 40,000-ha project; Freitas 2004).

Long lists of marketable timber-producing tree species present managers with both opportunities and risks. Greater numbers of commercial species increases a manager's flexibility in selecting trees to be harvested, trees to be retained as seed sources, and future crop trees to be favored by judicious thinning around their crowns. This flexibility is important given the uncertainties in timber markets and the wide range of conditions appropriate for the regeneration and growth of valuable tree species. On the other hand, there is a risk of over-harvesting, particularly where there is little control of forest harvesting operations or where harvesting decisions are based solely on minimum felling diameters without concern for the regeneration requirements of the harvested species.

Variation among Forests

Tropical forests are justly famous for their overall species diversity, but ecologists have only recently recognized how much diversity there is *among* forests in the tropics. Similarly, forest managers are becoming increasingly aware that the silvicultural treatments they apply must be appropriate for the particular characteristics of the species and forests they are managing. For example, retaining canopy cover by carefully harvesting spafpo-hi res

tially isolated trees is critical for managing forests for shade-tolerant trees that are abundant in the subcanopy and understory. The same approach to harvesting light-demanding species, in contrast, would not contribute to sustainability because these species only regenerate in large clearings. Foresters in the Dipterocarpaceae-dominated forests of southeast Asia as well as those working in the forests on the Guyana Shield of South America, where many of the commercial timber tree species are at least moderately shade-tolerant, are justifiably adamant about reducing the impacts of logging on the residual stand. Conversely, silvicultural intensification, including exposure of mineral soil in large canopy openings, is being called for in seasonal forests on the rim of the Amazon where most of the commercially important timber tree species are light-demanding (Fredericksen and Putz 2003). While many forest management practices are widely applicable, such as the need to avoid sediment loading of streams with runoff from logging roads, no single silvicultural system is appropriate for all tropical forests.

Figure D Oil palm plantations are becoming more common, replacing selective logging practices in much of Southeast Asia. (Photograph by M. Pinard).

Variation among forests also means that some forests may be easier to manage than others. For example, some of greatest success in management of tropical forests has been in low diversity forests with a high density of commercial timber trees. Mangrove and swamp forests are particularly notable, although low diversity forests can also be found in uplands. For example, silviculture in oak-dominated montane forests in Costa Rica has proven to be straightforward partially because the canopy trees produce very large crops of acorns that satiate their seed predators resulting in high seedling densities in the understory (Saenz and Guariguata 2001; Guariguata and Saenz 2002). The lowland forests of Peninsular Malaysia are extremely diverse, but their management is also relatively easy because the canopy is dominated by species of Dipterocarpaceae that share silvicultural requirements. Unfortunately, the successful regeneration of an extensive area by good forest management has been erased as most of these areas have been cut to make way for oil palm plantations (Figure D).

Working With Less Valuable and Fragmented Forests

After widespread deforestation for cattle ranching, industrial farming and other agricultural uses, as well as oil palm and wood fiber plantations, the land left for natural forest management for timber is mostly remote, steep, rocky, or swampy. The conditions that render land unsuitable for more intensive uses also add to the challenge of forest management. Natural forest managers have to be comfortable working in remote areas and need to be very sensitive to environmental issues where slopes are steep and soils are easily damaged by heavy equipment. Additionally, the costs of applying even the simplest of stand improvement treatments, such as cutting vines on future crop trees, can become excessively expensive under these adverse conditions.

Managers should also become aware that timber-producing forests are getting smaller. In the neotropics, while the *annual* cutting area of a single logging company in the Bolivian Amazon might average 2000 ha, the *total* area of production forest of individual concessionaires or forest owners in Nicaragua, Costa Rica, and Honduras rarely exceed this same figure (Table A; one

TABLE A ***A Regional (Central versus South American) Contrast in the Estimated Areas of Mixed-Species, Lowland Broad-Leaved Forest Currently Managed for Timber***

Country	Mean (range)[a]	N[b]	Observations
Honduras	1342 (196–4149)	45	Includes community and privately-owned forest in the northern lowlands
Nicaragua	2814 (5–42887)	39	Includes the entire country; management plans granted during 1999 only
Costa Rica	62 (2–481)	404	Privately-owned forests in the northern lowlands (excludes *Carapa-Pentaclethra* forests on poorly-drained soils)
Perú	17460 (2697–49620)	31	State and privately owned forest, Amazonian lowlands
Bolivia	62420 (1171–365847)	95	Concessions and community forests, Amazonian lowlands

Source: Data from the following governmental institutions: Corporación Hondureña de Desarrollo Forestal (COHDEFOR) and Instituto Nacional Forestal (INAFOR). Data also from the non-governmental organization Fundación para el Desarrollo de la Cordillera Volcánica Central (FUNDECOR), and from the bilateral/multilateral research initiative BOLFOR and Center for International Forestry Research (CIFOR).
[a] The mean (range) of the forest area is measured in hectares.
[b] Number of sites.

notable exception to this pattern is the forest community concessions in Petén, Guatemala that reach thousands of hectares [ha] [Ortiz and Ormeño. 2002]). Although generalizing how fragmentation affects the biological sustainability of timber management is currently difficult, penetration of light and wind into fragmented forests from their edges results in increased flammability, a huge concern given the frequency of human induced ignitions of wildfires in many areas of the tropics (Laurance and Cochrane 2001). Also, vines and other forest weeds proliferate on forest edges, and can greatly increase the mortality of edge-exposed trees (Laurance et al. 2001). Seed dispersal by vertebrates can also vary between fragmented and extensively forested areas (Guariguata et al. 2002).

Biological considerations aside, a potential constraint on timber production in small fragments of forest relates to landscape-level planning of management operations. Forest fragmentation may limit the viability of selective logging schemes that might work well in extensive forests because of the low probability of securing an adequate volume of a given timber species. Even well intentioned policies can exacerbate this problem. By law in Costa Rica, for example, harvesting quotas for a given timber species should not exceed 60% of the total number of harvestable individuals (Comisión Nacional de Certificación Forestal 1999). Given that most Costa Rican forests destined for timber production are only a few tens of ha in extent, harvesting quotas guided by the "60%" rule may be financially unrealistic in many forest patches due to the small absolute number of trees.

How the Challenges of Tropical Forestry Can Be Confronted

Many approaches may be helpful in reducing unsustainable forestry practices. Among these, demand from consumers, adjusted markets, policy changes, and technological advances all may play a part, often together.

Pressure from Socially and Environmentally Concerned Consumers

Frustrated by continued unsustainable forestry practices in the tropics, environmentally concerned consumers of forest products are using their market power to promote better management. Initially, boycotts of tropical forest products were staged, but they back-fired—driving down the market price of tropical timber only served to increase the rate of logging as companies strove to maintain their profits. Much more successful has been an international program of voluntary third-party certification of good forest management practices coordinated by the Forest Stewardship Council (FSC).

While every year the area of tropical forest certified as well managed according to FSC Principles (Table B) increases by about 1 million ha, global demand for certified forest products continues to exceed the supply. Unfortunately, consumer awareness of the beneficial influences of selecting certified forest products in the U.S. still lags far behind Europe. As more and more Americans move from the countryside to cities and suburban areas where they have few opportunities to learn the difference between sound and unsound forest management practices, efforts to promote forest management as a conservation strategy will become increasingly challenging. Counterbalancing this trend, country of origin labeling, organic food certification, "fair-trade" programs, and marketing of "bird-friendly, shade-grown" coffee, are all helping to make consumers in the U.S. aware of their potential power to increase social welfare and protect the environment.

Paying the true value for tropical timber

One way to reduce the opportunity costs inherent in managing forests for timber is to capture the full economic value of tropical forests. Many of the values of forests are not included in traditional market transactions for timber and even most non-timber forest resources (e.g., rattan canes, Brazil nuts, and palm hearts). Although we recognize the roles of tropical forests as storehouses of fantastic biodiversity and for their effects on local and global climates, forest owners are generally not financially compensated for these values. The costs or benefits of forests that accrue to people other than the property owners are known as externalities. Economists are working with ecologists around the world to capture these externalities in economic analyses by creating markets for sequestered carbon, transpired water, and protected biodiversity. In these efforts, Costa Rica has been a world leader.

An innovative mechanism for forest conservation, Payment for Environmental Services, was included in Costa Rica's most recent forestry law and implemented through a decentralized body (National Forestry Financing Fund [FONAFIFO]). These payments represent an attempt to financially compensate small landholders for the services their forests provide including carbon sequestration, watershed functions, maintenance of biological diversity, and protection of scenic beauty, going some way to reduce the opportunity costs of maintaining forest cover.

Markets for sequestered carbon are developing all over the world, but use of carbon credits to promote forest conservation through improved management faces a number of serious challenges. Unfortunately, reforestation of deforested areas, afforestation of naturally nonforested areas (e.g., grasslands and savannas), and, to a lesser extent, strict forest protection have all received more support from international policymakers than reduced-impact logging and other changes in forest management that promote carbon sequestration (e.g., Putz and Pinard 1993). Part of the problem is that many policymakers cannot recognize the difference between well and poorly managed forests, and doubt that anyone else can either.

Policy and legal reform

Policy and legal reform are often prerequisite to the removal of disincentives to sustainable forest management. For example, *ejidatarios* (communal owners) or indigenous communities control 80% of the forest resources of Mexico. Initially they were

TABLE B ***Ten Principles of Forest Stewardship According to the Forest Stewardship Council***

Principle 1: Compliance with laws and FSC principles Forest management shall respect all applicable laws of the country in which they occur, and international treaties and agreements to which the country is a signatory, and comply with all FSC principles and criteria.
Principle 2: Tenure and use rights and responsibilities Long-term tenure and use rights to the land and forest resources shall be clearly defined, documented and legally established.
Principle 3: Indigenous peoples' rights The legal and customary rights of indigenous people to own, use and manage their lands, territories, and resources shall be recognized and respected.
Principle 4: Community relations and worker's rights Forest management operations shall maintain or enhance the long-term social and economic well-being of forest workers and local communities.
Principle 5: Benefits from the forest Forest management operations shall encourage the efficient use of the forest's multiple products and services to ensure economic viability and a wide range of environmental and social benefits.
Principle 6: Environmental impact Forest management shall conserve biological diversity and its associated values, water resources, soils, and unique and fragile ecosystems and landscapes, and, by so doing, maintain the ecological functions and the integrity of the forest.
Principle 7: Management plan A management plan—appropriate to the scale and intensity of the operations—shall be written, implemented, and kept up to date. The long term objectives of management, and the means of achieving them, shall be clearly stated.
Principle 8: Monitoring and assessment Monitoring shall be conducted—appropriate to the scale and intensity of forest management —to assess the condition of the forest, yields of forest products, chain of custody, management activities and their social and environmental impacts.
Principle 9: Maintenance of high conservation value forests Management activities in high conservation value forests shall maintain or enhance the attributes which define such forests. Decisions regarding high conservation value forests shall always be considered in the context of a precautionary approach.
Principle 10: Plantations Plantations shall be planned and managed in accordance with principles and criteria 1–9, and principle 10 and its criteria. While plantations can provide an array of social and economic benefits, and can contribute to satisfying the world's needs for forest products, they should complement the management of, reduce pressures on, and promote the restoration and conservation of natural forests.

Source: Modified from Forest Stewardship Council website, http://www.fscoax.org/.

obliged by law to sell their forest products to companies and thus had limited real control over the fates of their forests. This legal arrangement discouraged sustainable use and fuelled conflicts between the companies and the *ejidatorios*. The companies were not interested in sustainable management because their concessions were short term and they had no prospects of becoming forest owners. The *ejidatario*s, in turn, had little interest in the forests because they had such little control over their use. This conflict was resolved in the 1980s when a new law allowed *ejidatarios* to manage their forests directly. Today, the best examples of good forest management in Mexico come from *ejidatarios* and indigenous communities that recognize the long-term value of keeping their forests (Flachsenberg and Galletti 1998; Bray 2004). Moreover, some of the indigenous communities actively promote reforestation of lands formerly cleared for agriculture (Bocco et al. 2000).

Policy reforms are only effective in improving forest management practices when supported by the appropriate regulations and the institutions needed to implement and enforce the new policies. In Bolivia, for example, the passage of new forestry legislation in 1996 was followed by the creation of a new institution that was assigned the task of assuring compliance with the legislation. In the first year of activity, the new national forestry authority resolved millions of hectares of conflicting land claims, issued long-term cutting contracts, and increased tax revenue to the Bolivian government four-fold (Nittler and Nash 1999).

Technological strategies

Tropical silviculturalists have approached the problem of managing high diversity in tropical forests in various ways. In the 1960s, uniform silvicultural systems (e.g., shelterwood systems or patch clearcuts) were promoted as a means of domesticating the forest and increasing productivity by favoring a few light-demanding species at the expense of other more slow-growing, shade tolerant species. Polycyclic management systems (those more commonly used today) were considered less appropriate because of the high losses of volume caused by incidental damage associated with selective timber harvesting, the risk of a shift in forest composition to more shade-tolerant species, and the risk of over-harvesting if cutting cycles are too short (Dawkins and Philip 1998).

Domestication of tropical forests through intensive silvicultural interventions is generally not practiced today despite the fact that the silvicultural objectives of increasing stocking and growth rates appear to have been met in many forests treated as early as the 1950s (e.g., Alder 1993; Manokaran 1998; Osafo 1968). Two factors appear related to the lack of support for radical domestication—one is the relatively high risk of forest clearing for agriculture during the first decades in the management cycle when the forest holds little value, and the other is an assumed incompatibility between intensive silviculture and biodiversity conservation (Dawkins and Philip 1998; but see de Graaf 2000).

Typical approaches to timber management in natural tropical forests currently are conservative, aimed at reducing the impacts of interventions (Fredericksen and Putz 2003). To a great extent, reduced-impact logging has become synonymous with sustainable forest management, even though the former is only one component of the latter. Where light-demanding species are being harvested yet failing to regenerate, more intensive, locally imposed interventions are being promoted (Dickinson and Whigham 1999; Fredericksen and Mostacedo 2000; Snook 1996). For example, thinning interventions that liberate individual crop trees and maintain overall diversity in structure are sometimes recommended (see Wadsworth 1997 for review). In forests in which the commercial timber is produced by both light-demanding and shade-tolerant species, a mixed system would seem most appropriate. For example, single-tree selection might be applied where there is advance regeneration of shade-tolerant species, while in other areas large gaps might be created near potential seed trees to promote regeneration of light-demanding species (Pinard et al. 2000).

Looking Forward: Where Will the Next Decades Lead?

Whilst uncertainty in timber prices, politics, and priorities make it difficult to predict where the next decades will lead tropical forestry, a few pathways seem more likely than others. Overall, while deforestation rates are likely to remain high, forest management practices should continue to improve under the influence of the FSC's timber certification processes (see Table B). These improvements will be a consequence of more forest owners working towards certification, certified producers improving their practices through the monitoring and feedback programs built into the certification process, and in response to indirect influences of certification such as the exchange of information and experience among forest owners, managers, and regulators.

It is also clear that the focus of the timber industry will increasingly move to marginal lands where opportunity costs are low and natural forest management is relatively attractive as a land use. With widespread devolution of control of forest lands to indigenous groups and other rural communities, timber buyers will be motivated to develop socially acceptable approaches to company–community partnerships (Mayers and Vermeulen 2002). Farm forestry will also continue to develop, contributing to a shift in milling capacity to process smaller stems. As the big profit margins associated with exploiting old growth forest give way to the more modest profits associated with sustainable harvests, smaller operators are likely to be attracted to the business. Provision of technical support to many small operators may be more difficult than to fewer large operators, but levels of motivation and innovation may also be higher. Where managers are committed to sustainable practices, more silviculture will be introduced into management. Meanwhile, integration of inventory data, harvest planning, and monitoring operations into geographic information systems (GIS) will facilitate the implementation of more intensive and directed operations.

The trends in policy towards broadening societal participation in forestry are likely to continue with more efforts to devolve forest management to rural communities. But early experience gained across a broad range of socio-political and economic conditions emphasizes the need for strategies that combine both short- and long-term objectives (du Toit et al. 2004), institutional development, conflict resolution (Castro and Nielson 2001), and a recognition that in some cases, it will take a lot of time and effort for communities of subsistence farmers to become sustainable forest managers.

As pressure to place remaining tracts of natural forest under protection, the divide between those arguing for sustainable use and those arguing for complete protection may grow wider (see Dickinson et al. 1996 and Pearce et al. 2003 for summaries and primary literature therein), one consequence being increased competition for sources of funds for development. All progress towards sustainable forest management depends on good governance. Where corruption and illegal logging continue, it will be difficult to improve forest management practices (Ravenal et al. 2004).

The challenges facing tropical forest management are many. The field of natural forest management in the tropics needs energetic and dedicated people who are willing to put up with the rigors of tropical forestry work. Input from biologists is needed to ensure that the development of good practices, and the criteria and indicators used to assess and monitor these practices, are based on relevant biological and ecological information (Putz and Viana 1996).

Summary

1. Overexploitation is ranked second only to habitat loss as a cause of extinction risk in species whose status has been assessed globally. It involves the unsustainable use of wild animals, plants, and their products for purposes such as food, medicines, shelter, and fiber. The motivations for such exploitation are as varied as the plants and animals that are taken, ranging from subsistence hunting and fishing, to recreational and economic pursuits carried out by wealthy individuals and corporations. While most environmentalists are well aware that fisheries and large-bodied birds and mammals are often overexploited, recent studies have shown that these changes can be far more dramatic than previously recognized. Fisheries can reduce the biomass of targeted and nontargetted species by 80% or more in

10–20 years, and subsistence hunters in the Neotropics can create a vacuum of large-bodied species within 10–20 miles of their villages.

2. The biological theory of sustainable exploitation is firmly rooted in the field of population ecology, which seeks to understand the responses of populations to increased mortality of individuals through density-dependent compensation. This theory has produced a range of methods for estimating sustainable limits of exploitation from simple rules of thumb based on life histories to highly sophisticated models that are appropriate for only a small fraction of cases where the necessary input data are available. This theory cannot be put into practice to make exploitation sustainable without a clear understanding of the motivations of people who use wild animals and plants, the alternatives available to them, and the effects of management recommendations on their livelihoods. The "tragedy of the commons" often looms large in overexploitation in both terrestrial and aquatic ecosystems, exacerbated by "discounting," whereby we give wild populations a higher value for what we can get from them today than in the future. Yet there is a growing realization of the enormous economic and social benefits that we receive from ecosystem goods and services. With encouragement from processes such as the World Summit on Sustainable Development in 2002 and the Millennium Ecosystem Assessment, many people are now rising to the challenge of finding innovative ways helping people to reap the rewards of sustainable exploitation.

Please refer to the website www.sinauer.com/groom for Suggested Readings, Web links, additional questions, and supplementary resources.

Questions for Further Discussion

1. How can rich countries help encourage poor countries to exploit their plants and animals sustainably?
2. Actions taken to protect vulnerable species may affect some people's livelihoods. Because the decision to protect biodiversity is an expression of public will, do you think that governments have an obligation to assist families and businesses whose livelihoods are harmed by a conservation plan?
3. Many cases of overexploitation involve not only people's livelihoods, but their subsistence. How can we prioritize conservation versus human subsistence? What mechanisms might we foster to reduce this conflict?
4. In what ways can models help us exploit wild populations more sustainably? What are some of the limitations of the models typically used to estimate safe harvest levels?
5. Why is overexploitation so large a problem in the marine realm, and relatively less important in most terrestrial biomes?