# 11 Ecology, Evolution, Economics, and Ungulate Management

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Modern ungulate management must have three major components: research to increase its knowledge base, a choice of management objectives dictated in part by societal choices, and use of scientific knowledge to achieve those objectives. In addition to being valuable for management, research on ungulates has made major contributions to the development of ecological theory. The study of ungulates is particularly important, because their longevity, strong iteroparity, and overlapping generations produce unique patterns of population dynamics and life-history evolution (Gaillard et al. 2000, 2001). Wildlife management is motivated by human activities: wildlife would not need managers if it was not because of society's wishes to either exploit it, to minimize human impacts on ecosystems, or to avoid wildlife impacts on humans. As human populations expand, use more resources, and increasingly affect ecosystem functions, the need for scientific information to guide wildlife management increases. The diversity of wildlife management issues also increases. A few decades ago, ungulate management mostly involved setting hunting seasons and quotas to avoid overexploitation. In many cases, managers were reintroducing ungulates in areas where they had been extirpated (Komers and Curman 2000). Usually, the main preoccupation was that there were too few ungulates, not too many. The "client" of the fledgling wildlife management profession was the sport hunter, and some countries had no tradition of professional wildlife management based on ecological research.

Over the past 20 years, ungulate management has evolved. Conservation remains a guiding principle, and sport hunters remain a major user of ungulate populations, but ungulate overabundance is now an ecological and economic preoccupation in many parts of the world (Côté et al. 2004; Gordon et al. 2004). Large predators are recolonizing areas from where they had been absent for decades or centuries, some exotic ungulates are now widespread, and some ungulate populations have become a concern for human safety (through disease transmission or vehicle accidents), and for local economies (through damage to crops and forests, or disease transmission to livestock) (Gordon et al. 2004). On the other hand, some species that were abundant a few decades ago, such as woodland caribou (*Rangifer tarandus*) in North America, *Hippocamelus* deer in South America (Saucedo and Gill 2004),

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and several ungulates in Central Asia are now being threatened with extinction, because human-induced habitat changes (including forest harvests and exotic species) have modified both forage availability and predator–prey relationships (Wittmer et al. 2005a). Other species, such as chiru (*Pantholops hodgsonii*) (Li et al. 2000) and musk deer (*Moschus* spp.) (Yang et al. 2003), are over-exploited to obtain commercial products. Although the number of sport hunters is rapidly decreasing in many countries, "high-end" tourist hunting for trophy males is expanding and generating new ecological, social, and economic challenges and opportunities (Hofer 2002). "Alternative" hunting products such as penned hunts and hunts for exotic ungulates on game ranches are proliferating. These activities provide economic diversification and substantial gain for a few individuals, but have negative impacts on biodiversity and provide choice fodder for antihunting groups.

Wildlife scientists are increasingly preoccupied with habitat fragmentation, climate change (Thomas et al. 2004), and the negative impacts of high ungulate densities on biodiversity. Mounting public interest in conservation means that the "clients" of wildlife managers are now a very diverse group, often with conflicting values or objectives. Wildlife managers also face new legal obligations, such as endangered species legislations and requirements to consult with Aboriginal Peoples and various stakeholder groups. These changes require new ideas and initiatives from wildlife and social scientists. Ungulate managers are evolving from providers of hoofed targets to stewards of ecosystems.

Here, I briefly examine a few examples of how ungulate management has changed over the past few decades, then examine how advances in our understanding of ungulate population dynamics, population genetics, and evolutionary ecology could improve management. I will also discuss new challenges for wildlife managers over the next few decades. Most of those challenges hinge more on improving communication than on increasing our knowledge base. I suspect that managers often know what needs to be done to both manage ungulates and conserve biodiversity, but cannot do it because of social, political, or economic constraints.

## PREDATORS, EQUILIBRIA, AND LACK THEREOF

Ungulate management has always had a difficult relationship with large predators. "Predator control" used to be an acceptable part of management when predators were seen as competitors for sport hunters. The pendulum then swung to the opposite side (mostly pushed by people living in urban areas or in regions without large predators), and predator control became a controversial issue. Some populations of large predators now enjoy high levels of protection and are increasing in both abundance and geographical range. As society's awareness of the value of biodiversity increased, a combination of interest by nonhunters in conservation and a near-religious belief in the "Balance of Nature" contributed to elevate the wolf (*Canis lupus*), in some countries (including those whose last wolf was shot long ago), to a level of social reverence shared only by whales and baby seals. Increasing ungulate populations, changes in societal attitudes, and in some cases abandonment of rural areas have recently allowed large predators to reoccupy areas from where they had disappeared. Wolves were reintroduced in Yellowstone National Park (United States) (Vucetich et al. 2005), and have increased substantially in both numbers and range in the north-central United States (Harper et al. 2005) and in both southern and northern Europe (Valière et al. 2003; Vilà et al. 2003). Brown bears (*Ursus arctos*) have increased their range in Europe [partly through reintroductions (Apollonio et al. 2003)], North America, and in Hokkaido in Japan. Cougars (*Puma concolor*) have increased in numbers in much of western North America and may be spreading eastward, possibly supplemented by illegal releases of captive animals (Scott 1998). European lynx (*Lynx lynx*) [which, unlike Canadian lynx (*Lynx canadensis*), are effective predators of small- and medium-sized ungulates] have expanded their range in Scandinavia and have been reintroduced in the Alps (Molinari-Jobin et al. 2002).

Despite these welcome cases of recolonization or reintroductions, however, on a global scale the conservation status of large carnivores is deteriorating. Many populations face an uncertain future,
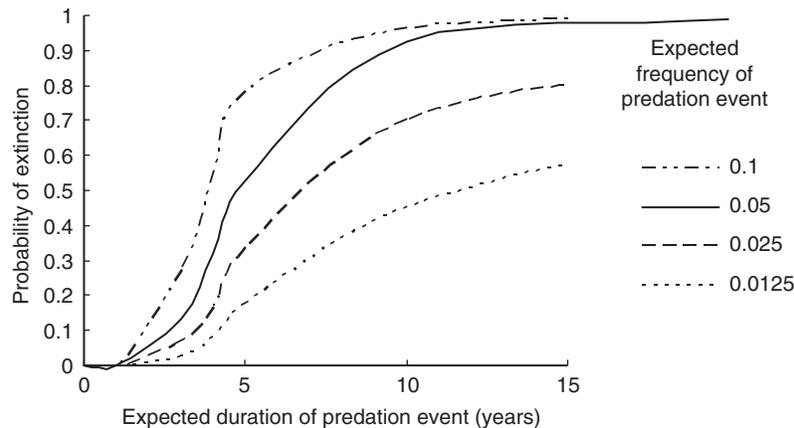
**FIGURE 11.1** An example of apparently unsustainable predation: Cougars and bighorn sheep at Ram Mountain, Alberta. The probability of population extinction increased with the frequency of occurrence of individual cougars that specialize on predation on bighorn sheep and with the duration of the predation "event." (From Festa-Bianchet et al. 2006. *Proc. R. Soc. B* 273:1537. With permission.)

and several species are threatened with extinction or extirpation over wide areas (Brashares 2003; Proctor et al. 2005). Even in countries where large carnivores have recently made some gains, the land surface from which they have been eliminated over the past two centuries is typically much greater than the area that they have reoccupied (Leonard et al. 2004). Nevertheless, some expanding carnivore populations are having an impact on ungulates and represent a challenge for wildlife managers, sometimes because of a public perception that large carnivores are under threat, which is true in much of the world (Cardillo et al. 2004), but not everywhere.

There are numerous recent examples of unsustainable predation on ungulates, leading to drastic declines or local extirpations (Figure 11.1). Woodland caribou are disappearing in the face of wolf and sometimes cougar predation (Wittmer et al. 2005b), bighorn sheep (*Ovis canadensis*) populations can be decimated by cougar predation (Festa-Bianchet et al. 2006), and several species of ungulates in the Kruger National Park in South Africa are declining rapidly, apparently because of lion (*Panthera leo*) predation (Owen-Smith et al. 2005).

Restoration of large carnivores is highly desirable for conservation of biodiversity (Berger et al. 2003). Sport hunting should be curtailed when predation increases natural mortality, and sometimes may have to cease. For example, sport hunting of nonmigratory woodland caribou is no longer permitted in most of Canada. In some cases, the impact of returning predators has been moderate. Clearly, more research is needed on how best to adjust ungulate harvests in the presence of predators (Nilsen et al. 2005), and the importance of other factors cannot be discounted: ungulate declines are not necessarily due to the return of large predators (Vucetich et al. 2005). But what should be done when ungulate populations are driven to extinction by predation, and more importantly, why do ungulate and predator populations sometimes not reach equilibrium? With the exception of some island populations, all extant species of ungulates were exposed to predation during their evolutionary history. It is normal for ungulates and large predators to coexist. Why then do we see cases where predation is a threat to the persistence of ungulate populations? I suggest that the answer lies in considering predator–prey equilibria over appropriate spatial and temporal scales. Unfortunately, the temporal scale at which equilibrium is likely to occur may not be acceptable to society, and the spatial scale required may no longer exist because of anthropogenic habitat modifications.

Managers could react to the threat of extinction caused by predation by removing some predators, but that measure is seldom taken (Ernest et al. 2002; Courchamp et al. 2003) because of social opposition. The problem in these situations is not the lack of tools to protect disappearing ungulate

populations from large predators, but rather an inability to convince the public that predator–prey equilibrium is not always possible. For example, public opinion in Canada generally opposes removal of wolves and cougars to protect endangered Vancouver Island marmots (*Marmota vancouverensis*), even though both predators are plentiful (on Vancouver Island and in many other areas) and the marmot is so rare (less than 40 in the wild) that it could go extinct within a few years (Bryant 1997). Most people typically oppose predator control because, intuitively, predator–prey equilibria seem inevitable, otherwise either the prey or the predator would have gone extinct. Equilibria over hundreds of years and thousands of square kilometers, however, do not imply short-term and small-scale equilibria, especially where habitats or community dynamics have been artificially modified (Darimont et al. 2005; Whitehead and Reeves 2005).

Over the long term, predators and prey typically reach an equilibrium, and many ungulate populations coexist with large predators, especially in remote areas (Messier 1994; Sinclair et al. 2003). There is no theoretical justification, however, to expect a fixed balance between prey and predators, particularly over small areas or short time spans (Sinclair and Pech 1996). Local extinctions due to predation, followed by recolonization, sometimes over a vast spatial scale, can be part of a long-term equilibrium even in pristine conditions (Kraus and Rödel 2004). Today, some ungulate species are rare because of habitat modifications through human activities, as is likely the case with caribou (~~which~~ are eas~~ier~~ to kill ~~and~~ need old-growth forests) living in areas where populations of moose (*Alces alces*) (~~those~~ wolves ~~which~~ find ~~it~~ difficult to kill and benefit from forestry operations) have increased partly because of forestry practices (Messier 1995; Stuarth-Smith et al. 1997; Schaefer et al. 1999) but see Hayes et al. (2000). In other places, the small amount of remaining habitat, or the lack of connectivity between habitat patches, make it unlikely that predators and prey will reach an equilibrium: that may be the current situation in the Kruger National Park in South Africa ~~and~~ that until recently was mostly fenced (Owen-Smith et al. 2005). In these cases, predator control may be an acceptable stopgap measure, but it is not a solution to the problem. If a predator–prey disequilibrium results from changes in the ecosystem, then the ecosystem requires management, not just the predators. Restoration of woodland caribou in Canada will require the restoration of mature forests. Over the long term, caribou conservation will involve cutting fewer trees, reclaiming roads, and limiting snowmobile access. It will not be accomplished just by killing wolves. Over the short term, however, some populations of caribou will disappear under the current level of predation (Wittmer et al. 2005b).

Recolonizing populations of large carnivores are a welcome development for biodiversity, but they present ungulate managers with several challenges. The widely held belief that predators and prey will reach equilibrium is fundamentally correct, but it requires an understanding of the temporal and spatial scales of predator–prey dynamics. For large mammals, those scales may involve decades or centuries, and thousands of square kilometers. Much of the public, however, expects that predator–prey equilibria will always occur, regardless of how small the area considered, how short the time frame, or how much the ecosystem has been compromised by human activities. Wildlife managers need more information on the effects of large predators on small populations of ungulates and on the interactions between predators, habitat changes, fragmentation, and the availability of alternative prey (including introduced exotic herbivores). Predator control on a large scale neither is nor should be socially acceptable, but an unjustified belief in an unfailing "Balance of Nature" may hamper conservation measures required to preserve populations threatened by predation (Courchamp et al. 2003).

## EXPONENTIAL POPULATION GROWTH AND UNGULATE IMPACTS ON BIODIVERSITY

Many ungulate species in Europe and North America are probably as numerous today as they have ever been. They live in areas where land-use practices have created good habitat, and are typically
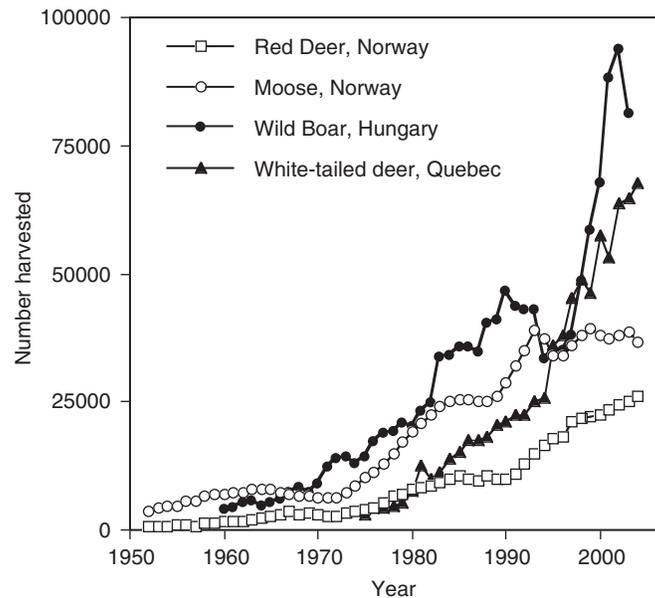
**FIGURE 11.2** Examples of increasing sport harvests of selected ungulates in Europe and North America.

harvested conservatively. Where large predators have been eliminated, ungulates suffer little if any predation, particularly on adults. The recent increase in ungulate density is typically viewed as a success story by sport hunters, and many hunting statistics suggest a continuing increase in the number of ungulates harvested over the past few decades (Figure 11.2). The number of red deer (*Cervus elaphus*) harvested in different European countries has increased by 400–700% over the past 30 years, yet in most countries that increase in harvest has not prevented an increase in both numbers and geographical range of red deer (Milner et al. 2006). The range of most species has expanded, and many are now sustaining sport harvests in areas where they were absent 15 or 20 years ago. For example, roe deer (*Capreolus capreolus*) are now found almost everywhere in Europe, including large open agricultural areas and mountains over 2000 m (Andersen et al. 1998). Unfortunately, the same is true for several exotic species, such as red deer in South America, New Zealand, and Australia, or sika deer (*Cervus nippon*) in Europe (Coomes et al. 2003; Pitra et al. 2005).

In this section, I will frequently refer to ungulate impacts on biodiversity as a bad thing, and I should explain why. Just like wildlife management "problems" would not exist if people did not create them, most "impacts on biodiversity" should not be seen as a bad thing unless they were caused by human actions. Over time, ecosystems change, species go extinct, distribution patterns change, and new species evolve. For example, over the past few hundreds of thousands of years, changes in ocean level allowed repeated waves of Old World species to enter North America. Those invasions certainly led to major ecological impacts and species extinctions, but there is no reason to see those events as negative: it is just what happens. If, however, deer browsing modifies habitats and causes local extinctions because people have removed the predators, built barriers to natural dispersal or migration, or introduced deer outside their natural range, then we have a problem and must fix it. There is accumulating evidence that higher biodiversity leads to greater ecosystem productivity and stability (Tilman et al. 1996; Sankaran and McNaughton 1999; Hughes et al. 2005) and, therefore, managers should attempt to limit the human-caused impacts of ungulates on other species. Because ecosystems naturally vary over time, it is always difficult to determine what a "normal" range of impacts is, particularly over short time scales. A useful rule of thumb is that impacts that can be attributed to human actions should generally be seen as negative.

When resources are not limiting, animal populations typically increase exponentially and not linearly. Consequently, protected or lightly hunted predator-free ungulate populations can increase rapidly and reach very high densities (Caughley 1970). Harvest quotas are often not increased sufficiently to contain expanding populations (Milner et al. 2006), because managers have to work with outdated population estimates (Fryxell et al. 1991; Solberg et al. 1999), sport hunters typically like more ungulates rather than fewer, and in some cases hunters simply cannot harvest enough deer (Giles and Findlay 2004). Ungulates can have substantial impacts on vegetation (Gordon et al. 2004). Those impacts are perhaps most obvious following artificial introductions, such as the effects of both wild and domestic ungulates in Australia, New Zealand, and many other islands (Choquenot 1993; Fraser et al. 2000). Although introduced bovids can be the focus of concern, such as mountain goats (*Oreamnos americanus*) in Olympics National Park, United States (Hutchings 1995), most of the current preoccupation with impacts of ungulates on biodiversity focuses on effects of browsing by cervids on the regeneration of woody species or on the persistence of rare plants (Côté et al. 2004). Not all populations of ungulates without either predation or harvests expand uncontrollably: Red deer on the unhunted part of the Isle of Rum or alpine ibex (*Capra ibex*) in the Gran Paradiso National Park in Italy seem to have reached an equilibrium with their environment (at least over a scale of decades) (Coulson et al. 2004; Jacobson et al. 2004). In general, negative impacts of ungulates on biodiversity are greater for browsers than for grazers (Mysterud 2006). Here I am concerned with cases where a herbivore-vegetation equilibrium does not appear possible without human intervention.

Wildlife managers have long been aware of the potential impacts of ungulates on vegetation, but that impact has greatly increased over the past two decades, prompting much concern and research, as recently reviewed by Côté et al. (2004). Extremely high deer densities are reached on islands and in protected areas, but densities sufficiently high to affect succession and prevent forest regeneration are now common over very wide areas. Unfortunately, deer can prevent regeneration of forests at densities well below their short-term carrying capacity (Coomes et al. 2003; Côté et al. 2004). The impacts of high deer density on biodiversity have been reviewed elsewhere in considerable detail (Augustine and McNaughton 1998; Berger et al. 2003; Côté et al. 2004) and I will only briefly summarize them here. Most of the attention has been devoted to impacts on vegetation structure and composition, and on bird diversity, because browsing removes nesting habitat and food resources. In addition, deer likely affect nutrient cycling and soil moisture characteristics, and modify the abundance and distribution of other animal groups such as invertebrates. Wild boar damage to many ecosystems and cultivations is increasing in many areas where boars or feral pigs are introduced exotics, and includes predation on nesting birds, small vertebrates, and invertebrates (Geisser and Reyer 2004). Additional undesirable consequences of high ungulate density are increased vehicle collisions and transmission of diseases to wild and domestic ungulates and to humans, including Lyme disease, brucellosis, tuberculosis, giant liver fluke, and chronic wasting disease (Brownstein et al. 2005). There is no question that ungulates can have a negative impact on biodiversity and on economic activities in areas where they are abundant. The question is what to do about it.

Two aspects of high-density populations of ungulates are particularly relevant to their management: Negative impacts on biodiversity are often evident at densities where ungulate populations still grow rapidly (Coomes et al. 2003), and the density required to limit environmental or economic damage is typically much lower than the density favored by sport hunters (Côté et al. 2004). Consequently, ungulate populations may not stabilize at levels where forest regeneration is possible. Management decisions to maintain low ungulate density in favor of biodiversity are likely to result in substantially lower harvest and therefore unsatisfied sport hunters, an important group of users of wildlife. Alternatives such as exclosures to allow forest regeneration are being experimented with. In parts of Europe, there is a long tradition of artificial feeding of deer in winter, and in some central European countries landowners have a legal obligation to provide supplementary winter food (Putman and Staines 2004). In many countries, hunters also pay compensation for forest and agricultural damage caused by wild ungulates. In France, in recent years, about US $22 million a year have been paid to landowners and farmers in compensation for damage caused by wild ungulates

(Office National de la Chasse 2003). In extreme situations, deer are baited into large enclosures and artificially fed for much of the winter. These practices may allow both maintaining a high deer density and limiting impacts on biodiversity, but they tend to be costly, produce an artificial system that requires continued human intervention, and are typically only feasible over a small scale.

Although several studies have documented severe impacts of high deer density on vegetation [reviewed in Côté et al. (2004)], few have directly addressed its long-term effects on both deer and biodiversity. Over a few decades, even if forest regeneration is prevented by browsing, high densities of deer may be sustained by litter fall and blowdown of mature trees (Tremblay et al. 2005). That system is unsustainable, however, because the mature trees will eventually die, presumably leaving a high-density deer population with no winter forage. Ungulate populations using resources that are not renewing themselves will eventually decline. An unresolved important concern is whether corrective measures (such as a drastic and sustained decrease in deer density) will result in a return to the original vegetation community, or whether some of the changes caused by deer are irreversible (Côté et al. 2004). There is an urgent need for research on both long-term impacts of high ungulate densities on ecosystems, and effectiveness of possible remedial measures (Coomes et al. 2003).

Because negative ecological consequences of overbrowsing often occur at much lower ungulate densities than those that lead to density-dependent reduction in population growth, and because high ungulate density can be sustained by "ecological subsidies" such as litter fall from mature trees (or artificial feeding programs), a superficial assessment of the situation may lead to a false sense of security, particularly by people strongly influenced by ideas about harmony in nature. Wildlife managers may not have an easy task in arguing for ungulate culls when the public thinks that there is no problem, such as in the case of protected areas with no large predators, where hunting is forbidden. That situation is akin to the person falling from a 25-floor building: asked how he was doing as he flew past the tenth floor, he answered "so far, so good." Unfortunately, much of the public still equates "protection of biodiversity" with "no hunting," because long-term ecosystem deterioration is difficult to portray in a 10-sec TV news item.

## WITHER THE BALANCE OF NATURE?

I trust that by now readers will wonder how I can first warn about unsustainable predation on ungulates by large carnivores and immediately after lament the negative impacts of predator-free, overabundant ungulates on biodiversity. I argued that ungulates do not need wildlife managers in the absence of human-caused problems. What I have illustrated since is a series of human-caused problems: predator extirpation followed by ungulate overabundance, complicated by habitat alterations and occasionally a return of predators to landscapes modified by habitat fragmentation, changes in land-use practices, and sometimes the introduction of exotic species. Under those circumstances, a "hands-off" approach is inexcusable, particularly when other sectors of society, such as agriculture, resource extraction industries, land developers, and various recreational industries, are not keeping their hands off. Wildlife managers face two challenges: to defeat the simplistic expectation of a short-term and ubiquitous balance between predators and prey, herbivores and forage, which is so ingrained in much of society, and to base management decisions on scientific knowledge. Management actions that involve killing either predators or ungulates typically face public opposition. They must be based on a combination of solid scientific evidence and professional integrity. There is a fine line between killing a wolf to save endangered caribou and a smokescreen to hide inaction on protecting caribou habitat from logging, snowmobiles, hydrocarbon exploration, and expanding road networks. When controversial policies are justified by the conservation of biodiversity, however, wildlife managers cannot simply shirk away from them just because they may be unpopular. Unfortunately, most politicians will typically select the path of least resistance and opt for policies guided by public opinion rather than by science. Consequently, it may fall upon wildlife scientists in academic institutions,

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rather than those working for government agencies, to provide an independent assessment of the scientific basis of unpopular management decisions.

## SELECTIVE HUNTING SELECTS!

Over the past few years, realization that humans can affect evolution of harvested species has become ~~firmly~~ established in the fisheries literature (Rochet 1998). This realization also led to changes in fishery management practices in the small subset of cases where fishery management is driven partly by scientific knowledge and not just by short-term political objectives (Hutchings et al. 1997; Olsen et al. 2004). Many sport-fishing regulations, for example, now emphasize the importance of protecting large individuals, and harvest of some species is regulated through maximum size limits rather than ~~just the~~ minimum size limits. Evolutionary effects of overfishing preoccupy fisheries managers, because if fish are artificially selected to reproduce at an earlier age and at a smaller body size, then both their fertility and the fish biomass available to be exploited will decrease (Hutchings 2004). Natural mortality may also increase if earlier reproduction lowers life expectancy and decreases reproductive success (Walsh et al. 2006). If fishing mortality is extremely high, however, reduced life expectancy will be irrelevant, as most fish die young, scooped up in a net.

In many populations of ungulates, most adult mortality is due to hunting (Langvatn and Loison 1999; Ballard et al. 2000; Biederbeck et al. 2001; Nixon et al. 2001; Bender et al. 2004). Hunters are typically selective of the sex–age or morphological characteristics of what they harvest, either because of hunting regulations or of social preferences (Hartl et al. 1995; Maher and Mitchell 2000; Solberg et al. 2000; Strickland et al. 2001; Martinez et al. 2005). Therefore, it is important that wildlife scientists examine the effects of sport harvest on evolution of exploited populations (Law 2001; Harris et al. 2002; Festa-Bianchet 2003).

Two characteristics of sport hunting of ungulates are particularly likely to lead to artificial selection: the preference for hunters to shoot males with large horns or antlers ("trophy" males), and the reduction in age-specific survival imposed by hunting. I have considered elsewhere the potential selective effects of sport hunting on life history strategies (Festa-Bianchet 2003) and I will only briefly summarize them here. I underline, however, that very few studies have addressed this issue. Therefore, although sport hunting may be a selective pressure, there are very few data available to assist scientists in assessing the extent (if any) of artificial selection in ungulates.

In an isolated population of bighorn sheep at Ram Mountain, Alberta, Canada, three decades of trophy hunting selected for rams with genetically smaller horns, mostly by creating a negative correlation between horn size and male reproductive success (Figure 11.3). This result was greeted with indignation by some hunter groups, skepticism by some managers, much interest by other managers, and a yawn by many evolutionary ecologists, who thought that the outcome was rather obvious. In bighorn sheep, horn length affects mating success for mature rams that can defend estrous ewes, but not for rams younger than about 7 years (Coltman et al. 2002). Young rams use alternative mating tactics and father some lambs (Hogg and Forbes 1997), but neither horn size nor social dominance appear to affect their mating success (Hogg and Forbes 1997; Coltman et al. 2002). Presumably, a subordinate ram's mating success is determined by his speed, agility, and willingness to risk being hit by other rams. Because bighorn rams complete much of their horn growth by 5 years of age (Jorgenson et al. 1998), however, Alberta's hunting regulations that require a minimum horn size of 4/5 curl (Figure 11.4) allow fast-growing rams to be shot at age 4. Therefore, large horns will increase a male's mating success from age 7, but will put him at risk of being shot from age four. With a harvest rate of about 30% for "legal" rams, about 10% natural mortality (Jorgenson et al. 1997), and a prerut hunt, a male "legal" at age 4 has only about a 15% chance of surviving to rut as a 7 year old. Males with small horns that never reach legal size see most of their potential competitors eliminated by hunters, and consequently father many lambs (Coltman et al. 2003).
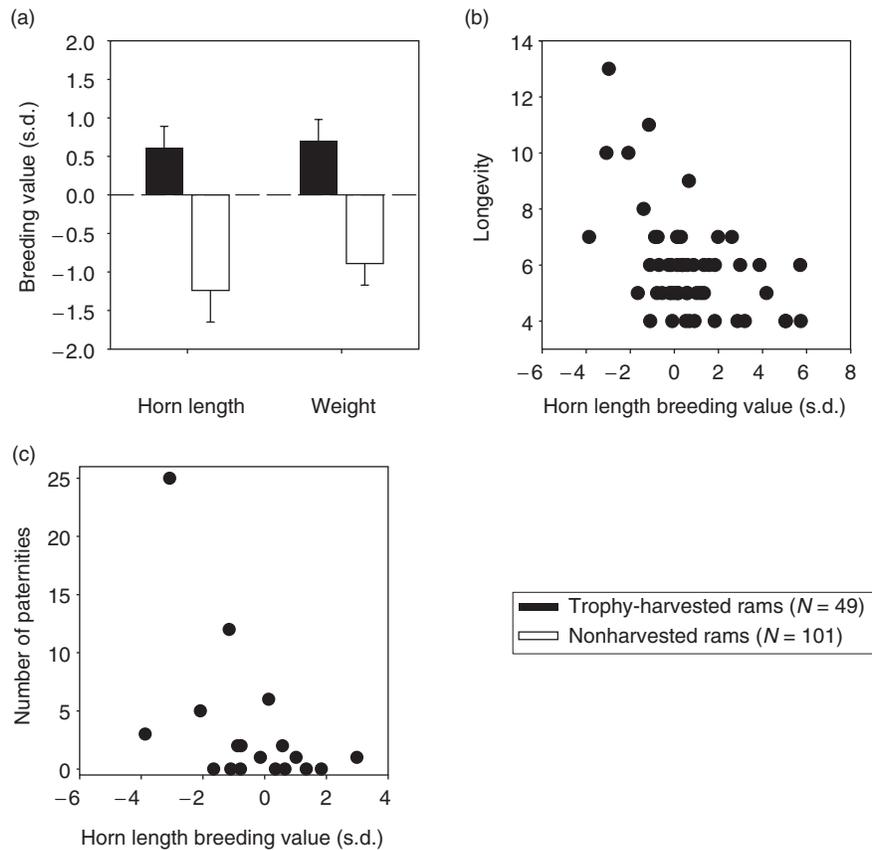
**FIGURE 11.3** At Ram Mountain, Alberta, Canada, selective removal of large-horned rams by hunters led to rams with high breeding values for both horn length and body weight having a greater probability of being shot (a), a negative relationship between horn length breeding value and longevity (b), and a negative correlation between horn length breeding value and lifetime reproductive success measured by the number of lambs fathered as determined by DNA analysis (c). Breeding value is a representation of the genetic component of a given trait. (From Coltman et al. 2003. *Nature* 426:655. With permission.)

Artificial selection through trophy hunting is possibly more likely at Ram Mountain than elsewhere, because the population is isolated. There is no immigration from protected refugia such as national parks, where rams with rapidly growing horns should have high mating success, because they will become dominant at a younger age (Pelletier and Festa-Bianchet 2006). During the rut, high- but not top-ranking rams from protected populations may move to areas where many of their potential competitors are removed through trophy hunting, undertaking "breeding commutes" over linear distances of ~~at least~~ 50 km (Hogg 2000). Consequently, a network of protected areas may retard or possibly even negate the selective effects of trophy hunting, if those areas can serve as a source of immigrants. In addition, lower levels of harvest will presumably result in a lower (and possibly negligible) evolutionary impact. There is little reliable information on the harvest rate of "trophy" males in any ungulate population, but the 30% rate measured at Ram Mountain is probably typical for mountain sheep in areas with limited access (Festa-Bianchet 1989). In populations that are easily accessible and where there are no limits to the number of permits issued, it is likely that most rams are shot the year they become "legal."

Ungulate managers are mostly concerned with population dynamics and habitat characteristics that may affect productivity of ungulate populations and, therefore, the sustainable level of hunting.

**FIGURE 11.4**   A 4-year-old bighorn ram shot in 2005 in southwestern Alberta. A line (represented here by the Plexiglas sheet) drawn from the base of the horn to the tip of the eye intercepts the tip of the horn, making this ram legal for harvest. Had its horn been one cm shorter, it would have been illegal to shoot it. Only rams with exceptionally large horns become "legal" at four years of age.

In many populations, sport hunting is the main source of adult mortality, and much of the harvest is selective, either through regulations or through hunter preferences. Therefore, managers should be concerned about potential evolutionary impacts of sport hunting (Festa-Bianchet 2003). Selective hunting could have several undesirable consequences on morphology, life history traits, and eventually population performance of ungulates. The evidence of artificial selection for small horns in trophy-hunted bighorn sheep, and the genetic correlation between traits that favor large horns and fitness-related traits in both sexes (Coltman et al. 2005) is both a conservation and an economic concern. Similar conclusions have recently been reached for fish under very high levels of experimental selective harvest (Walsh et al. 2006). These studies suggest that a harvest regime that targets the largest individuals can quickly lead to negative demographic consequences, as low-quality individuals are left to do most of the breeding.

When the artificial selective pressure is strong, evolution can happen surprisingly quickly. In the study by Walsh et al. (2006), major differences in reproductive performance were induced by just five generations of selection. It is, therefore, urgent to obtain empirical data on intensity of artificial selective pressures caused by sport hunting. An excellent research opportunity is provided by the ongoing drive towards "quality deer management" and by the patchwork of different hunting regulations over different geographical areas (Bishop et al. 2005). An assessment of the selective effects of hunting regulations is likely to be rewarding from both an applied and a fundamental viewpoint, and offers great opportunities for collaborations between wildlife managers and academic scientists.

Vast sums of money are generated through tourist hunting of trophy ungulates, yet a high level of selective removal of "trophy" males may have negative consequences. Hunters are willing to pay large amounts of money for the opportunity to shoot a large-horned male; therefore, a management regime that selects small-horned males appears rather counterproductive. Ecologically sensible harvest schemes, however, are unlikely to generate the same revenues given the current social preferences of trophy hunters. The person who pays $40,000 to shoot an argali (*Ovis ammon*) ram is

unlikely to pay that much to shoot a lamb, even if harvesting juveniles would mimic natural mortality and allow a much greater harvest rate. In those cases where some of the revenue generated through trophy hunting is used for conservation (Harris and Pletscher 2002), the potential loss of that revenue through ineffective management would be a serious conservation (as well as economic) concern. Unfortunately, however, while many trophy-hunting programs in developing countries claim to contribute to conservation, most of them only contribute to trophy hunting. Currently, very little, if any, of the money generated through most trophy-hunting of mountain ungulates in Asia benefits either conservation or the local economy (Hofer 2002).

Socially, trophy hunting is less acceptable than other forms of sport hunting and "trophy hunters" are a favorite target of antihunting groups. Yet, if properly managed, trophy hunting can be sustainable and used to finance protection of biodiversity, particularly in developing countries (Leader-Williams et al. 2001). Over the short and medium term, the challenge for managers and researchers is to identify trophy-hunting management practices that do not affect evolution. Possible solutions include reductions in harvest of mature males, greater selectivity for those that have had opportunities to breed (rather than killing high-quality males before they can pass on their genes) and a network of protected areas to provide unselected immigrants. Over the long term, however, the greater challenge is to do away with the competitive aspect of trophy hunting. An end to "scoring" mentality (the "mine-is-bigger-than-yours" approach to hunting) and to bizarre traditions such as "slams" (the "stamp collecting" approach to hunting) would be a good start.

## UNGULATE POPULATION DYNAMICS WITH AND WITHOUT HUNTING

Population dynamics and life history evolution are inevitably connected: reproductive strategies, mating systems, maternal investment strategies, and mate choice are all influenced by age-specific survival and reproduction probabilities, and by sex ratio (Stearns 1992). In turn, reproductive strategies can affect age- and sex-specific mortality. It has long been assumed that higher mortality of males than of females among adult ungulates is due to a greater reproductive effort of males during the rut, although the evidence supporting that contention is not very convincing (Toïgo and Gaillard 2003). In particular, it is far from clear that highly successful males suffer higher natural mortality than less successful ones (McElligott et al. 2002; Pelletier et al. 2006). Recent research has revealed that sex–age structure is a major determinant of population dynamics in ungulates (Coulson et al. 2001; Festa-Bianchet et al. 2003), which is not surprising, given how strongly the reproduction and survival probabilities of ungulates vary with age (Gaillard et al. 2000). If mortality induced by sport hunting differs from that due to natural causes, it will almost inevitably affect both evolution (as argued in the previous section) and population dynamics of ungulates.

Three characteristics of sport hunting mortality usually differ drastically from natural mortality: age, sex, and timing. These differences can increase population productivity but can also increase impacts of changes in both density and weather upon population growth rate.

There are now several unhunted or lightly hunted populations of ungulates in North America and Europe where the sex- and age-specific survival of marked individuals has been monitored for many cohorts. The results for females are remarkably similar (Figure 11.5): Juvenile survival is generally low (averaging about 50%) and very variable from year to year, yearling survival is typically 5–10% lower than the survival of adults, then there is a "prime-age" phase (typically from 2 to about 7–9 years of age) when female survival is very high (92–95% or higher) and stable from year to year, followed by a senescent phase where yearly survival gradually declines to about 50% at 17–19 years, an age reached by extremely few individuals (Gaillard et al. 2000; Loison et al. 1999a). Male age-specific survival is usually lower than female survival but follows a similar pattern, although with much more interspecific variability (Figure 11.5). A review of recent studies by Gaillard et al. (2000) revealed that these sex- and age-specific patterns of mortality apply to
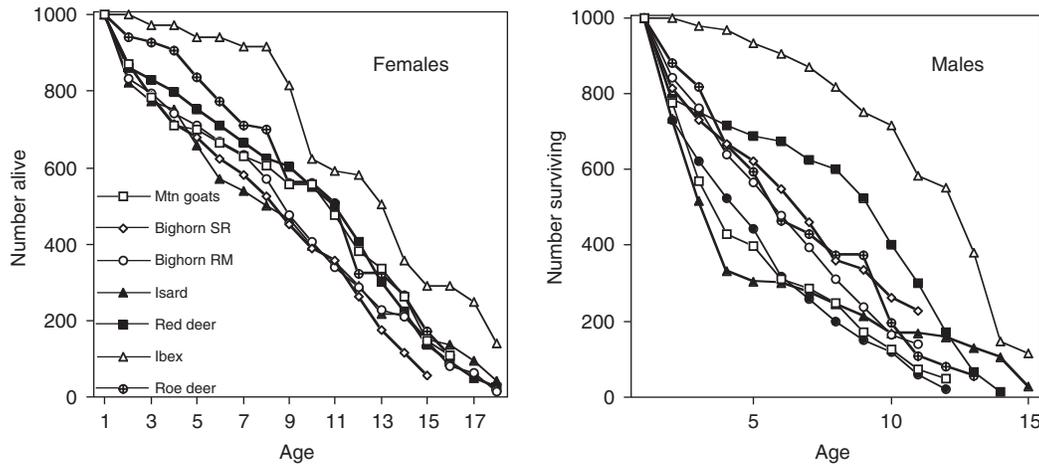
**FIGURE 11.5**   Natural local survival of cohorts of 1000 yearling females and males in unhunted populations of ungulates, based upon the age-specific survival measured through long-term monitoring of marked individuals: bighorn sheep at Sheep River and Ram Mountain, Alberta (Canada) (Loison et al. 1999a), mountain goats at Caw Ridge, Alberta (M. Festa-Bianchet and S. D. Côté, unpublished data), isard (*Pyrenean chamois*) at Orlu (France) (Loison et al. 1999a), fallow deer (males only, filled circles) at Phoenix Park, Ireland (McElligott et al. 2002), alpine ibex at Belledonne, France (C. Toïgo, unpublished data), red deer on Rum, Scotland (Catchpole et al. 2004) and roe deer at Chizé, France (J.-M. Gaillard, unpublished data). For mountain goat and isard males, some disappearances of animals aged 1–3 years are due to emigration rather than mortality.

most ungulate species: in unhunted populations most mortality affects young of the year, yearlings, and individuals aged 10 years or more (although mortality of males aged 6–10 years can also be substantial in several species; Figure 11.5). Most populations examined in that review had no large predators, but predation can lead to substantial adult mortality (Owen-Smith and Mason 2005). Often, however, predation on ungulates is most severe for very young and very old individuals (Kunkel et al. 1999). Gaillard et al. (1998) suggested that juveniles, yearlings, and possibly senescent individuals are most susceptible to yearly variation in mortality due to changes in weather, population density, and predation. On the other hand, very few studies that accounted for age effects on survival found significant yearly variability in the survival of prime-aged adults, particularly females. Evidence of weather or density effects on the survival of prime-aged adult female ungulates is particularly scarce. It appears that most ungulates evolved under conditions of low and variable juvenile survival and high and stable survival of presenescent adults (Gaillard and Yoccoz 2003).

In contrast, in most hunted populations of ungulates, mortality of prime-aged adults is high, so that few (if any) individuals reach senescence, or even the age of asymptotic mass or horn/antler size. In many hunted populations, mortality of very young males is extreme, leading to the somewhat bizarre situation where hunters think of a 4-year-old as an "old" male, or of a ratio of 5 bulls per 100 cows in elk as normal (Bender et al. 2002). Although there are few precise data on age-specific survival of ungulates in hunted populations, a harvest rate of 20% of adult females, assuming an additional 2% natural mortality, would mean that only about 38% of yearlings would reach the age of five years, half as many as the average of 75% (range 66–94%) in seven unhunted populations of ungulates monitored over the long term (Figure 11.5). For males, a harvest rate of 35% and natural mortality of 3% (both very conservative assumptions) would let only 10% of yearlings survive to age 5, much less than the average of 57% (range 31–93%) for the eight unhunted populations [including mountain goats and isard (*Rupicapra pyrenaica*), where some disappearances of young males were due to emigration] shown in Figure 11.5. Sport hunting of ungulates leads to a truncated age distribution and a strong female bias among adults (Solberg et al. 2002). I have discussed

elsewhere the potential evolutionary consequences of shortened life expectancy and biased adult sex ratio (Festa-Bianchet 2003). Here, I will examine some potential consequences for population dynamics.

First, compared with unhunted populations of ungulates, many hunted populations contain few or no senescent individuals, almost no mature males (aged six years and older in most species), and a high proportion of young females that typically enjoy extremely high natural survival (Gaillard et al. 2000). Hunted populations should therefore experience low natural mortality of adults (Festa-Bianchet et al. 2003) and high productivity. Particularly if hunters avoid harvesting juveniles, however, a very high proportion of the post-hunt population will be made up of young of the year and yearlings, the age classes that are most sensitive to the effects of weather and population density (Gaillard et al. 1998). Therefore, heavily harvested populations may show greater changes in numbers according to winter weather than unhunted populations, particularly in interaction with high population density (Portier et al. 1998). A heavily juvenile-biased age structure should also result in stronger density-dependence of overall survival.

Second, male mortality is very high in hunted populations, usually through a combination of hunter preference and management regulations. Consequently, males have a very short life expectancy. In Norway, only 5% of male moose shot by hunters were aged 5 years or older, and 60% were yearlings (Mysterud et al. 2005). In hunted elk populations in Oregon, 7% or less of males survived to 4 years of age (Biederbeck et al. 2001). A female-biased adult sex ratio will increase overall "adult" survival (because males have lower natural survival than females) and increase recruitment compared with naturally regulated populations (Solberg et al. 1999). In extreme cases, however, a scarcity of reproductive males may lower recruitment or increase the proportion of females that fail to conceive in their first estrus (Milner-Gulland et al. 2003; Sæther et al. 2003). The resulting late-born juveniles are likely to experience high mortality (Festa-Bianchet 1988). Although it is sometimes assumed that males are "superfluous" in ungulate populations, theory and data both suggest that males play an important role in population dynamics (Gaillard et al. 2003; Mysterud et al. 2002). The age distribution of males may even affect juvenile sex ratio (Saether et al. 2004). Therefore, the effects of changes in adult sex ratio or male age structure in hunted populations are worth investigating.

Third, the timing of mortality is very different in hunted and unhunted populations. In unhunted populations of northern ungulates, most mortality occurs in late winter, when body condition is at its yearly minimum (Loison et al. 1999b). In hunted populations, much of the mortality is during the autumn hunting season, when animals are typically in peak body condition. In unhunted high-density populations, all animals compete with many conspecifics until late winter, when finally those in worse condition (typically juveniles and senescent individuals) die (Clutton-Brock et al. 1987). In contrast, in heavily hunted populations the survivors of the hunting season face winter with a much-reduced number of competitors. Presumably, the lower level of competition will improve overwinter survival. Consequently, the dynamics of a hunted and an unhunted population with the same summer density are likely to be very different. In the hunted population, survivors of both the hunting season and the winter should be in better condition in the spring and may have higher reproductive success than survivors from the unhunted population that faced a higher level of intraspecific competition during winter (Boyce et al. 1999).

Because of opposing (and possibly interacting) effects of biases in sex and age structure and of difference in timing of natural and hunting mortality, it is difficult to predict how the dynamics of hunted and unhunted populations may differ in the face of changes in weather or density. Demographic and life history theories developed for unhunted populations may see their basic assumptions (sex–age distribution, timing of mortality, strength of the effects of weather, and density-dependence) violated in hunted populations. If harvest levels of adults of both sexes are very high, and higher for males than for females, the surviving population would include mostly juveniles, yearling males, and females aged 1–3 years. Such a population would be highly productive but also very vulnerable to harsh winter weather. On the other hand, a heavy

harvest of males and of juveniles of both sexes could maintain a highly productive population with high survival, as intraspecific competition during winter will be lowered by autumn harvests. Finally, the sudden cessation of harvests (as may occur following changes in land tenure) could lead to unpredictable changes in density and sex–age structure (Coulson et al. 2004).

## CONCLUSIONS: WHAT TO DO?

Wildlife management should minimize the impacts of humans (including hunters) on biodiversity. Sport hunting must be sustainable, but "sustainable" should not simply mean that enough animals are left to hunt again the following year. It should also mean a management regime that will not drastically alter either the selective pressures acting on wild ungulates, or their impact on the ecosystem. The potential consequences of alternative management strategies must be considered over the long term, because both the ungulates and some of the species they interact with have long generation times. Management leading to artificial selection, or to negative impacts of ungulates on biodiversity, is not sustainable even if it fulfills the short-term goal of providing recreational opportunities.

Sport hunting is and should be a component of conservation, because it generates both interest and education in biodiversity, and income that can be used for conservation. Providing sustainable sport hunting opportunities is an acceptable goal of a democratic society. Inevitably, hunted populations will differ from those that are not hunted. Wildlife managers must know what those possible differences may be, and select a strategy that provides recreational opportunities while minimizing any consequences that are undesirable from an ecological or societal viewpoint.

Sometimes ungulate hunting is necessary, for example, to limit their impacts on ecosystems where large predators have been removed, or to control exotic species. In many other cases, hunting is tolerable, because it does not severely affect biodiversity. Ungulate removals are at times necessary in protected areas where ungulates alter ecosystem functions. Sport hunting of exotic ungulates is encouraged in national parks in New Zealand and may be required in some parks elsewhere if natural predators have been eliminated and cannot be reintroduced.

Sustainable sport harvest should not be selective for morphological attributes and should attempt to mimic natural mortality. Ideally, it would mostly remove young of the year and older individuals. In many species, however, hunters cannot distinguish juveniles from adults, and in most species, they cannot recognize senescent individuals (especially females). There is often a cultural resistance to killing juveniles. When asked about the best sport-hunting strategy for mountain goats, I reply that hunters should only shoot kids. That is because mountain goats have a late age of primiparity, low recruitment, and are highly susceptible to the harvest of adults, especially females (Côté and Festa-Bianchet 2003). Given that mountain goat kids are as cute as baby seals, however, my suggestion usually elicits a negative reaction. Hunters should always be encouraged to harvest juveniles rather than adult females or prime-aged males. Directing most of the harvest to young of the year has been used very successfully for Scandinavian moose (Nilsen et al. 2005) and other cervids (Milner et al. 2006). Although I consider trophy hunting to be ecologically undesirable, it is not realistic to advocate its immediate end, and some harvest of adult males is sustainable. The tradition of seeking to harvest males with large horns or antlers is deeply engrained in the social fabric, and generates revenues that could be (and occasionally are) directed to conservation (Leader-Williams et al. 2001; Harris and Pletscher 2002). More research is required to establish what trophy hunting programs are sustainable and do not affect the evolution of harvested populations. Males with large horns or antlers should only be harvested after they have had a chance to benefit from those large weapons by obtaining a high mating success. For most species, it means harvesting males at least 9–10 years old (Clutton-Brock et al. 1988; Coltman et al. 2002). Clearly, this will require a reduction in the numbers that can be shot. For the eight unhunted populations illustrated in Figure 11.5,

the average male survival from yearling to 5 years is 57%, but survival to 10 years averages only 27%.

Wildlife managers and scientists should speak out against the emphasis on trophy size over everything else. That emphasis is motivated by economic gain and does not serve either sport hunting or conservation. It is reflected in attempts to artificially feed ungulates to increase trophy size, the popularity of penned "hunts," and the increasing efforts of outfitters and providers of private "pay-per-hunt" facilities to boost trophy size (Geist 1994). Market-driven hunting industries predictably seek to maximize revenue, and they can best do so by encouraging a hunting ethic that identifies horn or antler size with hunt satisfaction or with personal prestige. Those interested in promoting hunting as a conservation tool rather than as a source of income, however, must advocate ecologically responsible hunting practices. This includes both a limitation of ungulate density to prevent negative effects on biodiversity, and harvest plans that attempt to mimic natural mortality. It also requires policies that maintain sport hunting within the reach of most sectors of society, not restrict it to a small elite group (Geist 1992, 1994).

Although they share many broad similarities in population ecology and life history strategies, not all ungulates have identical ecological attributes, and basic knowledge of the biology of each species (or of the same species in different ecological situations) is required to manage them sustainably. Although age-specific survival of adult females in different species appears broadly similar, for males it can be very different (Figure 11.5). One should not manage the harvest of mountain goats or ibex based on the assumption that they have sex- and age-specific schedules of survival and reproduction similar to those of most cervids. Recent examples of research on marked individuals that underlined interspecific differences among ungulates include the extremely high susceptibility of mountain goats to sport harvest (Hamel et al. 2006), possibly due to a very late age of first reproduction (Côté and Festa-Bianchet 2001), and the unusually high survival of adult male ibex (Toïgo et al. 1997). Already, management of mountain goats based on the assumption that they were similar to other ungulates led to overharvesting: goats may be the only North American ungulate for which sport hunting led to local extirpations or drastic declines (Côté and Festa-Bianchet 2003). For alpine ibex, the high survival rate of males means that harvest of young and middle-aged males would produce an artificial age structure with many fewer older males than in unhunted populations. The same harvest practices would have a much lower impact on the age structure of moose, deer, or mountain sheep.

I conclude with a plea for research on marked individuals in hunted populations. Long-term monitoring of marked individuals is not always possible and presents many challenges. It requires access to a study area that does not undergo drastic changes in accessibility, land tenure, or administration for decades. For long-lived species such as ungulates, however, it is the best way to document basic biological attributes that are relevant to management, such as age-specific survival and reproduction, or how density-dependent and density-independent factors affect reproduction, growth, and survival of different sex–age classes. Results from long-term studies of marked individuals have been instrumental in affecting ungulate management policies (Gordon et al. 2004), yet basic biological information is still lacking for many sport-hunted species. For example, I am unaware of data on sex- and age-specific mortality of white-tailed deer or caribou that could be comparable to those available for roe deer, red deer, or bighorn sheep (Gaillard et al. 1998). There is almost no comparable information for any ungulate species from Asia, Africa, or South America (or for macropod marsupials). Both wildlife management and ecological theory stand to benefit from long-term studies of marked individuals in hunted populations, because hunting affects both population and evolutionary ecology. Most long-term research on marked ungulates investigated populations that were either lightly hunted or not hunted at all. Because most ungulate populations are subject to sport hunting, however, questions remain about the applicability of results from long-term, individual-based research to hunted populations (Festa-Bianchet 2003). In particular, heavy sport harvest may select for different reproductive strategies in both sexes, which could have important (but currently unknown) effects on both population ecology and evolution.

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## ACKNOWLEDGMENTS

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