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Exploitative Wildlife Management as a Selective Pressure for Life-History Evolution of Large Mammals

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This chapter explores the usefulness of behavioral ecology when sport hunting is either a component or the major objective of a wildlife management strategy. I examine the potential selective effects of different management practices, and argue that wildlife managers' ignorance of those effects could have long-term negative ecological and economic consequences. Knowledge of the selective pressures caused by sport harvest could help define harvesting programs that avoid or reduce artificial changes in the genetic makeup of harvested populations. I will assume that the main goal of sport hunting is to provide recreational opportunities, not to maximize meat production or the number of animals killed. Within that framework, I suggest that minimizing the impact of sport hunting on the evolution of the hunted species should be a major preoccupation of wildlife managers.

Until recently, most wildlife management was concerned with numbers of animals within a hunted population, and their relationships with their habitat. Hunting regulations and harvest quotas are typically based on population goals. Managers either seek to harvest enough animals to prevent some

type of habitat or health degradation (such as allowing forest regeneration or decreasing the risk of epizootics), or to avoid overharvesting and thereby maintain the ability to harvest the population in the future or to increase long-term yield (Caughley and Sinclair 1994). Consequently, much management-oriented research has focused on population dynamics, particularly questions of density-dependence and of time lags in population and habitat responses, or on the relationships between herbivores and predators (Fryxell et al. 1991, Clutton-Brock and Loneragan 1994, Messier 1994, Solberg et al. 1999). Hunting regulations often direct the harvest to particular sex/age categories, depending on the harvest or population goals (Kokko, Lindström, and Ranta 2001). For example, male-only harvest is used in cases where female harvests are expected to decrease the population below the management goal. Adult male and young-of-the-year harvests are often used when populations are at the desired density, and finally all sex/age classes, including adult females, are taken where either the population would grow rapidly in the absence of harvests, or a reduction in density is desired.

In North America, little attention has been paid to the potential selective effects of sport hunting (Harris, Wall, and Allendorf 2002). In parts of Europe, on the contrary, there is a rich tradition of “selective” hunting, sometimes with painstakingly detailed hunting regulations that direct the harvest to particular sex/age classes or even to particular phenotypes. Some of these practices include the selective removal of individuals that appear weak, or with “undesirable” antler or horn shape and size. In some cases, the apparent intent of selective harvests is to decrease intraspecific competition and maintain future recruitment by removing those individuals that are least likely to survive. In other cases, however, the goal of selective harvest is indeed to select, by favoring certain phenotypes over others. There is evidence that European harvest practices can affect the genetic variability of hunted populations, at least for red deer (*Cervus elaphus*) (Hartl et al. 1995, 1991) and foxes (*Vulpes vulpes*) (Frati, Lovari, and Hartl 2000).

In North America, hunting rules are not as detailed as some European regulations, but often go beyond specifying the sex of the animals that can be harvested. For example, a minimum horn size is often set for male pronghorn (*Antilocapra americana*), mountain goat (*Oreamnos americanus*), and mountain sheep (*Ovis* spp.), and a minimum number of antler points for cervids.

In addition to legal requirements, hunters’ preferences affect the type of animals they are more likely to harvest. Hunters may avoid shooting females accompanied by young (Solberg et al. 2000). Given a choice, most hunters will take the largest individual, or the one with the largest horns or antlers. Because in many populations of ungulates sport hunting is the principal

cause of death for adult animals (Langvatn and Loison 1999), it is reasonable to suppose that nonrandom hunting mortality may have a selective effect. Recent studies of wild ungulates have shown strong heritabilities for morphological traits such as body size, and varying levels of heritability for life-history traits, particularly those affecting female fertility (Hewison 1997; Réale, Festa-Bianchet, and Jorgenson 1999; Kruuk et al. 2000). Hunting-induced mortality of nonlactating females may select for increased investment in reproduction by generating an artificial positive correlation between reproductive effort and survival, whereas hunter selection for large-horned males could lead to either a selective advantage for small-horned males or selection for an earlier investment in rutting activities (Heimer, Watson, and Smith 1984).

Trophy hunting is well developed in many parts of the world and is a major economic activity. There is considerable interest in the use of sport hunting as part of a conservation strategy. Trophy hunting of ungulates is particularly appealing from a conservation viewpoint because a very large income can be generated from the harvest of a small number of animals (Lewis and Alpert 1997). Consider for example the markhor (*Capra falconeri*), an endangered species. Like many other ungulates in Asia, it is threatened by poaching and habitat destruction (Shackleton 1997). Trophy hunters will pay several tens of thousands of dollars to kill a mature male. That money could be used for conservation and could show the value of habitat protection to the local population. At the same time, the demographic impact of removing a few mature males is minor. Indeed, although the markhor is listed in Appendix I of the Convention on International Trade of Endangered Species (CITES), a program in Pakistan for limited trophy hunting of this species is supported by the World Conservation Union (IUCN) Caprinae Specialist Group.

There are two questions related to the potential selective effects of trophy hunting. First, what is the effect of increasing the mortality of males with a trait (large horns or antlers) that is favored by sexual selection and is likely correlated with individual reproductive success? Second, if trophy hunting selects for smaller horns or antlers, then it will decrease the availability of large-horned or large-antlered males over the long term. Therefore, what management strategies may ensure that trophy hunting can be sustained, particularly given the direct relationship between the expected trophy size and the amount of money hunters are willing to pay?

There are many possible selective effects of sport hunting upon the hunted species. For example, about half of the adult mortality of snow geese (*Anser caerulescens*) in North America is due to hunting (Gauthier et al. 2001), and there are untested speculations that wild geese have evolved (or

learned and then culturally transmitted) behaviors to avoid sport hunters. Sport fishing has been suggested to select for “smarter” fish (Miller 1957), more adept at avoiding anglers’ lures. I will consider two specific cases where sport hunting may have a selective effect on large mammals: changes in reproductive strategy caused by high hunting-induced adult mortality, and changes of horn and antler morphology caused by trophy hunting. The evidence for or against a selective effect of sport hunting is limited because this problem has apparently attracted little attention from either wildlife managers or behavioral ecologists (Law 2001). Rather than review all the available evidence, therefore, my goal is to point out that artificial selection through sport hunting can be a serious ecological, economic, and ethical problem, and therefore research is urgently required to determine the extent to which it may occur.

Sport Harvest and Life-History Evolution

For many species of ungulates, hunting, legal or otherwise, is the most common cause of adult mortality. In areas where large predators have been eliminated, hunting and road accidents account for almost all adult mortality (McCorquodale 1999, Ballard et al. 2000). In Europe, outside protected areas, hunting probably accounts for most mortality of adult chamois (*Rupicapra rupicapra* and *R. pyrenaica*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), moose (*Alces alces*) and red deer. In North America, the same could be said for white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), pronghorn antelope, male bighorn (*Ovis canadensis*) and Dall sheep (*O. dalli*), and some populations of moose, wapiti, and black bear (*Ursus americanus*). Modern wildlife management can claim a numerical success: many hunted species are much more abundant now than they have been for several centuries. In these populations, high density coexists with high levels of hunter harvest, a situation made possible by past restraint in harvests, controls over poaching, good habitat, and absence or near-absence of predation on adults. Artificial feeding is also partly responsible for high ungulate densities, particularly in central Europe.

DEMOGRAPHIC EFFECTS OF HUNTING

What are the demographic characteristics of a hunted population, and how do they differ from those of ungulate populations limited by food availability or by predators? There are two major effects of hunting: an age distribution heavily skewed toward younger animals, and a sex ratio biased in favor of females (Squibb 1985, Ginsberg and Milner-Gulland 1994, Laurian et al. 2000).

These effects can be extreme: posthunt sex ratios of less than 5 males per 100 females have been reported for elk (Noyes et al. 1996).

Few studies have measured the survival of marked individuals in sport-hunted populations of ungulates. In a population of red deer in Norway, natural survival of stags from weaning to 5.5 years of age was 56%, but was reduced to 5% by hunting; in the same population and over the same age interval, survival of females was reduced from 59% to 32% (Langvatn and Loison 1999). In a trophy-hunted population of bighorn sheep in Alberta, natural survival of rams from 4 to 8 years was 58%, but actual survival was reduced to 27% by sport hunting. Because that population was partially protected by a wildlife sanctuary where most rams spent most of the hunting season (Festa-Bianchet 1989), it is likely that in other hunted populations survival to 8 years would be even lower. In one population in Alaska, 10 of 23 mature Dall rams were shot within 2 years of marking, an average harvest-induced yearly mortality of about 25% (Heimer, Watson, and Smith 1984). In a population of Norwegian moose, about 15% of adult females were shot each year, in addition to the 2.5% yearly natural mortality (Stubsjøen et al. 2000). Therefore, fewer than 50% of yearling female moose would survive to 5 years in hunted populations, compared to about 90% in unhunted populations. Data on survival of marked individuals from other hunted populations are scarce, but it is reasonable to suspect that in many heavily hunted species, fewer than 5 to 10% of yearling males and perhaps fewer than 15 to 20% of yearling females survive to 5 years. In unhunted populations the corresponding figures would be about 50 to 60% for males and 60 to 70% for females (Loison et al. 1999a, Gaillard et al. 2000). Because almost all studies of marked individuals report that adult survival of ungulates is not density-dependent, natural survival should not be lower in unhunted than in hunted populations (Gaillard et al. 2000).

SPORT HUNTING AS A SELECTIVE PRESSURE FOR REPRODUCTIVE STRATEGY

Sport hunting causes high mortality of prime-aged adults, whereas most natural mortality affects young of the year and senescent individuals (Gaillard 1998, Gaillard et al. 2000). Life-history strategy and demography are linked: early comparative approaches to life-history evolution suggested trade-offs between, for example, age of first reproduction and longevity (Harvey and Zammuto 1985), or litter size and juvenile survival (Promislow and Harvey 1990). Over the long term, however, those trade-off are inevitable: a species where first reproduction occurs late in life and average lifespan is short will go extinct and therefore will not be around for biologists to study. If adult

mortality is high, either fecundity or juvenile survival must be high, or extinction will follow. Conversely, if adult mortality is low, either fecundity or juvenile survival will decrease because populations cannot increase indefinitely.

If ungulates evolved with low adult mortality, what are the possible consequences of high adult mortality through hunting? The most likely consequence is an increase in reproductive investment by young adults. In ungulates, strong iteroparity and small litter size select for low maternal investment to avoid compromising the female's survival and future chances to reproduce, particularly when combined with high and temporally variable juvenile mortality, much of which is independent of the amount of maternal care (Festa-Bianchet and Jorgenson 1998). Indeed, interspecific comparisons show that the survival of prime-aged females (before senescence) in un-hunted populations is high and varies little, regardless of the causes of mortality (disease, predation, starvation, weather) (Gaillard et al. 1998b, Gaillard et al. 2000). A female with a 92 to 96% yearly survival probability should not increase her current maternal investment to a point where it may affect her viability, given that her offspring faces a much lower and widely varying probability of surviving to 1 year, and then a yearling survival that is typically lower than adult survival (Gaillard et al. 2000).

In heavily hunted populations, however, female survival is greatly diminished, independently of current reproductive effort. In addition, a dependent offspring may increase survival, as hunters are often reluctant to kill lactating females (Solberg et al. 2000). Hunting regulations for alpine chamois in many jurisdictions prohibit the killing of lactating females. Similar regulations protect members of grizzly (*Ursus arctos*) and black bear family groups in much of North America. In Alberta, there is a high proportion of 2-year-old ewes among the harvest of "nontrophy" bighorn sheep. Two-year-old ewes often do not produce lambs, and hunters may select ewes without lambs (W. D. Wishart, 1982, pers. comm.). In hunted populations, therefore, there could be selection for increased maternal expenditure. In species like chamois and bighorn sheep that are usually hunted in open areas, selection against females without dependent offspring is likely stronger than for forest-dwelling species such as white-tailed or roe deer, where hunters have fewer opportunities to evaluate female reproductive status before they shoot.

When populations are kept below carrying capacity through hunting, female reproductive performance is enhanced: age of primiparity decreases, whereas fecundity, juvenile survival, and litter size usually increase (Swenson 1985; Jorgenson, Festa-Bianchet, and Wishart 1993; Jorgenson et al. 1993; Swihart et al. 1998). Over the short to medium term, these effects can largely be explained by density-dependent mechanisms: observational and experimental studies of ungulates show that female reproduction, particularly age

of primiparity, is very sensitive to resource availability (Langvatn et al. 1996). An additional, potentially confusing variable is the modified age distribution, which in hunted populations is typically heavily skewed toward younger and more productive age classes. This latter effect, however, should be weak: reproductive senescence in female ungulates occurs at an age reached by a very small proportion of females even in unhunted populations (Benton, Grant, and Clutton-Brock 1995; Bérubé, Festa-Bianchet, and Jorgenson 1999). Age differences between hunted and unhunted populations, however, are very likely to cause differences in mortality because survival senescence typically sets in several years before reproductive senescence (Benton, Grant, and Clutton-Brock 1995; Loison et al. 1999a). Therefore one may expect greater natural (i.e., unhunted) female survival in hunted than in unhunted populations, simply because in hunted populations there are few if any females older than 8 to 10 years.

In addition to the ecological effects due to lowered intraspecific competition, I suggest that heavy harvest may select for a life-history strategy that is normally disadvantaged in natural populations. Consider a set of genes whose phenotypic expression led to females that invested heavily in early reproduction, leading to early primiparity and an increase in offspring survival at the expense of maternal survival. In a naturally regulated population of ungulates, that genotype would be selected against because longevity is the greatest determinant of lifetime reproductive success for females (Clutton-Brock 1988, Bérubé, Festa-Bianchet, and Jorgenson 1999). If very few females survive more than two to four hunting seasons, however, a reproductive strategy leading to greater reproductive success early in life would be favored even if it had a negative effect on lifespan. If the average lifespan including natural and hunting mortality is 5 years, a gene that decreased natural lifespan from 10 to 6 years would not be selected against. Selection for high maternal investment would be strengthened by hunter preference for females without dependent offspring. This scenario is not dissimilar to what may be expected in other ungulate populations under artificial selection, such as domestic sheep, cows, or goats. Domestic ungulates have a shortened life expectancy compared to their wild counterparts, possibly because of artificial selection for increased reproduction (or milk production) early in life.

We readily accept that many traits of domestic animals are the result of artificial selection, and some life-history traits of wild animals could also be affected by artificial selection. With sport hunting, most adult mortality is human-caused and human predation is not random with respect to reproductive status or morphology. Obviously, a major methodological challenge in studying the selective effects of hunting is to separate the environmental effects due to lowered intraspecific competition and the genetic effects due to

selection for a less iteroparous reproductive strategy. A modeling exercise (Benton, Grant, and Clutton-Brock 1995) suggested that the reproductive strategy of red deer hinds that were hunted until a few generations before the study may be suboptimal, possibly because it was shaped by culling that for many generations resulted in a high level of adult mortality. Researchers have recently expressed concern that the life-history strategies of moose in heavily harvested populations in Sweden may be affected by hunting-induced mortality, which may select for high reproductive effort in early life and lead to premature senescence (Ericsson and Wallin 2001, Ericsson et al. 2001).

My review concerns large herbivores (and possibly some bear populations) that are subject to intense sport hunting, but a similar line of reasoning could apply to large carnivores that are the target of both sport hunting and trapping (or even predator control programs): for example studies of wolves (*Canis lupus*) outside protected areas report very high levels of human-caused mortality (Potvin et al. 1992).

The potential selective effects of harvesting have preoccupied some fisheries scientists for a long time (Miller 1957). Heavy fishing pressure may have not only a demographic effect on fish populations but also a selective effect (Kirkpatrick 1993, Policansky 1993, Reznick 1993, Rochet et al. 2000). Fishing disproportionately increases mortality of adult fish, and nets with mesh sizes allowing the escape of some of the smaller individuals further select against large fish (Law 2001). A logical outcome of these selective pressures is an earlier age of maturity, as reported by a number of studies (Rijnsdorp 1993, Rowell 1993, Rochet 1998). It is often problematic to partition environmental and genetic effects: early reproduction could occur in the absence of selection simply because resources may be more abundant in heavily harvested populations (Rochet et al. 2000).

High predation on adult guppies (*Poecilia reticulata*) is associated with earlier maturation, higher reproductive effort, and more and smaller offspring compared to populations where predation is mainly on juveniles. Differences in life-history strategies are heritable. Translocation experiments to areas where predation was mostly on juveniles led to life-history changes in 11 years (30–60 generations) (Reznick, Bryga, and Endler 1990), providing experimental evidence that life-history traits respond quickly to strong selective pressures. Fisheries scientists are interested in the possible evolutionary impacts of fishing upon fish populations that are exploited either commercially or for sport fishing. Because most of these populations are very difficult to study, however, the evidence for genetic changes consists mostly of phenotypic measurements on exploited stocks and controlled experiments in short-lived species that are not exploited (Reznick, Bryga, and Endler 1990; Reznick 1993). A more direct approach is possible with exploited ungulates,

where individual-level information on morphology, life-history, and genotype can be obtained. Different ungulate hunting regimes in adjacent areas offer great potential to compare life-history differences associated with differences in age-specific mortality.

Trophy Hunting and Selective Pressures on Horns and Antlers

Trophy hunting has a competitive component. Complex scoring formulae measure various aspects of an animal's horns, antlers, or skull, and records are kept by a number of organizations. Trophy scores are strongly correlated with size, therefore most trophy hunters seek adult males with large horns or antlers. Trophy hunting is big business: hunters are willing to pay very large sums in the hope of harvesting a "record book" trophy. Guides and outfitters typically advertise the trophy scores of animals shot by their clients, and areas reputed for producing large trophies attract much greater revenues than areas where males have smaller horns or antlers. For example, consider the bids received by the Foundation for North American Wild Sheep during its auctions of special permits for bighorn sheep (Erickson 1988). These permits are offered by some American states and Canadian provinces to the highest bidder, and typically sell for tens to hundreds of thousands of dollars that should then be used for conservation, research, or wildlife management activities. Recent auction results reveal that, although most jurisdictions obtain bids for special permits of between \$20,000 and \$60,000, those with a reputation for producing large rams (Alberta, Montana, Arizona) regularly receive up to 10 times as much, with bids topping \$400,000 (<http://www.fnaws.org/page1.html>). Some hunters are willing to pay great sums of money to obtain a few extra centimeters of horn, and the availability of large trophy males can play a strong role in the economics of a wildlife management program.

By definition, the trophy hunter selects according to morphological criteria. For most bovids, the criterion is simply horn size, for cervids the number of tines, antler symmetry and branching pattern can affect a trophy's score. Given that a proportion of the variability in horn and antler size is genetically determined (Fitzsimmon, Buskirk, and Smith 1995; Hartl et al. 1995; Lukefahr and Jacobson 1998; Moorcroft et al. 1996), trophy hunting may create the somewhat paradoxical situation of selecting against the preferred phenotype. It is therefore surprising that wildlife managers, especially in North America, have paid so little attention to the genetic effects of trophy hunting (Harris, Wall, and Allendorf 2002).

ECOLOGICAL VARIABLES AND ARTIFICIAL SELECTION

The strength of artificial selection caused by trophy hunting will depend upon ecological variables and harvest regulations. Obviously, a high level of harvest of trophy-class males should have a stronger selective effect than a low level of harvest. Harvest regulations based on a simple morphological criterion, without a limit on the number of permits issued, are likely to have a stronger selective effect than management regimes that limit the number of males harvested within each age class or morphological grouping. The timing of the hunt in relation to the reproductive cycle will also affect the selective pressure caused by trophy hunting: a pre-rut hunt will have a stronger effect than a post-rut hunt. The pattern of age-specific horn growth may also play a strong role. For example, species like chamois, mountain goat, and roe deer have a relatively rapid horn or antler growth: mountain goats and chamois achieve over 90% of their horn growth by 3 years of age (Côté, Festa-Bianchet, and Smith 1998). In these species, males become desirable trophies at a relatively young age, and therefore large-horned individuals risk being killed before contributing to future generations. The horns of ibex (*Capra ibex*), on the other hand, grow substantially up to about 10 to 12 years, and ibex may reproduce actively for several years before being selected by trophy hunters (Toïgo, Gaillard, and Michallet 1999). Bighorn sheep are somewhat intermediate; the horns of 6-year-old rams are about 90% of the length they will attain by 9 or 10 years (Jorgenson, Festa-Bianchet, and Wishart 1998). The mating system will also affect the strength of artificial selection for small horns or antlers caused by trophy hunters: where alternative mating tactics account for a substantial proportion of paternities (Hogg and Forbes 1997), selection is likely weaker than where paternities are monopolized by a few highly successful males (Apollonio, Festa-Bianchet, and Mari 1989).

If mating success is affected by both weapon size and male age, an intense level of trophy hunting of young males will have a stronger selective effect than in species where only older males are removed by hunting. For example, although precise information on male reproductive success is not available, studies of both chamois and ibex suggest that in un hunted populations most matings are achieved by males 10 years of age and older (Lovari and Cosentino 1986; Toïgo, Gaillard, and Michallet 1999). An ibex male may not achieve “trophy” status until about 10 to 12 years of age, but the horns of a 5-year-old chamois are not much smaller than those of a 10-year-old. If in a trophy-hunted population of ibex most matings are done by 10-year-olds rather than 12-year-olds, there will still be 10 years of time for natural selection to potentially affect pre-mating male survival. In trophy-hunted popula-

tions of chamois, on the other hand, most matings may be by males aged 4 to 5 years because few males may survive to older ages, possibly allowing some reproduction by males that normally would not survive to mating age.

The potential selective strength of trophy hunting is illustrated by fallow deer (*Dama dama*), where a single male can mate with 25% of the females during one rut (Apollonio, Festa-Bianchet, and Mari 1989). If the traits that favor male reproductive success were the same as those selected by trophy hunters, a single male shot before the rut could lead to a large difference in the genetic makeup of fawns born the following year.

Male reproductive success in most ungulates appears to be determined mainly by an individual's ability to beat other males. Antler or horn size is, presumably, only one component of fighting ability: body size and condition can also play a role, especially if very large weapons suffer a risk of breakage (Alvarez 1994). Both size and shape of antlers and horns could be modified by selection to preserve their effectiveness as intraspecific weapons but make them less attractive as trophies. For example, in most of the Canadian province of Alberta, hunting regulations specify that only bighorn rams whose horns describe at least four-fifths of a curl can be shot.

A ram with a large body mass and whose horns were massive but did not reach the minimum legal size until 6 or 7 years of age would enjoy greater survival than a ram with fast-growing horns that became "legal" at 4 or 5 years of age (Jorgenson, Festa-Bianchet, and Wishart 1998). In areas with good hunter access, few rams survive more than one hunting season after becoming legal, and in areas with moderate access, about 30 to 40% of legal rams are shot each year (Festa-Bianchet 1986). A ram that survives the hunting season will face little competition during the following rut because many potential competitors will have been shot. It is therefore reasonable to predict that any genetic trait that retards the age at which a ram's horn becomes legal will be strongly selected for. There is considerable interindividual variability in the age at which rams reach legal status, from as early as 3 years in exceptional cases, to never (Jorgenson, Festa-Bianchet, and Wishart 1998). Rams that reach legal status later in life may have greater lifetime reproductive success than those whose horns are legal by 4 or 5 years of age. In addition, recent evidence suggests that horn size only plays an important role in male mating success after about 7 years of age (Coltman et al. 2002). Rams with fast-growing horns therefore risk being shot before their large horns give them a reproductive advantage, compounding the potential selection for small horns.

Similarly, imagine a wapiti or red deer male with large antlers but with only a few tines: such an individual would do well in an area where hunting regulations state a minimum number of tines for harvestable males, or could

enjoy greater survival under a trophy hunting regime simply because hunters would “pass him up” in favor of what they may see as a more attractive set of antlers. Trophy hunting favors a “nontrophy” phenotype by increasing its survival relative to the population mean, and by removing potential competitors. The harvesting scheme prevalent in parts of Europe, where “undesirable” horn or antler phenotypes are selectively harvested in addition to trophy-class males, would obviously complicate the situation.

Of course, the preceding scenario does not take into account potential gene flow among populations subject to different hunting regimes, changes in hunting regulation or harvest levels, and the strengths of several competing selective pressures, many of which are likely temporally variable. For example, there could be a net outflow of genes from protected into hunted areas because males who survived the hunting season by staying within protected areas would be in a very good position to compete for estrous females in neighboring populations where most resident males were shot by hunters (Hogg 2000).

In addition to selection for horn or antler morphology, a high level of trophy hunting may select for greater reproductive effort by young males. Over the short term, there may be a demographic effect without evolution of novel mating strategies: if most mature males are removed by hunters, younger males may take over the role of breeders and possibly suffer higher mortality as a result, as suggested by Geist (1971) and Heimer, Watson, and Smith (1984).

Over the long term, selection could favor males with high reproductive effort over their first few years of life, possibly including faster growth, lower fat reserves, and riskier behavior during the rut. A shortened life expectancy would weaken selective pressures for less risky behavior that may increase the chance to survive to breed again. The consequence could be higher nonhunting mortality for young males. Consider the many white-tailed deer, roe deer, chamois, or moose populations that are subject to very high harvest levels: in these populations very few males survive past 2 or 3 years of age. In three management areas in Oregon, over 90% of wapiti males were killed before 4 years of age (Biederbeck, Boulay, and Jackson 2001). High hunting mortality of males could lead to a high selective advantage for those few that survive beyond 4 years (possibly because they have small horns or antlers, or because their behavior decreases their chance of being shot), or strong selection for early reproduction. In either case, sport hunting could lead to evolutionary change.

The Implications for Consumptive Management

Harvest of large mammals through sport hunting can lead to economic and social benefits that can stimulate conservation. It is therefore important that management decisions be based upon the best available informa-

tion. It is reasonable to suspect that any selective harvest may have evolutionary consequences by altering selective pressures and gene frequencies compared to naturally regulated populations. There is clearly a need for more information, particularly about the levels and types of hunting that may lead to evolutionary change. Sexual selection and possibly female choice may favor males with large horns or antlers, and partly compensate for the effects of selective hunting. If the hunting mortality is not very high, it may be insufficient to change the genetic makeup of future generations. Immigration from protected areas may reduce the potential for selection for a “short and fast” reproductive strategy among both sexes. Finally, harvest schemes that simply stipulate a minimum size or minimum number of tines required for legal harvest will likely have stronger selective effects than the more complex harvest strategies prevalent in central Europe.

Three potential problems should be considered. First, some current harvest policies may select for unwanted morphological or life-history attributes that may lead to loss of economic and recreational opportunities. This would be the case for selection for small horns or antlers by high levels of trophy hunting, but also for selection of a reproductive strategy favoring high early investment in reproduction, if it increased nonhunting mortality of young adults. Selective hunting may lead to a loss of genetic variability (Hartl et al. 1995), which may negatively affect a population’s ability to survive environmental changes over the long term.

Poaching of African elephants (*Loxodonta africana*) for the illegal ivory trade may select for tusklessness (Jachmann, Berry, and Imae 1995). Second, artificial “adaptive” changes in hunted populations may compromise their long-term ability to persist. A cessation of hunting may have unpredictable consequences for a population that has undergone adaptations to a high level of hunting mortality: both evolutionary and demographic effects should be considered when hunting is stopped because of changes in land designation. Artificial selection is not necessarily reversible (Law 2001). Third, there are ethical concerns: should hunting shape evolution? Much of the nonhunting public and many hunters dislike the competitive nature of scoring trophies. The competitive aspect of trophy hunting spurs a negative reaction by many people that accept or even support other forms of sport hunting. As public attitudes change, the conservation of ungulates will increasingly require the support of people with little interest in hunting. I suggest that the best outcome for both hunting and conservation would be a decreased emphasis on trophy scores, and more emphasis on the enjoyment of hunting, independent of the particular attributes (sex, age, horn size) of the animals that are harvested.

Conclusions and Recommendations

The ideas I have put forth in this chapter, if correct, justify changes in several sport hunting practices. If these ideas are incorrect, however, changes in wildlife management would not be required and could have a negative effect. It is therefore important to test these ideas, ideally through long-term studies conducted in cooperation with researchers, wildlife management agencies, and sport hunting groups. Wildlife management agencies can do the required experiments by manipulating hunting regulations. For example, an experimental change in the definition of legal ram was approved in Alberta partly to test the effects of different management schemes on bighorn ram survival and harvest. Changes in regulations, however, require the support of the hunting public. Future research should combine the analysis of genotype frequencies, morphology, and life-history attributes in populations subject to different levels of hunting or to different harvest regimes.

An alternative to experimental manipulation of hunting regulations would to better exploit available information. There are vast repositories of data on morphology, sex, and age of harvested animals, in computers and file drawers of wildlife management agencies all over Europe and North America. Additional information on morphological measurements (or trophy scores) is available from private organizations and individuals, including records and actual specimens (stuffed heads) from several decades ago. This information could be used to investigate hypotheses about the selective effects of sport hunting, or to form the basis of future research programs. There are several recent examples of how long-term information gleaned from wildlife management agencies can provide very valuable scientific contributions (Loison, Gaillard, and Jullien 1996; Post et al. 1999; Schneider and Wasel 2000).

The diversity of wildlife management schemes in different areas, including different sex/age restrictions, could also be used to test specific hypotheses. The main difficulty will be teasing apart environmental and genetic effects: a high level of harvest that reduces population density will almost certainly lead to a phenotypic response, but it may or may not also select particular genotypes. The most powerful test of these hypotheses will be a long-term study of the survival and reproduction of a large sample of marked individuals. Long-term studies of marked large mammals are rare, and very few have been done in hunted populations (Festa-Bianchet 1989; Jorgenson, Festa-Bianchet, and Wishart 1993; Langvatn and Loison 1999), partly because researchers are reluctant to invest time and money for marking animals that may be shot within a few months or years. As a result, much of the information on the evolutionary ecology of wild ungulates comes from populations

that are either un hunted or very lightly hunted (Byers 1997; Clutton-Brock, Rose, and Guinness 1997; Festa-Bianchet, Gaillard, and Jorgenson 1998; Gaillard et al. 1998a), and little is known about the evolutionary effects of sport hunting. Because of the high cost of marking and monitoring programs, and because a long-term study in a hunted population would be unable to consider many questions of theoretical interest, there is a need for government agencies to become involved. The long-term monitoring program of polar bears (*Ursus maritimus*) in Canada (Messier, Taylor, and Ramsay 1992; Derocher and Stirling 1998) is an excellent example of a successful study supported by government agencies.

The effects of gene flow in and out of protected areas is an area of research that holds particular promise and particular urgency, for both its practical and its theoretical interest. The amount of gene flow among areas subject to different harvest regimes will likely decrease the selective pressures brought about by selective hunting. On the other hand, selective hunting may itself affect the rate and direction of gene flow (Hogg 2000). There are complex patchworks of protected and exploited ungulate populations that would lend themselves to a very productive study.

The possibility that life-history strategies of large mammals have been shaped by hunting also has potential applications for our understanding of interspecific differences in behavior and reproductive strategies (Benton, Grant, and Clutton-Brock 1995). Consider two mountain ungulates, the alpine ibex and the bighorn sheep. The former has been protected from hunting in most of its range since early in the twentieth century, and is still protected from legal harvests in both Italy and France. Bighorn sheep, on the other hand, have been and are heavily hunted for trophies in most of their range in North America. Ibex males have a very high survival rate until about 11 to 12 years of age (Girard et al. 1999, Toïgo, Gaillard, and Michallet 1997) and a very gradual pattern of age-specific horn development (Toïgo, Gaillard, and Michallet 1999), whereas bighorn rams have low survival at 3 to 8 years of age (Jorgenson et al. 1997, Loison et al. 1999a), rapid horn growth (Jorgenson, Festa-Bianchet, and Wishart 1998), and subadult adoption of risky but successful alternative mating strategies (Hogg and Forbes 1997). These interspecific differences could be due to a wide range of plausible ecological explanations but may also result from selection for greater reproductive effort at a younger age in bighorn sheep, brought about by high hunting mortality over the last century. If this is the case, then one may predict higher natural mortality rates and faster horn growth of ibex in areas where they are hunted, such as in Switzerland (Giacometti et al. 1997), and higher survival and slower horn growth (but not smaller asymptotic horn size) of bighorn rams in protected areas, such as large national parks. Information on genetic

differences, however, would also be required to test this prediction because differences in survival could be due to changes in age ratios and therefore in age-specific rutting behavior (Heimer, Watson, and Smith 1984), and changes in horn growth would be expected simply from differences in population density (Jorgenson, Festa-Bianchet, and Wishart 1998).

A Final Thought: Is Human-Induced Selection a Modern Phenomenon?

The current extinction crisis caused by human activities is unprecedented, but there is evidence that humans have had a strong impact on the species composition of several ecosystems for thousands of years (Kay 1994a, Balmford 1996, Caughley and Gunn 1996), although the exact nature and strength of historic human impacts are unclear and often controversial (Beck 1996, Choquenot and Bowman 1998). Nevertheless, it is reasonable to suspect that changes in density, distribution, and behavior of many species of large mammals have been affected by human hunters for a long time.

Consider the differences in behavior toward humans of brown bears in Europe and North America. European bears are less aggressive, possibly as a result of coevolution with humans, who may have selectively killed aggressive individuals. Similarly, although North American wolves appear unable to survive outside wilderness areas (Mladenoff, Sickley, and Wydeven 1999), in parts of Europe wolves coexist with very high human population densities (Okarma 1993, Meriggi and Lovari 1996). Differences in response to habitat fragmentation and other human activities also appear to vary according to the potential for coevolution of humans and other species, measured by the length of time since recorded human occupancy (Balmford 1996, Martin and Clobert 1996). Hunting by humans has likely affected adult mortality of many large mammal species in much of the world for several centuries, possibly for millennia. If this is the case, then the reverse argument of the one I have presented may have some merit: the “new” selective pressures may be those experienced by ungulates in several European and North American national parks, particularly southern parks without large predators.

We should be concerned about the potential selective effects of sport hunting because they may limit the future ability of populations to adapt to a changing environment, or future opportunities for trophy hunting. There is also an ethical concern that sport hunting may lead to “artificial” selection. If we wish to avoid the evolution of “artificial” phenotypes, however, we must know what is “natural.” Establishing what is “natural” for species whose evolution has been shaped by human predation may be very difficult.

Summary

Game management is mostly concerned with what determines the size and sex/age composition of populations of hunted animals. Consequently, principles of population dynamics are most often applied to wildlife management, including considerations of sex- and age-specific survival and reproductive rates. It is often assumed that sport hunting affects population dynamics but is not a selective force. For many game species, however, avoiding getting shot is a major selective force because most mortality is due to human hunters.

The age-specific mortality caused by sport hunting of large mammals is usually very different from natural mortality. Hunters often kill prime-aged individuals, which normally have a very high survival rate. Regulations often specify the sex and the age class of animals to be killed. Hunters may select prey according to sex, age, reproductive status, or morphology. In much of Europe, morphology-based harvests favor certain phenotypes, particularly with regard to antler or horn size. The term *selective hunting* is somewhat foreign to North American managers, but it is often used in Europe. In North America, harvest is directed to certain age classes through morphology-based definitions of what can be killed, particularly with regard to horn size and antler points. Principles of evolutionary theory suggest that “selective” harvesting may indeed “select,” but not necessarily with the results that managers or society may seek. Intensive hunting may select for precocious maturity and increased reproductive effort, and trophy hunting may select for small horns or antlers. Long-term management plans must take into account the potential selective pressures of alternative harvest schemes, as is recognized by some fisheries scientists. Because sport hunting is as much a social issue as a biological one, changes in wildlife management require changes in attitudes, particularly in the case of trophy hunting. Relegating the competitive attitude to the past will benefit both hunters and biodiversity.

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