

CHAPTER 6

Overexploitation

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In an increasingly human-dominated world, where most of us seem oblivious to the liquidation of Earth's natural resource capital (Chapters 3 and 4), exploitation of biological populations has become one of the most important threats to the persistence of global biodiversity. Many regional economies, if not entire civilizations, have been built on free-for-all extractive industries, and history is littered with examples of boom-and-bust economic cycles following the emergence, escalation and rapid collapse of unsustainable industries fuelled by raw renewable resources. The economies of many modern nation-states still depend heavily on primary extractive industries, such as fisheries and logging, and this includes countries spanning nearly the entire spectrum of per capita Gross National Product (GNP), such as Iceland and Cameroon.

Human exploitation of biological commodities involves resource extraction from the land, freshwater bodies or oceans, so that wild animals, plants or their products are used for a wide variety of purposes ranging from food to fuel, shelter, fiber, construction materials, household and garden items, pets, medicines, and cosmetics. Overexploitation occurs when the harvest rate of any given population exceeds its natural replacement rate, either through reproduction alone in closed populations or through both reproduction and immigration from other populations. Many species are relatively insensitive to harvesting, remaining abundant under relatively high rates of offtake, whereas others can be driven to local extinction by even the lightest levels of offtake. Fishing, hunting, grazing, and logging are classic consumer-resource interactions and in natural systems such interactions tend to come into equilibrium with the intrinsic productivity of a given

habitat and the rates at which resources are harvested. Furthermore, efficiency of exploitation by consumers and the highly variable intrinsic resilience to exploitation by resource populations may have often evolved over long periods. Central to these differences are species traits such as the population density (or stock size), the per capita growth rate of the population, spatial diffusion from other less harvested populations, and the direction and degree to which this growth responds to harvesting through either positive or negative density dependence. For example, many long-lived and slow-growing organisms are particularly vulnerable to the additive mortality resulting from even the lightest offtake, especially if these traits are combined with low dispersal rates that can inhibit population diffusion from adjacent unharvested source areas, should these be available. These species are often threatened by overhunting in many terrestrial ecosystems, unsustainable logging in tropical forest regions, cactus "rustling" in deserts, overfishing in marine and freshwater ecosystems, or many other forms of unsustainable extraction. For example, overhunting is the most serious threat to large vertebrates in tropical forests (Cunningham *et al.* 2009), and overexploitation, accidental mortality and persecution caused by humans threatens approximately one-fifth (19%) of all tropical forest vertebrate species for which the cause of decline has been documented [Figure 6.1; IUCN (International Union for Conservation of Nature) 2007].

Overexploitation is the most important cause of freshwater turtle extinctions (IUCN 2007) and the third-most important for freshwater fish extinctions, behind the effects of habitat loss and introduced species (Harrison and Stiassny 1999). Thus, while population declines driven by habitat

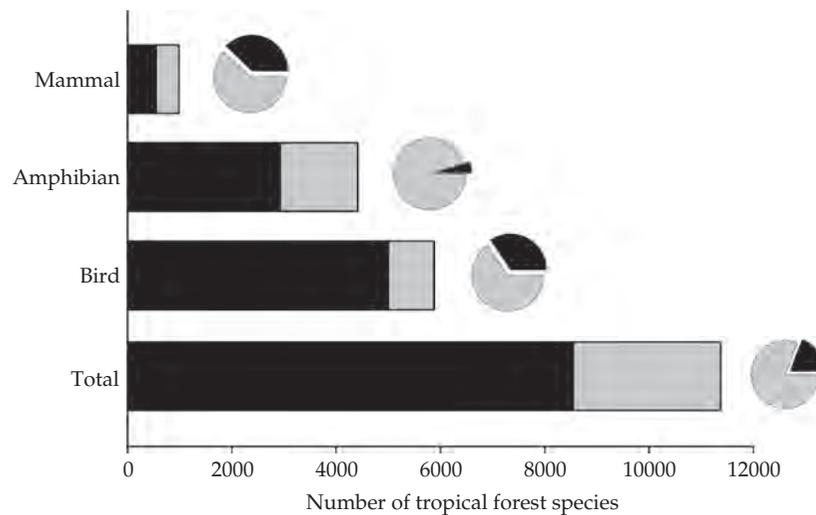


Figure 6.1 Importance of threats to tropical forest terrestrial vertebrate species other than reptiles, which have not yet been assessed. Horizontal bars indicate the total number of species occurring in tropical forests; dark grey bars represent the fraction of those species classified as vulnerable, endangered, critically endangered or extinct in the wild according to the IUCN (2007) Red List of Threatened Species (www.iucnredlist.org). Dark slices in pie charts indicate the proportion of species for which harvesting, accidental mortality or persecution by humans is the primary cause of population declines.

loss and degradation quite rightly receive a great deal of attention from conservation biologists (MEA 2006), we must also contend with the specter of the ‘empty’ or ‘half-empty’ forests, savannahs, wetlands, rivers, and seas, even if the physical habitat structure of a given ecosystem remains otherwise unaltered by other anthropogenic processes that degrade habitat quality (see Chapter 4). Overexploitation also threatens frogs: with Indonesia the main exporter of frog legs for markets in France and the US (Warkentin *et al.* 2009). Up to one billion wild frogs are estimated to be harvested every year for human consumption (Warkentin *et al.* 2009).

I begin this chapter with a consideration of why people exploit natural populations, including the historical impacts of exploitation on wild plants and animals. This is followed by a review of effects of exploitation in terrestrial and aquatic biomes. Throughout the chapter, I focus on tropical forests and marine ecosystems because many plant and animal species in these realms have succumbed to some of the most severe and least understood overexploitation-related threats to population viability of contemporary times. I

then explore impacts of exploitation on both target and non-target species, as well as cascading effects on the ecosystem. This leads to a reflection at the end of this chapter of resource management considerations in the real-world, and the clashes of culture between those concerned with either the theoretical underpinnings or effective policy solutions addressing the predicament of species imperiled by overexploitation.

6.1 A brief history of exploitation

Our rapacious appetite for both renewable and non-renewable resources has grown exponentially from our humble beginnings—when early humans exerted an ecological footprint no larger than that of other large omnivorous mammals—to currently one of the main driving forces in reorganizing the structure of many ecosystems. Humans have subsisted on wild plants and animals since the earliest primordial 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 and semi-subsistence farmers in tropical ecosystems, at varying stages of transition to an agricultural economy, still exploit a large number of plant and animal populations.

By definition, exploited species extant today have been able to co-exist with some background level of exploitation. However, paleontological evidence suggests that prehistoric peoples have been driving prey populations to extinction long before the emergence of recorded history. The late Paleolithic archaeology of big-game hunters in several parts of the world shows the sequential collapse of their majestic lifestyle. Flint spearheads manufactured by western European Cro-Magnons became gradually smaller as they shifted down to ever smaller kills, ranging in size from mammoths to rabbits (Martin 1984). Human colonization into previously people-free islands and continents has often coincided with a rapid wave of extinction events resulting from the sudden arrival of 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 and Wright 1967; Steadman 1995; McKinney 1997; Alroy 2001). These are relatively well corroborated in the (sub)fossil record but many more obscure target species extirpated by archaic hunters will remain undetected.

In more recent times, exploitation-induced extinction events have also been common as European settlers wielding superior technology greatly expanded their territorial frontiers and introduced market and sport hunting. One example is the decimation of the vast North American buffalo (bison; *Bison bison*) herds. In the 1850s, tens of millions of these ungulates roamed the Great Plains in herds exceeding those ever known for any other megaherbivore, but by the century's close, the bison was all but extinct. Another example is the extirpation of monodominant stands of Pau-Brasil legume trees (*Caesalpinia echinata*, Leguminosae-Mimosoidae) from eastern Brazil, a source of red dye and hardwood that gave Brazil its name. These were once extremely abundant

and formed dense clusters along 3000 km of coastal Atlantic forest. This species sustained the first trade cycle between the new Portuguese colony and European markets and was relentlessly exploited from 1500 to 1875 when it finally became economically extinct (Dean 1996). Today, specimens of Pau-Brasil trees are largely confined to herbaria, arboreta and a few private collections. The aftershock of modern human arrival is still being felt in many previously inaccessible tropical forest frontiers, such as those in parts of Amazonia, where greater numbers of hunters wielding firearms are emptying vast areas of its harvest-sensitive megafauna (Peres and Lake 2003).

In many modern societies, the exploitative value of wildlife populations for either subsistence or commercial purposes has been gradually replaced by recreational values including both consumptive and non-consumptive uses. In 1990, over 20 million hunters in the United States spent over half a billion days afield in pursuit of wild game, and hunting licenses finance vast conservation areas in North America. In 2006, ~87.5 million US residents spent ~US\$122.3 billion in wildlife-related recreational activities, including ~US\$76.6 billion spent on fishing and/or hunting by 33.9 million people (US Census Bureau 2006). Some 10% of this total is spent hunting white-tailed deer alone (Conover 1997). Consumptive uses of wildlife habitat are therefore instrumental in either financing or justifying much of the conservation acreage available in the 21st century from game reserves in Africa, Australia and North America to extractive reserves in Amazonia, to the reindeer rangelands of Scandinavia and the saiga steppes of Mongolia.

Strong cultural or social factors regulating resource choice often affect which species are taken. For example, while people prefer to hunt large-bodied mammals in tropical forests, feeding taboos and restrictions can switch "on or off" depending on levels of game depletion (Ross 1978) as predicted by foraging theory. This is consistent with the process of de-tabooing species that were once tabooed, as the case of brocket deer among the Siona-Secoya (Hames and Vickers 1982). However, several studies suggest that cultural factors breakdown and play a lesser role

when large-bodied game species become scarce, thereby forcing discriminate harvesters to become less selective (Jerzolimski and Peres 2003).

6.2 Overexploitation in tropical forests

6.2.1 Timber extraction

Tropical deforestation is driven primarily by frontier expansion of subsistence agriculture and large development programs involving resettlement, agriculture, and infrastructure (Chapter 4). However, animal and plant population declines are typically pre-empted by hunting and logging activity well before the *coup de grâce* of deforestation is delivered. It is estimated that between 5 and 7 million hectares of tropical forests are logged annually, approximately 68–79% of the area that was completely deforested each year between 1990 and 2005 [FAO (Food and Agriculture Organization of the United Nations) 2007]. Tropical forests account for ~25% of the global industrial wood production worth US\$400 billion or ~2% of the global gross domestic product [WCFS (World Commission on Forests and Sustainable Development) 1998]. Much of this logging activity opens up new frontiers to wildlife and non-timber resource exploitation, and catalyses 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 adequately reported. The best case studies come from the most valuable timber species that have already declined in much of their natural ranges. For instance, the highly selective, but low intensity logging of broadleaf mahogany (*Swietenia macrophylla*), the most valuable widely traded Neotropical timber tree, is driven by the extraordinarily high prices in international markets, which makes it lucrative for loggers to open-up even remote wilderness areas at high transportation costs. Mechanized extraction of mahogany and other prime timber species impacts the forest by creating canopy

gaps and imparting much collateral damage due to logging roads and skid trails (Grogan *et al.* 2008). Mahogany and other high-value tropical timber species worldwide share several traits that predispose them to commercial extirpation: excellent pliable wood of exceptional beauty; natural distributions in forests experiencing rapid conversion rates; low-density populations (often <1 tree/ha); and life histories generally characterized as non-pioneer late secondary, with fast growth rates, abiotic seed dispersal, and low-density seedlings requiring canopy disturbance for optimal seedling regeneration in the understory (Swaine and Whitmore 1988; Sodhi *et al.* 2008).

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. Economic logic often dictates that trees should be felled whenever their rate of volume increment drops below the prevailing interest rate (Pearce 1990). Postponing harvest beyond this point would incur an opportunity cost because profits from logging could be invested at a higher rate elsewhere. This partly explains why many slow-growing timber species from tropical forests and savannahs are harvested unsustainably (e.g. East African Blackwood (*Dalbergia melanoxylon*) in the Miombo woodlands of Tanzania; Ball 2004). This is particularly the case where land tenure systems are unstable, and where there are no disincentives against 'hit-and-run' operations that mine the resource capital at one site and move on to undepleted areas elsewhere. This is clearly shown in a mahogany study in Bolivia where the smallest trees felled are ~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 at only 1%, so that a 40-cm mahogany tree increases in value at about 5% annually, slowing down as the tree becomes larger. In contrast, real interest rates in Bolivia and other tropical countries are often >10%, creating a strong economic incentive to liquidate all trees of any value regardless of resource ownership.

6.2.2 Tropical forest vertebrates

Humans have been hunting wildlife in tropical forests for over 100 000 years, but the extent of consumption has greatly increased over the last few decades. Tropical forest species are hunted for local consumption or sales in distant markets as food, trophies, medicines and pets. Exploitation of wild meat by forest dwellers has increased due to changes in hunting technology, scarcity of alternative protein, larger numbers of consumers, and greater access infrastructure. Recent estimates of the annual wild meat harvest are 23 500 tons in Sarawak (Bennett 2002), up to 164 692 tons in the Brazilian Amazon (Peres 2000), and up to 3.4 million tons in Central Africa (Fa and Peres 2001). Hunting rates are already unsustainably high across vast tracts of tropical forests, averaging six-fold the maximum sustainable harvest in Central Africa (Fa *et al.* 2001). Consumption is both by rural and urban communities, who are often at the end of long supply chains that extend into many remote areas (Milner-Gulland *et al.* 2003). The rapid acceleration in tropical forest defaunation due to unsustainable hunting initially occurred in Asia (Corlett 2007), is now sweeping through Africa, and is likely to move into the remotest parts of the neotropics (Peres and Lake 2003), reflecting human demographics in different continents.

Hunting for either subsistence or commerce can profoundly affect the structure of tropical forest vertebrate assemblages, as revealed by both village-based kill-profiles (Jerozolinski and Peres 2003; Fa *et al.* 2005) and wildlife surveys in hunted and unhunted forests. This can be seen in the residual game abundance at forest sites subjected to varying degrees of hunting pressure, where over-hunting often results in faunal biomass collapses, mainly through declines and local extinctions of large-bodied species (Bodmer 1995; Peres 2000). Peres and Palacios (2007) provide the first systematic estimates of the impact of hunting on the abundances of a comprehensive set of 30 reptile, bird, and mammal species across 101 forest sites scattered widely throughout the Amazon Basin and Guianan Shield. Considering the 12 most harvest-sensitive species, mean aggregate population biomass was reduced almost eleven-fold from 979.8

kg/km² in unhunted sites to only 89.2 kg/km² in heavily hunted sites (see Figure 6.2). In Kilum Ijim, Cameroon, most large mammals, including elephants, buffalo, bushbuck, chimpanzees, leopards, and lions, have been lost as a result of hunting (Maisels *et al.* 2001). In Vietnam, 12 large vertebrate species have become virtually extinct over the last five decades primarily due to hunting (Bennett and Rao 2002). Pangolins and several other forest vertebrate species are facing regional-scale extinction throughout their range across southern Asia [Corlett 2007, TRAFFIC (The Wildlife Trade Monitoring Network) 2008], largely as a result of trade, and over half of all Asian freshwater turtle species are considered Endangered due to over-harvesting (IUCN 2007).

In sum, game harvest studies throughout the tropics have shown that most unregulated, commercial hunting for wild meat is unsustainable (Robinson and Bennett 2000; Nasi *et al.* 2008), and that even subsistence hunting driven by local demand can severely threaten many medium to large-bodied vertebrate populations, with potentially far-reaching consequences to other species. However, persistent harvesting of multi-species prey assemblages can often lead to post-depletion equilibrium conditions in which slow-breeding, vulnerable taxa are eliminated and gradually replaced by fast-breeding robust taxa that are resilient to typical offtakes. For example, hunting in West African forests could now be defined as sustainable from the viewpoint of urban bushmeat markets in which primarily rodents and small antelopes are currently traded, following a series of historical extinctions of vulnerable prey such as primates and large ungulates (Cowlshaw *et al.* 2005).

6.2.3 Non-timber forest products

Non-timber forest products (NTFPs) are biological resources other than timber which are extracted from either natural or managed forests (Peters 1994). Examples of exploited plant products include fruits, nuts, oil seeds, latex, resins, gums, medicinal plants, spices, dyes, ornamental plants, and raw materials such as firewood,

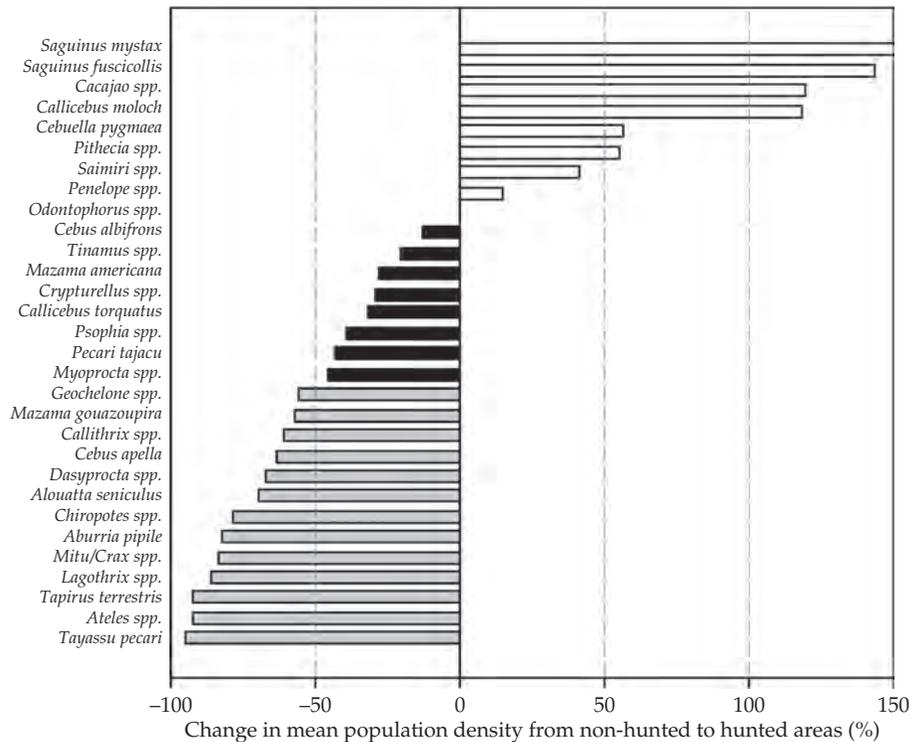


Figure 6.2 Changes in mean vertebrate population density (individuals/km²) between non-hunted and hunted neotropical forest sites (n = 101), including 30 mammal, bird, and reptile species. Forest sites retained in the analysis had been exposed to different levels of hunting pressure but otherwise were of comparable productivity and habitat structure. Species exhibiting higher density in hunted sites (open bars) are either small-bodied or ignored by hunters; species exhibiting the most severe population declines (shaded bars) were at least halved in abundance or driven to local extinction in hunted sites (data from Peres and Palacios 2007).

Desmoncus climbing palms, bamboo and rattan. The socio-economic importance of NTFP harvest to indigenous peoples cannot be underestimated. Many ethnobotanical studies have catalogued the wide variety of useful plants (or plant parts) harvested by different aboriginal groups throughout the tropics. For example, the Waimiri-Atroari Indians of central Amazonia make use of 79% of the tree species occurring in a single 1 ha terra firme forest plot (Milliken *et al.* 1992), and 1748 of the ~8000 angiosperm species in the Himalayan region spanning eight Asian countries are used medicinally and many more for other purposes (Samant *et al.* 1998).

Exploitation of NTFPs often involves partial or entire removal of individuals from the population, but the extraction method and whether vital parts are removed usually determine the

mortality level in the exploited population. Traditional NTFP extractive practices are often hailed as desirable, low-impact economic activities in tropical forests compared to alternative forms of land use involving structural disturbance such as selective logging and shifting agriculture (Peters *et al.* 1989). As such, NTFP exploitation is usually assumed to be sustainable and a promising compromise between biodiversity conservation and economic development under varying degrees of market integration. 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 form of NTFP exploitation in tropical forests has an ecological impact. The spatial 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 harvesting, and the particular species or plant part under exploitation.

Yet few studies have quantitatively assessed the demographic viability of plant populations sourcing NTFPs. One exception are Brazil nuts (*Bertholletia excelsa*, Lecythidaceae) which comprise the most important wild seed extractive industry supporting millions of Amazonian forest dwellers for either subsistence or income. This wild seed crop is firmly established in export markets, has a history of ~200 years of commercial exploitation, and comprises one of the most valuable non-timber extractive industries in tropical forests anywhere. 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 have succumbed to a process of senescence and demographic collapse, threatening this cornerstone of the Amazonian extractive economy (Peres *et al.* 2003).

A boom in the use of homeopathic remedies sustained by over-collecting therapeutic and aromatic plants is threatening at least 150 species of European wild flowers and plants and driving many populations to extinction (Traffic 1998). Commercial exploitation of the Pau-Rosa or rosewood tree (*Aniba rosaedora*, Lauraceae), which contains linalol, a key ingredient in luxury perfumes, involves a one-off destructive harvesting technique that almost invariably kills the tree. This species has consequently been extirpated from virtually its entire range in Brazilian Amazonia (Mitja and Lescure 2000). Channel 5[®] and other perfumes made with Pau-Rosa fragrance gained wide market demand decades ago, 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 accept replacing the natural Pau-Rosa fragrance with synthetic substitutes, and the last remaining populations of Pau-Rosa remain threatened. The same could be argued for a number of NTFPs

for which the harvest by destructive practices involves a lethal injury to whole reproductive individuals. 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 harvested? Are current extraction rates truly sustainable? These are key questions in terms of the demographic sustainability of different NTFP offtakes, which will ultimately depend on the ability of the resource population to recruit new seedlings either continuously or in sporadic pulses while being subjected to a repeated history of exploitation.

Unguarded enthusiasm for the role of NTFP exploitation in rural development partly stems from unrealistic economic studies reporting high market values. For example, Peters *et al.* (1989) reported that the net-value of fruit and latex extraction in the Peruvian Amazon was US\$6330/ha. This is in sharp contrast with a Mesoamerican study that quantified the local value of foods, construction materials, and medicines extracted from the forest by 32 indigenous Indian households (Godoy *et al.* 2000). The combined value of consumption and sale of forest goods ranged from US\$18 to US\$24 ha⁻¹ yr⁻¹, at the lower end of previous estimates (US\$49 - US\$1 089 ha⁻¹ yr⁻¹). NTFP extraction thus cannot be seen as a panacea for rural development and in many studies the potential value of NTFPs is exaggerated by unrealistic assumptions of high discount rates, unlimited market demands, availability of transportation facilities and absence of product substitution.

6.3 Overexploitation in aquatic ecosystems

Marine biodiversity loss, largely through overfishing, is increasingly impairing the capacity of the world's oceans to provide food, maintain water quality, and recover from perturbations (Worm *et al.* 2006). Yet marine fisheries provide employment and income for 0.2 billion people around the world, and fishing is the mainstay of the economy of many coastal regions; 41 million people worked as fishers or fish farmers in 2004,

operating 1.3 million decked vessels and 2.7 million open boats (FAO 2007). An estimated 14 million metric tons of fuel was consumed by the fish-catching sector at a cost equivalent to US\$22 billion, or ~25% of the total revenue of the sector. In 2004, reported catches from marine and inland capture fisheries were 85.8 million and 9.2 million tons, respectively, which was worth US\$84.9 billion at first sale. Freshwater catches taken every year for food have declined recently but on average 500 000 tons are taken from the Mekong river in South-East Asia; 210 000 tons are taken from the Zaire river in Africa; and 210 000 tons of fish are taken from the Amazon river in South America. Seafood consumption is still high and rising in the First World and has doubled in China within the last decade. Fish contributes to, or exceeds 50% of the total animal protein consumption in many countries and regions, such as Bangladesh, Cambodia, Congo, Indonesia, Japan or the Brazilian Amazon. Overall, fish provides more than 2.8 billion people with ~20% or more of their average per capita intake of animal protein. The oscillation of good and bad years in marine fisheries can also modulate the protein demand from terrestrial wildlife populations (Brashares *et al.* 2004). The share of fish in total world animal protein supply amounted to 16% in 2001 (FAO 2004). These 'official' landing statistics tend to severely underestimate catches and total values due to the enormous unrecorded contribution of subsistence fisheries consumed locally.

Although the world's oceans are vast (see Box 4.3), most seascapes are relatively low-productivity, and 80% of the global catch comes from only ~20% of the area. Approximately 68% of the world's catch comes from the Pacific and north-east Atlantic. At current harvest rates, most of the economically important marine fisheries worldwide have either collapsed or are expected to collapse. Current impacts of overexploitation and its consequences are no longer locally nested, since 52% of marine stocks monitored by the FAO in 2005 were fully exploited at their maximum sustainable level and 24% were overexploited or depleted, such that their current biomass is much lower than the level that would maximize their sustained yield (FAO 2007). The remaining one-

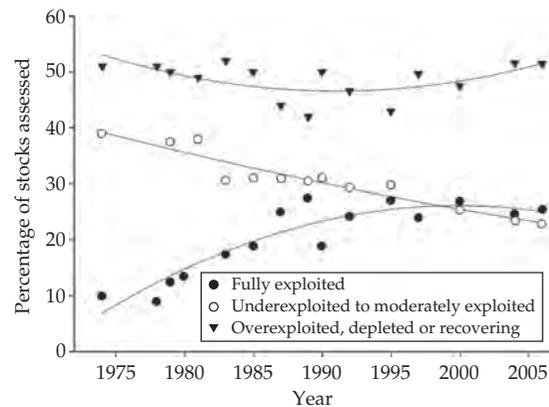


Figure 6.3 Global trends in the status of world marine fish stocks monitored by FAO from 1974 to 2006 (data from FAO 2007).

quarter of the stocks were either underexploited or moderately exploited and could perhaps produce more (Figure 6.3).

The Brazilian sardine (*Sardinella brasiliensis*) is a classic case of an overexploited marine fishery. In the 1970s hey-day of this industry, 200 000 tons were captured in southeast Brazil alone every year, but landings suddenly plummeted to <20 000 tons by 2001. Despite new fishing regulations introduced following its collapse, it is unclear whether southern Atlantic sardine stocks have shown any sign of recovery. With the possible exception of herring and related species that mature early in life and are fished with highly selective equipment, many gadids (e.g. cod, haddock) and other non-clupeids (e.g. flatfishes) have experienced little, if any, recovery in as much as 15 years after 45–99% reductions in reproductive biomass (Hutchings 2000). Worse still, an analysis of 147 populations of 39 wild fish species concluded that historically overexploited species, such as North Sea herring, became more prone to extreme year-on-year variation in numbers, rendering them vulnerable to economic or demographic extinction (Minto *et al.* 2008).

Marine fisheries are an underperforming global asset—yields could be much greater if they were properly managed. The difference between the potential and actual net economic benefits from marine fisheries is in the order of US\$50 billion per year—equivalent to over half the

value of the global seafood trade (World Bank 2008). The cumulative economic loss to the global economy over the last three decades is estimated to be approximately US\$2 trillion, and in many countries fishing operations are buoyed up by subsidies, so that the global fishery economy to the point of landing is already in deficit.

Commercial fishing activities disproportionately threaten large-bodied marine and freshwater species (Olden *et al.* 2007). This results in fishermen fishing down the food chain, targeting ever-smaller pelagic fish as they can no longer capture top predatory fish. This is symptomatic of the now widely known process of 'fishing down marine food webs' (see Box 6.1). Such sequential size-graded exploitation systems also take place in multi-species assemblages hunted in tropical forests (Jerolimski and Peres *et al.* 2003). In the seas, overexploitation threatens the persistence of ecologically significant populations of many large marine vertebrates, including sharks, tunas and sea turtles. Regional scale populations of large sharks worldwide have declined by 90% or more, and rapid declines of >75% of the coastal and oceanic Northwest Atlantic populations of scalloped hammerhead, white, and thresher sharks have occurred in the past 15 years (Baum *et al.* 2003; Myers and Worm 2003; Myers *et al.* 2007). Much of this activity is profligate and often driven by the surging global demand for shark fins. For example, in 1997 line-fishermen captured 186 000 sharks in southern Brazil alone, of which 83% were killed and discarded in open waters following the removal of the most lucrative body parts (C.M. Vooren, pers. comm.). Of the large-bodied coastal species affected by this trade, several have virtually disappeared from shallow waters (e.g. grey nurse sharks, *Carcharias taurus*). Official figures show that 131 tons of shark fins, corresponding to US \$2.4 million, were exported from Brazil to Asia in 2007.

Finally, we know rather little about ongoing extinction processes caused by harvesting. For example, from a compilation of 133 local, regional and global extinctions of marine fish populations, Dulvy *et al.* (2003) uncovered that exploitation was the main cause of extinctions (55% of all

populations), but these were only reported after a median 53-year lag following their real-time disappearance. Some 80% of all extinctions were only discovered through historical comparisons; e.g. the near-extinction of large skates on both sides of the Atlantic was only brought to the world's attention several decades after the declines have occurred.

6.4 Cascading effects of overexploitation on ecosystems

All extractive systems in which the overharvested resource is one or more biological populations, can lead to pervasive trophic cascades and other unintended ecosystem-level consequences to non-target species. Most hunting, fishing, and collecting activities affect not only the primary target species, but also species that are taken accidentally or opportunistically. Furthermore, exploitation often causes physical damage to the environment, and has ramifications for other species through cascading interactions and changes in food webs.

In addition, overexploitation may severely erode the ecological role of resource populations in natural communities. In other words, overexploited populations need not be entirely extirpated before they become ecologically extinct. In communities that are "half-empty" (Redford and Feinsinger 2001), populations may be reduced to sufficiently low numbers so that, although still present in the community, they no longer interact significantly with other species (Estes *et al.* 1989). Communities with reduced levels of species interactions may become pale shadows of their former selves. Although difficult to measure, severe declines in large vertebrate populations may result in multi-trophic cascades that may profoundly alter the structure of marine ecosystems such as kelp forests, coral reefs and estuaries (Jackson *et al.* 2001), and analogous processes may occur in many terrestrial ecosystems. Plant reproduction in endemic island floras can be severely affected by population declines in flying foxes (pteropodid fruit bats) that serve as strong mutualists as pollinators and seed dispersers (Cox *et al.* 1991).

In some Pacific archipelagos, several species may become functionally extinct, ceasing to effectively disperse large seeds long before becoming rare (McConkey and Drake 2006). A key agenda for future research will involve understanding the non-linearities between functional responses to the numeric abundance of strong interactors reduced by exploitation pressure and the quality of ecological services that depleted populations can perform. For example, what is the critical density of any given exploited population below which it can no longer fulfill its community-wide ecological role?

In this section I concentrate on poorly known interaction cascades in tropical forest and marine environments, and discuss a few examples of how apparently innocuous extractive activities targeted to one or a few species can drastically affect the structure and functioning of these terrestrial and aquatic ecosystems.

6.4.1 Tropical forest disturbance

Timber extraction in tropical forests is widely variable in terms of species selectivity, but even highly selective logging can trigger major ecological changes in the understory light environment, forest microclimate, and dynamics of plant regeneration. Even reduced-impact logging (RIL) operations can generate enough forest disturbance, through elevated canopy gap fracture, to greatly augment forest understory desiccation, dry fuel loads, and fuel continuity, thereby breaching the forest flammability threshold in seasonally-dry forests (Holdsworth and Uhl 1997; Nepstad *et al.* 1999; Chapter 9). During severe dry seasons, often aggravated by increasingly frequent continental-scale climatic events, extensive ground fires initiated by either natural or anthropogenic sources of ignition can result in a dramatically reduced biomass and biodiversity value of previously unburnt tropical forests (Barlow and Peres 2004, 2008). Despite these undesirable effects, large-scale commercial logging that is unsustainable at either the population or ecosystem level continues unchecked in many tropical forest frontiers (Curran *et al.* 2004; Asner *et al.* 2005). Yet surface fires aggravated by logging disturbance

represent one of the most powerful mechanisms of functional and compositional impoverishment of remaining areas of tropical forests (Cochrane 2003), and arguably the most important climate-mediated phase shift in the structure of tropical ecosystems (see also Chapters 8 and 9).

6.4.2 Hunting and plant community dynamics

Although the direct impacts of defaunation driven by overhunting can be predicted to some degree, higher-order indirect effects on community structure remain poorly understood since Redford's (1992) seminal paper and may have profound, long-term consequences for the persistence of other taxa, and the structure, productivity and resilience of terrestrial ecosystems (Cunningham *et al.* 2009). Severe population declines or extirpation of the world's megafauna may result in dramatic changes to ecosystems, some of which have already been empirically demonstrated, while others have yet to be documented or remain inexact.

Large vertebrates often have a profound impact on food webs and community dynamics through mobile-linkage mutualisms, seed predation, and seedling and sapling herbivory. Plant communities in tropical forests depleted of their megafauna may experience pollination bottlenecks, reduced seed dispersal, monodominance of seedling cohorts, altered patterns of seedling recruitment, other shifts in the relative abundance of species, and various forms of functional compensation (Cordeiro and Howe 2003; Peres and Roosmalen 2003; Wang *et al.* 2007; Terborgh *et al.* 2008; Chapter 3). On the other hand, the net effects of large mammal defaunation depends on how the balance of interactions are affected by population declines in both mutualists (e.g. high-quality seed dispersers) and herbivores (e.g. seed predators) (Wright 2003). For example, significant changes in population densities in wild pigs (*Suidae*) and several other ungulates and rodents, which are active seed predators, may have a major effect on seed and seedling survival and forest regeneration (Curran and Webb 2000).

Tropical forest floras are most dependent on large-vertebrate dispersers, with as many as

97% of all tree, woody liana and epiphyte species bearing fruits and seeds that are morphologically adapted to endozoochorous (passing through the gut of an animal) dispersal (Peres and Roosmalen 2003). Successful seedling recruitment in many flowering plants depends on seed dispersal services provided by large-bodied frugivores (Howe and Smallwood 1982), while virtually all seeds falling underneath the parent's canopy succumb to density-dependent mortality—caused by fungal attack, other pathogens, and vertebrate and invertebrate seed predators (see review in Carson *et al.* 2008).

A growing number of phytodemographic studies have examined the effects of large-vertebrate removal. Studies examining seedling recruitment under different levels of hunting pressure (or disperser abundance) 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 depends on the patterns of depletion across different prey species. In persistently hunted Amazonian forests, where large-bodied primates are driven to local extinction or severely reduced in numbers (Peres and Palacios 2007), the probability of effective dispersal of large-seeded endozoochorous plants can decline by over 60% compared to non-hunted forests (Peres and Roosmalen 2003). Consequently, plant species with seeds dispersed by vulnerable game species are less abundant where hunters are active, whereas species with seeds dispersed by abiotic means or by small frugivores ignored by hunters are more abundant in the seedling and sapling layers (Nuñez-Iturri and Howe 2007; Wright *et al.* 2007; Terborgh *et al.* 2008). However, the importance of dispersal-limitation in the absence of large frugivores depends on the degree to which their seed dispersal services are redundant to any given plant species (Peres and Roosmalen 2003). Furthermore, local extinction events in large-bodied species are rarely compensated by smaller species in terms of their population density, biomass,

diet, and seed handling outcomes (Peres and Dolman 2000).

Large vertebrates targeted by hunters often have a disproportionate impact on community structure and operate as “ecosystem engineers” (Jones *et al.* 1994; Wright and Jones 2006), either performing a key landscaping role in terms of structural habitat disturbance, or as mega-herbivores that maintain the structure and relative abundance of plant communities. For example, elephants exert a major role in modifying vegetation structure and composition as herbivores, seed dispersers, and agents of mortality for many small trees (Cristoffer and Peres 2003). Two similar forests with or without elephants show different succession and regeneration pathways, as shown by long-term studies in Uganda (Sheil and Salim 2004). Overharvesting of several other species holding a keystone landscaping role can lead to pervasive changes in the structure and function of ecosystems. For example, the decimation of North American beaver populations by pelt hunters following the arrival of Europeans profoundly altered the hydrology, channel geomorphology, biogeochemical pathways and community productivity of riparian habitats (Naiman *et al.* 1986).

Mammal overhunting triggers at least two additional potential cascades: the secondary extirpation of dependent taxa and the subsequent decline of ecological processes mediated by associated species. For instance, overhunting can severely disrupt key ecosystem processes including nutrient recycling and secondary seed dispersal exerted by relatively intact assemblages of dung beetles (Coleoptera: Scarabaeinae) and other coprophagous invertebrates that depend on large mammals for adult and larval food resources (Nichols *et al.* 2009).

6.4.3 Marine cascades

Apart from short-term demographic effects such as the direct depletion of target species, there is growing evidence that fishing also contributes to important genetic changes in exploited populations. If part of the phenotypic variation of target species is due to genetic differences among

individuals then selective fishing will cause genetic changes in life-history traits such as ages and sizes at maturity (Law 2000). The genetic effects of fishing are increasingly seen as a long-term management issue, but this is not yet managed proactively as short-term regulations tend to merely focus on controlling mortality. However, the damage caused by overfishing extends well beyond the main target species with profound effects on: (i) low-productivity species in mixed fisheries; (ii) non-target species; (iii) food webs; and (iv) the structure of oceanic habitats.

Low-productivity species in mixed fisheries

Many multi-species fisheries are relatively unselective and take a wide range of species that vary in their capacity to withstand elevated mortality. This is particularly true in mixed trawl fisheries where sustainable mortality rates for a productive primary target species are often unsustainable for species that are less productive, such as skates and rays, thereby leading to widespread depletion and, in some cases, regional extinction processes. Conservation measures to protect unproductive species in mixed fisheries are always controversial since fishers targeting more productive species will rarely wish to sacrifice yield in order to spare less productive species.

Bycatches

Most seafood is captured by indiscriminate methods (e.g. gillnetting, trawl netting) that haul in large numbers of incidental captures (termed bycatches) of undesirable species, which numerically may correspond to 25–65% of the total catch. These non-target pelagic species can become entangled or hooked by the same fishing gear, re-

sulting in significant bycatch mortality of many vulnerable fish, reptile, bird and mammal populations, thereby comprising a key management issue for most fishing fleets (Hall *et al.* 2000). For example, over 200 000 loggerhead (*Caretta caretta*) and 50 000 leatherback turtles (*Dermochelys coriacea*) were taken as pelagic longline bycatch in 2000, likely contributing to the 80–95% declines for Pacific loggerhead and leatherback populations over two decades (Lewison *et al.* 2004). While fishing pressure on target species relates to target abundance, fishing pressure on bycatch species is likely insensitive to bycatch abundance (Crowder and Murawski 1998), and may therefore result in “piggyback” extinctions. Bycatches have been the focus of considerable societal concern, often expressed in relation to the welfare of individual animals and the status of their populations. Public concerns over unacceptable levels of mortality of large marine vertebrates (e.g. sea turtles, seabirds, marine mammals, sharks) have therefore led to regional bans on a number of fishing methods and gears, including long drift-nets.

Food webs

Overfishing can create trophic cascades in marine communities that can cause significant declines in species richness, and wholesale changes in coastal food webs resulting from significant reductions in consumer populations due to overfishing (Jackson *et al.* 2001). Predators have a fundamental top-down role in the structure and function of biological communities, and many large marine predators have declined by >90% of their baseline population levels (Pauly *et al.* 1998; Myers and Worm 2003; see Box 6.1). Fishing affects

Box 6.1 The state of fisheries **Daniel Pauly**

Industrial, or large-scale and artisanal, or small-scale marine fisheries, generate, at the onset of the 21st century, combined annual catches of 120–140 million tons, with an ex-vessel value of about US\$100 billion. This is much higher than officially reported landings (80–90 million tons), which do not account for illegal, unreported and undocumented (IUU) catches

(Pauly *et al.* 2002). IUU catches include, for example, the fish discarded by shrimp trawlers (usually 90% of their actual catch), the catch of high sea industrial fleets operating under flags of convenience, and the individually small catch by millions of artisanal fishers (including women and children) in developing countries, which turns out to be very high in the

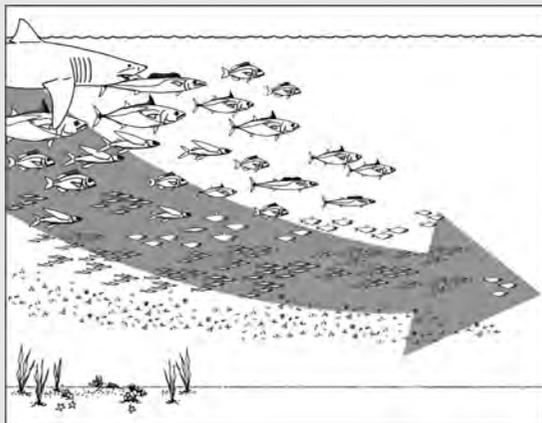
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Box 6.1 (Continued)

aggregate, but still goes unreported by national governments and international agencies.

This global catch, which, depending on the source, is either stagnating or slowly declining, is the culmination of the three-pronged expansion of fisheries which occurred following the Second World War: (i) an offshore/depth expansion, resulting from the depletion of shallow-water, inshore stocks (Morato *et al.* 2006); (ii) a geographic expansion, as the fleets of industrialized countries around the North Atlantic and in East Asia, faced with depleted stocks in their home waters, shifted their operations toward lower latitudes, and thence to the southern hemisphere (Pauly *et al.* 2002); and (iii) a taxonomic expansion, i.e. capturing and marketing previously spurned species of smaller fish and invertebrates to replace the diminishing supply of traditionally targeted, larger fish species (Pauly *et al.* 1998; see Box 6.1 Figure).

In the course of these expansions, fishing effort grew enormously, especially that of industrial fleets, which are, overall, 3–4 times larger than required. This is, among other things, a result of the US\$30–34 billion they



Box 6.1 Figure Schematic representation of the process, now widely known as ‘fishing down marine food webs’, by which fisheries first target the large fish, then, as these disappear, move on to smaller species of fish and invertebrates, lower in the food web. In the process, the functioning of marine ecosystems is profoundly disrupted, a process aggravated by the destruction of the bottom fauna by trawling and dredging.

receive annually as government subsidies, which now act to keep fleets afloat that have no fish to exploit (Sumaila *et al.* 2008). In addition to representing a giant waste of economic resources, these overcapitalized fishing fleets have a huge, but long-neglected impact on their target species, on non-targeted species caught as by-catch, and on the marine ecosystems in which all species are embedded. Also, these fleets emit large amounts of carbon dioxide; for example trawlers nowadays often burn several tons of diesel fuel for every ton of fish landed (and of which 80% is water), and their efficiency declines over time because of declining fish stocks (Tyedmers *et al.* 2005).

Besides threatening the food security of numerous developing countries, for example in West Africa, these trends endanger marine biodiversity, and especially the continued existence of the large, long-lived species that have sustained fisheries for centuries (Worm *et al.* 2006).

The good news is that we know in principle how to avoid the overcapitalization of fisheries and the collapse of their underlying stocks. This would involve, besides an abolition of capacity-enhancing subsidies (e.g. tax-free fuel, loan guarantees for boat purchases (Sumaila *et al.* 2008), the creation of networks of large marine protected areas, and the reduction of fishing effort in the remaining exploited areas, mainly through the creation of dedicated access privilege (e.g. for adjacent small scale fisher communities), such as to reduce the ‘race for fish’.

Also, the measures that will have to be taken to mitigate climate change offer the prospect of a reduction of global fleet capacity (via a reduction of their greenhouse gas emissions). This may lead to more attention being paid to small-scale fisheries, so far neglected, but whose adjacency to the resources they exploit, and use of fuel-efficient, mostly passive gear, offers a real prospect for sustainability.

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predator-prey interactions in the fished community and interactions between fish and other species, including predators of conservation interest such as seabirds and mammals. For example, fisheries can compete for the prey base of seabirds and mammals. Fisheries also produce discards that can provide significant energy subsidies especially for scavenging seabirds, in some cases sustaining hyper-abundant populations. Current understanding of food web effects of overfishing is often too poor to provide consistent and reliable scientific advice.

Habitat structure

Overfishing is a major source of structural disturbance in marine ecosystems. The very act of fishing, particularly with mobile bottom gear, destroys substrates, degrades habitat complexity, and ultimately results in the loss of biodiversity (see Box 4.3). These structural effects are compounded by indirect effects on habitat that occur through removal of ecological or ecosystem engineers (Coleman and Williams 2002). Many fishing gears contact benthic habitats during fishing and habitats such as coral reefs are also affected by changes in food webs. The patchiness of impacts and the interactions between types of gears and habitats are critical to understanding the significance of fishing effects on habitats; different gears have different impacts on the same habitat and different habitats respond differently to the same gear. For some highly-structured habitats such as deep water corals, recovery time is so slow that only no fishing would be realistically sustainable (Roberts *et al.* 2006).

6.5 Managing overexploitation

This chapter has repeatedly illustrated examples of population declines induced by overexploitation even in the face of the laudable goals of implementing conservation measures in the real-world. This section will conclude with some comments about contrasts between theory and practice, and briefly explore some of the most severe problems and management solutions that can minimize the impact of harvesting on the integrity of terrestrial and marine ecosystems.

Unlike many temperate countries where regulatory protocols preventing overexploitation have been developed through a long and repeated history of trial and error based on ecological principles and hard-won field biology, population management prescriptions in the tropics are typically non-existent, unenforceable, and lack the personnel and scientific foundation on which they can be built. The concepts of game wardens, bag limits, no-take areas, hunting or fishing licenses, and duck stamps are completely unfamiliar to the vast majority of tropical subsistence hunters or fishers (see Box 6.2). Yet these resource users are typically among the poorest rungs in society and often rely heavily on wild animal populations as a critical protein component of their diet. In contrast, countries with a strong tradition in fish and wildlife management and carefully regulated harvesting policy in private and public areas, may include sophisticated legislation encompassing bag limits on the age and sex of different target species, as well as restrictions on hunting and fishing seasons and

Box 6.2 Managing the exploitation of wildlife in tropical forests

Douglas W. Yu

Hunting threatens the persistence of tropical wildlife, their ecological functions, such as seed dispersal, and the political will to maintain forests in the face of alternative land-use options. However, game species are important sources of protein and income for millions of forest dwellers and traders of wildlife (Peres 2000; Bulte and van Kooten 2001; Milner-Gulland *et al.* 2003; Bennett *et al.* 2007; this chapter).

Policy responses to the overexploitation of wildlife can be placed into two classes: (i) demand-side restrictions on offtake, to increase the cost of hunting, and (ii) the supply-side provisioning of substitutes, to decrease the benefit of hunting (Bulte and Damania 2005; Crookes and Milner-Gulland 2006). Restrictions on offtake vary from no-take areas, such as parks, to various partial limits, such as reducing the density of hunters via private property rights, and establishing quotas and bans on specific species, seasons, or hunting gear, like shotguns (Bennett *et al.* 2007). Where there are commercial markets for wildlife, restrictions can also be applied down the supply chain in the form of market fines or taxes (Clayton *et al.* 1997; Damania *et al.* 2005). Finally, some wildlife products are exported for use as medicines or decoration and can be subjected to trade bans under the aegis of the Convention on International Trade in Endangered Species (CITES) (Stiles 2004; Bulte *et al.* 2007; Van Kooten 2008).

Bioeconomic modeling (Ling and Milner-Gulland 2006) of a game market in Ghana has suggested that imposing large fines on the commercial sale of wild meat should be sufficient to recover wildlife populations, even in the absence of forest patrols (Damania *et al.* 2005). Fines reduce expected profits from sales, so hunters should shift from firearms to cheaper but less effective snares and consume more wildlife at home. The resulting loss of cash income should encourage households to reallocate labor toward other sources of cash, such as agriculture.

Offtake restrictions are, however, less useful in settings where governance is poor, such that fines are rarely expected and incursions into no-take areas go unpunished, or where subsistence hunting is the norm, such as over much of the Amazon Basin (Peres 2000). In the latter case, markets for wild meat are small or nonexistent, and human populations are widely distributed, exacerbating the already-difficult problem of monitoring hunting effort in tropical forests (Peres and Terborgh 1995; Peres and Lake 2003; Ling and Milner-Gulland 2006). Moreover, the largest classes of Amazonian protected areas are indigenous and sustainable development reserves (Nepstad *et al.* 2006; Peres and Nascimento 2006), within which inhabitants hunt legally.

Such considerations are part of the motivation for introducing demand-side remedies, such as alternative sources of protein. The logic is that local substitutes (e.g. fish from aquaculture) should decrease demand for wild meat and allow the now-excess labor devoted to hunting to be reallocated to competing activities, such as agriculture or leisure.

However, the nature of the substitute and the structure of the market matter greatly. If the demand-side remedy instead takes the form of increasing the opportunity cost of hunting by, for example, raising the profitability of agriculture, it is possible that total hunting effort will ultimately increase, since income is fungible and can be spent on wild meat (Damania *et al.* 2005). Higher consumer demand also raises market prices and can trigger shifts to more effective but more expensive hunting techniques, like guns (Bulte and Horan 2002; Damania *et al.* 2005). More generally, efforts to provide alternative economic activities are likely to be inefficient and amount to little more than 'conservation by distraction' (Ferraro 2001; Ferraro and Simpson 2002).

In many settings, the ultimate consumers are not the hunters, and demand-side remedies could take the form of educational programs aimed at changing consumer preferences or,

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Box 6.2 (Continued)

alternatively, of wildlife farms (e.g. crocodylian ranches) that are meant to compete with and depress the price of wild-caught terrestrial vertebrates. The latter strategy could, however, lead to perverse outcomes if the relevant market is dominated by only a few suppliers, who have the power to maintain high prices by restricting supply to market (Wilkie *et al.* 2005; Bulte and Damania 2005; Damania and Bulte 2007). Then, the introduction of a farmed substitute can, in principle, induce intense price-cutting competition, which would increase consumer demand and lead to more hunting and lower wildlife stocks. Also, farmed substitutes can undermine efforts to stigmatize the consumption of wildlife products, increasing overall demand. Given these caveats, the strategy of providing substitutes for wildlife might best be focused on cases where the substitute is different from and clearly superior to the wildlife product, as is the case for *Viagra* versus aphrodisiacs derived from animal parts (von Hippel and von Hippel 2002).

Ultimately, given the large numbers of rural dwellers, the likely persistence of wildlife markets of all kinds, and the great uncertainties that remain embedded in our understanding of the ecology and economics of wildlife exploitation, any comprehensive strategy to prevent hunting from driving wildlife populations extinct must include no-take areas (Bennett *et al.* 2007)—the bigger the better. The success of no-take areas will in turn depend on designing appropriate enforcement measures for different contexts, from national parks to indigenous reserves and working forests to community-based management (Keane *et al.* 2008).

A potential approach is to use the economic theory of contracts and asymmetric information (Ferraro 2001, 2008; Damania and Hatch 2005) to design a menu of incentives and punishments that deters hunting in designated no-take areas, given that hunting is a hidden action. In the above bioeconomic model in Ghana (Damania *et al.* 2005), hidden hunting effort is revealed in part by sales in markets, which can be monitored, and the imposition of a punishing fine causes changes in the behavior of households that result ultimately in higher game populations.

It should also be possible to employ positive incentives in the form of payments for ecological services (Ferraro 2001; Ferraro and Simpson 2002; Ferraro and Kiss 2002). For example, in principle, the state might pay local communities in return for abundant wildlife as measured in regular censuses. In practice, however, the high stochasticity of such a monitoring mechanism, and the problem of free riders within communities, might make this mechanism unworkable. Alternatively, in the case of landscapes that still contain vast areas of high animal abundance, such as in many parks that host small human populations, a strategy that takes advantage of the fact that central-place subsistence hunters are distance limited is appropriate (Ling and Milner-Gulland 2008; Levi *et al.* 2009). The geographic distribution of settlements is then an easily monitored proxy for the spatial distribution of hunting effort. As a result, economic incentives to promote settlement sedentarism, which can range from direct payments to the provision of public services such as schools, would also limit the spread of hunting across a landscape.

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capture technology. Despite the economic value of wildlife (Peres 2000; Chardonnet *et al.* 2002; Table 6.1), terrestrial and aquatic wildlife in many tropical countries comprise an ‘invisible’ commodity and local offtakes often proceed unrestrained until the sudden perception that the resource stock is fully 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 harvest over 700 000 wild white-tailed deer (*Odocoileus virginianus*) every year, whereas Costa Rica can hardly sustain an annual harvest of a few thousand without pushing the same cervid species, albeit in a different food environment, to local extinction (D. Janzen, pers. comm.).

An additional widespread challenge in managing any diffuse set of resources is presented when resources (or the landscape or seascape which

they occupy) have no clear ownership. This is widely referred to as the 'tragedy of the commons' (Hardin 1968) in which open-access exploitation systems lead to much greater rates of exploitation than are safe for the long-term survival of the population. This is dreadful for both the resource and the consumers, because each user is capturing fewer units of the resource than they could if they had fewer competitors. Governments often respond by providing perverse subsidies that deceptively reduce costs, hence catalyzing a negative spiral leading to further overexploitation (Repetto and Gillis 1988). The capital invested in many extractive industries such as commercial fisheries and logging operations cannot be easily reinvested, so that exploiters have few options but to continue harvesting the depleted resource base. Understandably, this leads to resistance against restrictions on exploitation rates, thereby further exacerbating the problems of declining populations. In fact, exploitation can have a one-way ratchet effect, with governments propping up overexploitation when populations are low, and supporting investment in the activity when yields are high.

Laws against the international wildlife and timber trade have often failed to prevent supplies sourced from natural populations from reaching their destination, accounting for an estimated US \$292.73 billion global market, most of it accounted for by native timber and wild fisheries (see Table 6.1). Global movement of animals for the pet trade alone has been estimated at ~350 million live animals, worth ~US\$20 billion per year (Roe 2008; Traffic 2008). At least 4561 extant bird species are used by humans, mainly as pets and for food, including >3337 species traded internationally (Butchart 2008). Some 15 to 20 million wild-caught ornamental fish are exported alive every year through Manaus alone, a large city in the central Amazon (Andrews 1990).

Regulating illegal overharvesting of exorbitant-priced resource populations—such as elephant ivory, rhino horn, tiger bone or mahogany trees—presents an additional, and often insurmountable, challenge because the rewards accrued to violators often easily outweigh the enforceable penalties or the risks of being caught.

Table 6.1 Total estimated value of the legal wildlife trade worldwide in 2005 (data from Roe 2008).

Commodity	Estimated value (US\$ million)
Live animals	
Primates	94
Cage birds	47
Birds of prey	6
Reptiles (incl. snakes and turtles)	38
Ornamental fish	319
Animal products for clothing or ornaments	
Mammal furs and fur products	5000
Reptile skins	338
Ornamental corals and shells	112
Natural pearls	80
Animal products for food (excl. fish)	
Game meat	773
Frog legs	50
Edible snails	75
Plant products	
Medicinal plants	1300
Ornamental plants	13 000
Fisheries food products (excl. aquaculture)	81 500
Timber	190 000
Total	\$292.73 bill

For example, giant bluefin tuna (*Thunnus thynnus*), which are captured illegally by commercial and recreational fishers assisted by high-tech gear, may be the most valuable animal on the planet, with a single 444-pound bluefin tuna sold wholesale in Japan a few years ago for US \$173 600! In fact, a ban on harvesting of some highly valuable species has merely spawned a thriving illegal trade. After trade in all five species of rhino was banned, the black rhino became extinct in at least 18 African countries [CITES (Convention on International Trade in Endangered Species) 2008]. The long-term success of often controversial bans on wildlife trade depends on three factors. First, prohibition on trade must be accompanied by a reduction in demand for the banned products. Trade in cat and seal skins was crushed largely because ethical consumer campaigns destroyed demand at the same time as trade bans cut the legal supply.

Second, bans may curb legal trade, which often provides an economic incentive to maintain wildlife or their habitat. Some would therefore argue they undermine conservation efforts and may even create incentives to eliminate them. The American bison was doomed partly because its rangelands became more valuable for rearing cattle (Anderson and Hill 2004). Third, international trade agreements must be supported by governments and citizens in habitat-countries, rather than only conscious consumers in wealthy nations. But even well-meaning management prescriptions involving wildlife trade 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 (*Saiga tatarica*) horn to the Chinese traditional medicine market as a substitute for the horn of endangered rhinos. In October 2002, saiga antelopes were finally placed on the Red List of critically endangered species following this population crash (Milner-Gulland *et al.* 2001). In sum, rather few happy stories can be told of illegal wildlife commerce resulting in the successful recovery of harvested wild populations. However, these tend to operate through a 'stick-and-carrot' approach at more than one linkage of the chain, controlling offtakes at the source, the distribution and transport by intermediate traders, and/or finally the consumer demand at the end-point of trade networks. In fact, successful management of any exploitation system will include enforceable measures ranging from demand-side disincentives to supply-side incentives (see Box 6.2), with the optimal balance between penalties on bad behavior or rewards on good behavior being highly context-specific.

Faced with difficulties of managing many semi-subsistence exploitation systems, such as small-scale fisheries and bushmeat hunting, conservation biologists are increasingly calling for more realistic control measures that manipulate the large-scale spatial structure of the harvest. One such method includes no-take areas, such as wildlife sanctuaries and marine protected areas

(MPAs) that can be permanently or temporarily closed-off to maximize game and fish yields. Protection afforded by these spatial restrictions allows populations to increase through longer lifespans and higher reproductive success. Recovery of animal biomass inside no-take areas increases harvest levels in surrounding landscapes (or seascapes), and as stocks build up, juveniles and adults can eventually spill over into adjacent areas (e.g. Roberts *et al.* 2001). However, the theoretical and empirical underpinnings of marine reserves have advanced well beyond their terrestrial counterparts. Several typical life history traits of marine species such as planktonic larval dispersal are lacking in terrestrial game species, which differ widely in the degree to which surplus animals can colonize adjacent unharvested areas. However, many wild meat hunters may rely heavily on spillovers from no-take areas. A theoretical analysis of tapir hunting in Peruvian Amazonia showed that a source area of 9300 km² could sustain typical levels of hunting in a 1700 km² sink, if dispersal was directed towards that sink (Bodmer 2000). The degree to which source-sink population dynamics can inform real-world management problems remains at best an inexact science. In tropical forests, for example, we still lack basic data on the dispersal rate of most gamebird and large mammal species. Key management questions thus include the potential and realized dispersal rate of target species mediated by changes in density, the magnitude of the spillover effect outside no-take areas, how large these areas must be and still maintain accessible hunted areas, and what landscape configuration of no-take and hunted areas would work best. It is also critical to ensure that no-take areas are sufficiently large to maintain viable populations in the face of overharvesting and habitat loss or degradation in surrounding areas (Peres 2001; Claudet *et al.* 2008). In addition to obvious differences in life-history between organisms in marine and terrestrial systems, applying marine management concepts to forest reserves may be problematic due to differences in the local socio-political context in which no-take areas need to be accepted, demarcated and implemented (see Chapter 11). In particular, we need a better understanding of the opportunity costs in terms of

income and livelihoods lost from community activities, such as bushmeat hunting and timber extraction, from designating no-take areas.

Finally, conservation biologists and policy-makers who bemoan our general state of data scarcity are akin to fiddlers while Rome burns. Although more fine-tuning data are still needed on the life-history characteristics and population dynamics of exploited populations, we already have a reasonably good idea of what control measures need to be implemented in many exploitation systems. Whether qualitative or quantitative restrictions are designed by resource managers seeking yield quotas based on economic optima or more preservationist views supporting more radical reductions in biomass extraction, control measures will usually involve reductions in harvest capacity and mortality in exploited areas, or more and larger no-take areas (Pauly *et al.* 2002). Eradication of perverse subsidies to unsustainable extractive industries would often be a win-win option leading to stock recovery and happier days for resource users. Co-management agreements with local communities based on sensible principles can also work provided we have the manpower and rural extension capacity to reach out to many source areas (Chapters 14 and 15). Ultimately, however, uncontrolled exploitation activities worldwide cannot be regulated unless we can count on political will and enforcement of national legislation prescribing sustainable management of natural resources, which are so often undermined by weak, absent, or corrupt regulatory institutions.

Summary

- Human exploitation of biological commodities involves resource extraction from the land, freshwater bodies or oceans, so that wild animals, plants or their products are used for a wide variety of purposes.
- Overexploitation occurs when the harvest rate of any given population exceeds its natural replacement rate.
- Many species are relatively insensitive to harvesting, remaining abundant under relatively high

rates of offtake, whereas others can be driven to local extinction by even the lightest levels of offtake.

- This chapter reviews the effects of overexploitation in terrestrial as well as aquatic biomes. Options to manage resource exploitation are also discussed.

Relevant websites

- Bushmeat Crisis Task Force: <http://www.bushmeat.org/portal/server.pt>.
- Bioko Biodiversity Protection Program: <http://www.bioko.org/conservation/hunting.asp>.
- Wildlife Conservation Society: <http://www.wcs.org/globalconservation/Africa/bushmeat>.

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