Genetic consequences of hunting: what do we know and what should we do?

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Abstract  Possible evolutionary consequences of sport hunting have received relatively little consideration by wildlife managers. We reviewed the literature on genetic implications of sport hunting of terrestrial vertebrates and recommend research directions to address current uncertainties. Four potential effects can be ascribed to sport hunting: 1) it may alter the rate of gene flow among neighboring demes, 2) it may alter the rate of genetic drift through its effect on genetically effective population size, 3) it may decrease fitness by deliberately culling individuals with traits deemed undesirable by hunters or managers, and 4) it may inadvertently decrease fitness by selectively removing individuals with traits desired by hunters. Which, if any, of these effects are serious concerns depends on the nature and intensity of harvest as well as the demographic characteristics and breeding system of the species at issue. Undesirable genetic consequences from hunting have been documented in only a few cases, and we see no urgency. However, studies specifically investigating these issues have been rare, and such consequences require careful analysis and long time periods to detect. Existing information is sufficient to suggest that hunting regimes producing sex- and age-specific mortality patterns similar to those occurring naturally, or which maintain demographic structures conducive to natural breeding patterns, will have fewer long-term evolutionary consequences than those producing highly uncharacteristic mortality patterns.

Key words  alleles, effective population size, evolution, gene flow, genetics, heterozygosity, hunting, selection

Commentary  Wildlife managers have historically placed great emphasis on demographic issues and relatively little on how hunting influences genetic characteristics or the evolution of populations (Rhodes and Smith 1992). However, speaking as hunters as well as biologists, we value hunting as an experience of the wild, which in our view is linked inextricably to the forces of natural selection that have produced our native species. Few hunters would find interest or fulfillment in stalking animals housed in a zoo; similarly, we believe our descendents deserve opportunities to interact with species shaped principally by their native environments, rather than artificially molded in adaptation to human desires. In our opinion, integrity of a wild species’ gene pool deserves respect similar to that accorded to maintenance of its natural habitat.

Unlike in fisheries, however (e.g., Sutherland 1990, Stokes et al. 1993, Law 2000), North American game managers have paid little attention to the
long-term effects hunting may have on the genetic makeup of game species. This is surprising because sport hunting alters population density, sex ratio, and age distribution (Wall 1989, Ginsberg and Milner-Gulland 1994, Solberg et al. 2000), all of which potentially influence the genetics of populations.

We addressed four questions relating to common sport hunting practices and their long-term genetic consequences: 1) Can hunting alter natural patterns of gene flow among demes? 2) Can hunting lower genetic variation, through increasing genetic drift caused by reduction of effective population size? 3) Can deliberate selection against traits viewed as undesirable by hunters or managers reduce fitness? and 4) Can unintentional selection pressures, usually arising from management based on demographic criteria alone, have unintended consequences? We reviewed the existing literature to examine these questions, and provide some interpretations and suggest areas where further research is needed.

Hunting and gene flow

Genetic procedures recently described genetic differentiation within populations that appear morphologically uniform. Localized genetic differentiation has been documented for many hunted species, including pronghorn antelope (Antilocapra americana, Lec et al. 1989), mouflon (Ovis gmelini, Petit et al. 1997), red deer (Cervus elaphus, Strandgaard and Simonsen 1993), red fox (Vulpes vulpes, Frati et al. 1998), ring-necked pheasants (Phasianus colchicus, Warner et al. 1988, Robertson et al. 1995), and bobwhite quail (Colinus virginianus, Nedbal et al. 1997). In white-tailed deer (Odocoileus virginianus), considerable differentiation exists among neighboring subpopulations on a genetic level (Sheffield et al. 1985, Scribner et al. 1997). It appears that local differences in white-tailed deer are maintained by philopatry among females, but subpopulations are prevented from becoming too subdivided by male dispersal (Mathews and Porter 1993, Purdue et al. 2000; see Cronin et al. 1991 for similar findings in mule deer, O. hemionus). If males become rare through hunting, one concern is that the existing level of gene flow may be reduced further, strengthening population differentiation at the expense of genetic variability within localized demes (Ellsworth et al. 1994). Conversely, for species that are naturally philopatric or territorial, local genetic adaptations might be lost if gene flow among demes is increased due to the alteration of social structure caused by hunting. Kurt et al. (1993) examined populations of European roe deer (Capreolus capreolus) living in both forested and open habitats. In forest habitats, male roe deer were territorial, controlled access to a number of females, and variance of reproductive success among males was high. In open habitats, males were more migratory, a larger proportion of adult males succeeded in breeding, and genetic mixing within populations was greater. These differences evidently reflected adaptive responses to the variability of environmental resources, and were maintained locally by low levels of gene flow. However, under high hunting rates, gene flow between the 2 social systems increased, and this differentiation began to break down.

Similarly, among territorial greywing francolin (Francolinus africanaus), Little et al. (1993) found no difference in heterozygosity (H, the percentage of loci that are heterozygous in an average individual) between hunted and unhunted populations, but higher levels of inbreeding in unhunted populations. They concluded that any reduction in H caused by lower population size was compensated by greater gene flow within the hunted population. The net effect on H was neutral (i.e., higher migration rates were balanced by fewer potential migrants), but hunting clearly had contributed to a breakdown in the usual territorial structure.

Frati et al. (2000) interpreted lower genetic variability among unhunted populations than hunted populations of red fox in Europe as reflecting changes in fox social structure following the loss of larger predators. Historically, with the presence of wolves (Canis lupus), leopards (Panthera pardus), and lynx (Lynx lynx, L. pardinus), fox social structure was flexible and outbreeding common. They suggested that hunting, by increasing turnover and decreasing inbreeding, could partially mimic the effects of predation pressure under which foxes had evolved.

Hogg (2000) found that mid-ranking male bighorn sheep (Ovis canadensis) from an unhunted population made temporary migrations during rut to an adjacent hunted population. These rams faced less competition for mates from the relatively few high-ranking males in the hunted population and enhanced their breeding opportunities by moving. Here, gene flow from one deme to another was again increased, but in this case the probable determinant was not hunting per se but rather the abrupt contrast in density of older, larger-horned males between adjacent demes.
The available evidence suggested to us that alterations in naturally occurring patterns of gene flow would seem possible from any type of hunt; some level of social disruption must accompany any removal of individuals. We found this troublesome only when locally adapted gene complexes were compromised by hunting-induced gene flow, where gene flow would otherwise be discouraged by social behaviors. As the red fox example suggested, a hunting-induced increase of gene flow among adjacent demes may help mitigate other man-made reductions of gene flow.

**Hunting and genetic drift**

Genetic drift is the random change in gene frequencies caused by sampling (via sexual reproduction) from a finite population. Genetic drift occurs in all populations, but its effects become pronounced only if effective population size \( N_e \) is small. \( N_e \) is the number of individuals in an ideal population expected to lose genetic variation at the same rate as the census population \( N \) (Wright 1969, Harris and Allendorf 1989). With small \( N_e \), \( H \) is expected to decline, rare alleles are expected to be lost, and alleles may become fixed regardless of their effect on fitness.

Relevant questions were whether \( N_e \) of hunted populations might be small enough for drift to be a legitimate concern, and whether hunting regimes further reduce it. Concern about small \( N_e \) was expressed for introduced herds of bighorn sheep (Fitzsimmons et al. 1997) and upland birds (Little et al. 1993). Ryman et al. (1981) simulated moose (Alces alces) and white-tailed deer populations, calculating \( N_e \) based on various approximations from demographic statistics. They found that \( N_e \) was likely to be much lower than \( N \), even in a population exposed to no selective hunting. \( N_e/N \) ratios were additionally reduced under most hunting scenarios simulated. Although reductions in \( N_e/N \) under hunting were not large, Ryman et al. (1981) did not simulate hunting featuring extreme selection for males. They found \( N_e/N \) ratios as low as 0.2 (i.e., a population of 100 would experience genetic drift at the rate of an ideal population of 20), but pointed out that extreme selectivity for males in the hunt could further reduce this ratio.

Harris and Allendorf (1989) varied hunting regimes for hypothetical grizzly bear (Ursus arctos) populations, finding relationships between the type of hunt and \( N_e \). In some cases, \( N_e/N \) increased from the nonhunted situation, because reproductive success among males became more equitable. However, in hunting scenarios where the number of males became limiting, \( N_e/N \) declined from its unhunted level.

Wall (1989) examined demographics and heterozygosity of white-tailed deer populations in Texas exposed to hunts with differing selectivities. Although he was unable to estimate variation in reproductive success, an important determinant in \( N_e \) (Harris and Allendorf 1989), Wall (1989) compared “maximum \( N_e \)” among populations based on the demographic parameters and assuming no differences in variance of reproductive success. Variable hunting strategies had profound effects on \( N_e/N \). However, because those hunting regimes reducing \( N_e/N \) often were designed to keep \( N \) high, \( N_e \) generally varied less than did \( N_e/N \). For example, populations exposed to buck-only harvest had low \( N_e/N \) (because few bucks dominated breeding), but high \( N_e \) (because census population size remained high, being primarily a female population). In contrast, hunting regimes with a relatively high female harvest (and more equitable sex ratios) had the highest \( N_e/N \) ratios, but lower \( N_e \) (because the total population was lower). His sampling of genetic attributes suggested, however, that genetic drift (as documented by \( H \)) was a substantial concern only in the smallest, most isolated population.

Concerns about low \( N_e \) have been appropriately focused on small or declining populations (Allendorf and Ryman 2002) rather than on the larger populations typically subjected to sport hunting. Managers of sport hunts should be mindful, however, of the potential for undesirable genetic consequences of low \( N_e \) where high harvest rates produce severely skewed sex ratios. Sex ratios of about 1 adult male:10 adult females were documented for elk (Cervus elaphus, Leptich and Zager 1991, Noyes et al. 1996) and mule deer (Scribner et al. 1991), and are probably common in other species where males are selectively hunted. We agree with Scribner et al. (1991) that large population size substantially reduces the concern about genetic drift. Nevertheless, smaller breeding groups of related individuals may occur within larger populations because of strong site fidelity by females (Scribner et al. 1991). Therefore, highly skewed sex ratios may increase the frequency of inbreeding even in the presence of little population-wide genetic drift. Most managers of ungulate populations attempt to prevent adult sex ratios from reaching such extremes in order to maintain normal breeding behavior. We believe that loss of
genetic variability, even if nested within a larger population, is another reason to avoid highly skewed sex ratios.

**Hunting and deliberate selection**

Many European wildlife managers have traditionally attempted to alter antler or horn characteristics of artiodactyls by selectively culling those considered inferior (Webb 1960, Taber 1961, Hartl 1991, Sforzi and Lovari 2000). Culling of yearling white-tailed deer with poor antler development was also suggested in the southeast United States (Harmel 1983, Cook 1984, Newsome 1984, but see Lukefahr and Jacobson 1998). Although such management might be seen as a partial correction to practices where only the largest animals are taken, it is not without risks. By selecting for one particular trait of perceived value to humans, we believe it likely that management simultaneously (if inadvertently) selects against other traits potentially of adaptive significance for the species (Voipio 1950, Klein et al. 1992). In particular, relatively rare alleles that might be important in a long-term evolutionary perspective are vulnerable to loss when such selection for other traits takes place.

Research on red deer in Europe provided compelling evidence that deliberate selection could have unintended consequences. In France, Hartl et al. (1991, 1995) found that alleles at loci *Idb-2*, *Me-1*, and *Acp-1* were associated with body and antler size in red deer. Deliberate culling of yearling bulls with undesirable antler characteristics rapidly increased the frequency of an allele (*Idb-2*125) positively correlated with number of antler points. Importantly, Pemberton et al. (1988) found that juvenile survival among juvenile female red deer in Scotland heterozygous at this same *Idb-2* locus was higher than among homozygous individuals. Thus, by selectively removing males with small antlers and thus reducing the frequency of the alternate allele at *Idb-2*, it appeared that French hunters may have also unwittingly selected for poor juvenile survival (Hartl 1991). In general, when one phenotypic trait is maximized other traits are inevitably (and probably unknowingly) affected because life-history strategies inevitably involve trade-offs among various fitness components related to demographic equilibrium (Pemberton et al. 1991). Thus, human attempts to “improve” hunted species through selective culling seem certain to produce unforeseen consequences. Similarly, releasing penned deer bred specifically for antler growth (Cook 1984) into the wild (to produce large “super bucks”) seems to us careless disregard for this fundamental concept.

**Hunting and unintentional selection**

North American managers have often downplayed possible genetic consequence of selective hunting, focusing instead on maximizing yield either of total animals or of trophy males. However, harvest regimes that are focused on removing large males risk producing inadvertent directional selection against the very characteristics (usually large antlers or horns in artiodactyls) that hunters desire. We distinguished the effects that selective hunting may have on genetic diversity generally (as indicated by *H*) from those leading to loss of specific alleles.

**Selective hunting and **

*H* is often (albeit not universally) thought to be related to fitness in natural populations (Allendorf and Leary 1986, Britten 1996, Colman et al. 1999). In white-tailed deer, studies have reported positive correlations between *H* and twinning (Johns et al. 1977, Chesser and Smith 1987), fetal growth (Cothran et al. 1983), body weight (Smith et al. 1982), body size (Chesser and Smith 1987), and antler size (Scribner et al. 1989). The last-named authors considered it likely that higher *H* resulted in higher metabolic efficiency, and thus decreased maintenance-energy requirements, leading to larger antlers. Fitzsimmons et al. (1995) found slightly greater yearly horn growth among ≥6-year-old bighorn sheep rams that were heterozygous at ≥2 loci than among those heterozygous at a zero or one locus.

However, other studies have found no correlations between *H* and body mass or number of antler points in white-tailed deer (Sheffield et al. 1985) and red deer (Hartl et al. 1991). Chesser and Smith (1987) reported negative as well as positive correlations between *H* and components of reproduction related to fitness. Further, the relationships involving antler or horn growth observed by Scribner et al. (1989) and Fitzsimmons et al. (1995) occurred only for older age-classes. Because the majority of antler and horn growth occurred in younger classes (for which no correlation with *H* was found), the total amount of variation attributable to *H* class was low. Antler and horn growth also are known to respond to environmental factors (and the largest single determinant of size usually is
age class), so it is difficult to distinguish the effects of $H$ on horn or antler size.

Can selection imposed by hunting reduce $H$? Fitzsimmons et al. (1995) voiced concerns that selectively removing the largest rams by hunting would, perhaps unintentionally, reduce genetic variability in such populations. Although not specifically designed to examine such a possibility, the work of Wall (1989) provided some insight. Despite widely varying hunting regimes (and thus standing age structures), he found no differences in $H$, as measured by allozymes from harvested deer, among populations examined. If antler quality were related to $H$, we might expect hunter-harvested samples from those hunts featuring the greatest selectivity for trophies to exhibit higher $H$ than those from less selective hunts.

We found that the evidence for selective removal of relatively more heterozygous individuals within natural populations was weak. Perhaps more importantly, loss of $H$ caused by removal of individuals that tend to be heterozygous at specific loci is a reversible process. That is, even if heterozygotes were selectively removed, heterozygous progeny would be regenerated the next generation by matings between individuals that are homozygous for different alleles (Mitton 1997). Thus, although possible deleterious effects from selective removal of heterozygous individuals bears monitoring, it does not appear to be a serious problem.

**Selective hunting and changes in allele frequency**

A slightly different mechanism may come into play where hunter selectivity is based on phenotypic traits such as horns or antlers. Such hunts may unintentionally select against those very traits by reducing the life span (and thus the reproductive contribution) of individuals carrying specific alleles. Festa-Bianchet (2002) suggested that heavy hunting can alter selective pressures of female artiodactyls from those favoring high survival and low maternal investment per litter to those favoring early reproduction and lower survival. We share with Festa-Bianchet (2002) additional concerns about long-term genetic consequences of trophy hunts on phenotypic characteristics of males.

The empirical literature is ambiguous on whether hunting regimes focused on taking males with large horns or antlers unintentionally alters allele frequencies (as evidenced by phenotypic changes). Dubas and Jezierski (1989) documented declining antler quality and carcass weight by age over a 6-year time period in European red deer, speculating that selective hunting may have played a part. However, population density also increased during their study, confounding interpretation (Clutton-Brock et al. 1982). Ludwig and Hoefs (1995) discounted hunting as a possible factor in their finding that Dall sheep (Ovis dalli) in a hunted population had shorter horns than did those in the adjacent (unhunted) Kluane National Park despite similar age distributions (horn circumferences in the 2 populations did not differ). Solberg and Sæther (1994) reported no decline in antler size over a 23-year period of moose harvest. In contrast, Shea and Vanderhoof (1999) observed a reduction in antler size of 2.5-year-old white-tailed deer 5 years after initiation of a hunting regime intended to increase antler size by prohibiting harvest of small-antlered bucks. They attributed the unexpected reduction to “high-grading” (i.e., selective killing) of bucks born earlier during their year of birth. Their data also showed that early birth was associated with larger antlers, leaving predominantly late-born bucks to survive to 2.5 years. Shea and Vanderhoof (1999) evidently did not examine the genetic basis of these changes, but selective hunting of larger bucks may have changed frequencies of alleles that contributed to antler size.

In most cases hunters prefer to harvest large artiodactyls, and horn or antler size is generally correlated with male fitness. However, it does not follow that hunting removes relatively more fit individuals in all cases. Artiodactyl males begin with small horns or antlers that become progressively larger with age. Hunters selecting for individuals with the largest horns or antlers remove predominantly old individuals, not necessarily those with genomes conducive to producing large secondary sexual characteristics. Changes in allele frequencies caused by selective hunting of large males may be buffered by the genetic contributions of females, which will have most of the same alleles as males but are likely to be subject to differing selective pressures. Finally, other factors may affect vulnerability to hunting independent of hunter selectivity. For example, DuFour et al. (1993) found that mallards in poorer body condition were more vulnerable to hunting than those in better condition.

Given these complexities and ambiguities, we believe the simulation model constructed by Thelen (1991; see also Hundertmark et al. 1993, 1998) currently provides the best indication of how selective hunting might unintentionally alter the genetic constitution of big game populations.
Thelen (1991) assumed that antler characteristics of elk were polygenic traits, inherited in simple Mendelian fashion but with no dominance or epistasis. Antler size increased with age, but antler characteristics were also assumed to be an additive function of multiple loci (i.e. the greater the number of alleles favorable for large antlers, the larger the antlers). Heritability, the proportion of variation in antler size attributable to genotype, varied from 25% to 75%. Breeding success was controlled by both age and antler size. Age-specific survival of bulls was also negatively correlated with antler size (i.e., a survival cost of carrying heavy antlers was assumed). Hunting strategies were modeled to reflect various possible management objectives. Hunting regimes that specified minimum antler sizes always reduced the frequency of large antler alleles in modeled populations. When heritability of antler traits was modeled as 50%, allele frequencies were altered by approximately 10–20% after 50 years. When heritability was assumed to be 75%, the 50-year reduction in favorable allele frequency was on the order of 20–25%; with heritability of 25%, the 50-year reduction was about 10% (Figure 1).

By contrast, other hunting regimes had little effect on the frequency of existing alleles in the population. A nonrestricted harvest strategy, in which the sex and age of individuals harvested was directly proportional to their abundance in the population, had little effect on allele frequency after 50 years. The nonrestricted hunting regime also resulted in relatively high yield overall, but low yield of trophy males. But a split hunting regime, in which spike (mostly yearling) and ≥5 point (trophy) males were legally taken (but 2–4 point males protected) resulted simultaneously in moderate overall harvest, moderate harvest of trophy males, and little change in large-antler alleles (Figure 1).

It is likely not coincidental the mortality pattern produced by the split hunting regime resembled that of an ungulate population experiencing only nonhunting mortality (high mortality in young age classes, low among mature animals, high again as animals senesce). Thelen’s (1991) model suggested the possibility of achieving a sustainable harvest (including of trophy males) while avoiding substantial alterations in allele frequencies, by moderating hunting pressure focused on large males and simultaneously harvesting young males vulnerable to natural mortality. Klein et al. (1992) also recommended a split hunting regime as one that would produce a good compromise between hunter satisfaction and long-term evolutionary concerns.

Thelen’s results were sensitive to heritability of antler size (Figure 1). There is little doubt that antler characteristics are heritable traits (Harmel 1983, Williams et al. 1994, Lukefahr and Jacobson 1998, Wang et al. 1999). However, all studies to date have estimated heritability under captive conditions, thus the “unexplained” portion of antler variability (i.e., that remaining after inheritance is explained) has been low. In the wild, we would expect age-specific antler size to vary considerably with nutritional status as well as with genotype (Brown 1990).

An additional, important factor in such models is the strength of reproductive advantage enjoyed by males with desired traits. Conventional wisdom suggests that males with the largest horns and antlers have the highest reproductive success (Solberg and Sæther 1994). But just how much higher? The rate of loss of alleles affecting horn and antler size on the population caused by hunter selection of large males would be higher if males vulnerable to hunting dominate the breeding, and lower if smaller males (which would presumably survive a selective hunt) also make substantial contributions under natural conditions.

In unhunted red deer, paternity data showed not only that dominant bulls had greater reproductive
success than did subordinates, but also that their relative success was even greater than had been estimated from behavioral data (Pemberton et al. 1992). Younger, smaller, or less dominant bulls did relatively little breeding. In contrast, paternity data on bighorn sheep in two intensively studied populations showed that high-ranking rams, while still more successful than lower ranking rams, fathered fewer lambs than would have been estimated from only observing their success at tending estrous ewes (Hogg and Forbes 1997). Rams using “unconventional” courting tactics associated with lower rank were surprisingly effective in contributing their genes to subsequent generations. Thus, a variety of alleles in bighorns may be transmitted to subsequent generations by smaller, younger rams that would be unaffected by strongly selective hunts.

We suspect that long-term changes in allele frequencies are a common attribute of terrestrial populations subjected to strongly selective hunting. It is difficult to see how it could be otherwise, given that hunting often constitutes the largest source of mortality (Festa-Bianchet, 2002). However, because age and environment exert major influences on size, mating systems are often flexible, gene flow among adjacent populations that vary in mortality patterns may replenish vulnerable alleles, heritabilities of phenotypic traits observable to hunters may be low, and offtake rates usually are moderated in the most strongly selective hunts, we expect such changes to occur gradually and to be undetectable for many generation lengths.

**Research directions**

Research into genetic effects of hunting has been much less common than research into demographic and behavioral effects of hunting. Several important questions remain unanswered: 1) under what conditions is the alteration of gene flow among population subdivisions resulting from hunting of sufficient magnitude to cause problems? 2) does selective hunting preferentially take more heterozygous individuals than would a random hunt, and if so, does this reduce heterozygosity in the population? and 3) how much breeding is conducted by subordinate males, and how does that change under various hunting regimes? Answers to these questions are likely to vary by species, and perhaps also geographically.

Now that genetic techniques allow paternity determination (e.g., Hogg and Forbes 1997, Cronin et al. 1999), researchers are in a much better position to understand male reproductive success, its correlates, and its variance. Understanding patterns of male reproductive success has implications for the survival effects on other age classes of removing dominant males, influences of removing dominant males on breeding activity of females, and of the effects of management on genetically effective population size \((N_e)\), which, in turn, tells us about the magnitude of genetic drift. It is most useful to add paternity studies to populations already under intensive demographic study, but where these conditions exist, the laboratory expenses usually will be justified by the insight gained. Where paternity studies are conducted and phenotypic information also obtained, the opportunity exists to document the heritability of secondary male sexual characteristics of interest to hunters (usually horns or antlers) under wild conditions. The strength of heritability remains a critical, but largely unknown, piece of the puzzle in considering the long-term evolutionary consequences of selective hunting in ungulates (Rèale et al. 1999, Kruuk et al. 2000).

Indirect information on possible directional selection of genomes can also be obtained from existing data sources (e.g., hunter check-stations) by careful examination of long-term data sets comparing hunting intensity to trends in horn/antler size by age. Confounding effects, such as population density and varying environmental conditions, will need to be carefully considered. Further laboratory analyses (e.g., using carcasses at hunter check-stations) correlating the presence of specific alleles, as well as estimates of \(H\), with male characteristics (coupled with sampling of unhunted individuals) would further elucidate whether selective hunting has disruptive effects on \(H\) and allelic diversity.

**Conclusions**

We began by expressing concern about the long-term genetic consequences of hunting, but our review of the literature suggested little empirical evidence of such consequences. We have hypothesized a number of characteristics of hunting and hunted species that may act to mitigate expected negative effects. However, we found no grounds for complacency; studies designed to quantify genetic effects have been rare, and the effects eliciting our greatest level of concern are subtle and difficult to detect without long-term monitoring.

We stress that demographic and genetic changes occur on different time scales. Demographic
effects are often immediate and easily recognized; genetic changes occur over evolutionary time scales of many generations. Thus, although short-lived actions are unlikely to have genetic effects over the long term, any genetic changes will be difficult to detect because of the time scale over which they occur. For example, it would require careful study to detect the effects of a hunting management scheme that decreased mean antler size by 4% per generation (i.e., 1% reduction/yr in a species where the mean age of reproduction was 4 years). However, such a rate of change may have substantial effects over the long term. For example, this rate of change would reduce mean antler size by 30% in 50 years.

We urge managers to consider not only the maintenance of genetic diversity, but also whether the primary selective forces influencing adaptations in hunted populations have become artificial rather than natural. Where concern is justified, it is prudent to manage hunting such that the age-specific survival pattern (and thus age-specific breeding structure) emulates that occurring in the absence of hunting (Klein et al. 1992, Hundertmark et al. 1995). Such hunting regimes will generally produce little alteration in allele frequencies, have low chance of causing extinction of rare alleles, minimize extremely skewed sex ratios (and thus have less effect on $N_e$), and still allow for the hunting opportunities we cherish.

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