

PERSPECTIVE

When does selective hunting select, how can we tell, and what should we do about it?

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ABSTRACT

Potential evolutionary consequences of selective hunting of mammals are controversial because of limited evidence and important socio-economic impacts. Several ecological and management variables facilitate evolutionary responses to selection for horn, tusk or antler size, including strong selective hunting pressure; harvest of males with large horns, tusks or antlers before they can breed; unavailable or ineffective sources of unselected immigrants; and age-dependent relationships between horn, tusk or antler size and male mating success. Plastic responses of male horns, tusks and antlers to environment are probably more common than evolutionary changes. Evidence for evolutionary effects of selective hunting is strong for large mammals where biological characteristics and hunting regulations combine to favour them.

INTRODUCTION

Many ecological processes are now dominated by the actions of our species. Those actions include climate change, habitat destruction and alteration, pollution, overharvest and the spread of exotic species, including pathogens. Human activities also have widespread evolutionary consequences, from life-history changes in heavily harvested fish (Uusi-Heikkilä et al. 2015) to adaptations to human-modified environments (Altermatt & Ebert 2016). Evolutionary effects are increasingly taken into consideration by fisheries scientists, less so by fisheries managers (Kuparinen & Hutchings 2012). Their prevalence and consequences for wildlife management, however, have mostly been ignored (Myserud 2011). Here, I examine when harvests may affect the evolution of horn, tusk or antler size (also described as 'weapon size') in sport-hunted species, focussing on large mammals that are selectively harvested based on the size or shape of their horns, antlers or tusks. Trophy hunting has a very low demographic impact and often generates revenues that could be used for the conservation of biodiversity (Di Minin et al. 2016). Trophy hunting also generates much controversy, limiting its social acceptance as a component of a conservation strategy (Ripple et al. 2016). Possibly because of the

controversy surrounding trophy hunting, many hunting groups react negatively to the suggestion that selective hunting may in some circumstances lead to evolutionary changes in physical traits. It is therefore important to examine what circumstances may favour an evolutionary response to artificial selection through trophy hunting.

EVOLUTION REQUIRES HERITABILITY AND SELECTION

Long-term studies of wild ungulates with deep pedigrees show that heritability accounts for about 30–40% of variability in horn or antler size (Kruuk et al. 2002, Poissant et al. 2008). Therefore, given strong selective pressures, horns, tusks, and antlers can evolve rapidly.

SELECTION DOES NOT NECESSARILY LEAD TO EVOLUTION

Evolutionary changes may not follow selection. For example, red deer *Cervus elaphus* antler mass has a strong genetic component and is under directional selection because stags with large antlers have high reproductive success, but antlers do not increase in size over generations because of the overwhelming effect of the

environment on antler growth (Kruuk et al. 2014). For trophy hunting to lead to evolution of smaller horns, tusks or antlers, it must act on the genetic component of horn, tusk or antler size and must be sufficiently strong to counter sexual selection that usually favours individuals with larger horns, tusks or antlers (Coltman et al. 2002).

MANY FACTORS AFFECT THE PROBABILITY THAT SELECTIVE HARVEST WILL LEAD TO AN EVOLUTIONARY CHANGE

Variables that increase the probability that selective hunting for male mammals with large horns, tusks or antlers will lead to evolutionary changes in the size of the horns, tusks or antlers include aspects of a species' biology but also many variables under the control of wildlife managers (Table 1). The strongest evidence for evolutionary effects of trophy hunting comes from wild sheep *Ovis canadensis*, *Ovis dalli* and *Ovis aries* (Garel et al. 2007, Douhard et al. 2016, Pigeon et al. 2016). Sheep have many characteristics making them particularly prone to showing genetic changes in horn size and shape under intense trophy hunting. Most importantly, regulations that allow hunters to harvest rams with a minimum degree of horn curl ('legal' rams) ensure that those with fast-growing horns can be shot 2–3 years before those large horns lead to increases in their mating success (Coltman et al. 2002). Combined with unlimited harvests of 'legal' rams, the current practice in most of Canada, these regulations provide small-horned rams with excellent opportunities to be successful breeders at 7–9 years of age, because their large-horned competitors are shot. It is well-known in evolutionary biology that selective pressures that occur early in life are most effective in changing gene frequencies because they affect

a larger proportion of a cohort than selective pressures later in life, when many individuals have died (Williams 1957). Directing the harvest to older males, or ensuring that some of those with large horns, tusks or antlers have a chance to breed before they are shot, will weaken the effects of artificial selection.

THE MATING SYSTEM AND MALE MATING SKEW RELATIVE TO HORN, TUSK OR ANTLER SIZE DETERMINE WHETHER SELECTIVE HUNTING MAY CAUSE GENETIC CHANGES

With high male mating skew, removal of one or a few males can dramatically change the distribution of mating success among survivors (Apollonio et al. 1989). If the main determinant of male mating success is not the trait sought by hunters, however, we should expect a weaker selective effect. For example, in mountain goats *Oreamnos americanus* the strongest correlate of male mating success is body mass, not horn size, and the phenotypic correlation between horn size and body mass in mature males is weak (Mainguy et al. 2009). If hunters target mountain goat males with the largest horns they will not necessarily impose a radical change in the distribution of male mating success. Unfortunately, this prediction is difficult to test because we know little about the determinants of male mating success or the degree of mating skew in wild ungulates. Reliable data exist for only a handful of species, including bighorn sheep, feral sheep, red deer, fallow deer *Dama dama*, mountain goats and pronghorns *Antilocapra americana* (Festa-Bianchet 2012). With the exception of bighorn sheep, all researchers studying male mating success monitored unharvested populations, so it is difficult to predict what might happen in other species when age structure and age-specific horn, tusk or antler

Table 1. Ecological and management variables that increase the probability that selective hunting for male mammals with large tusks, horns or antlers will lead to an evolutionary change in horn, tusk or antler size

Ecology

Strong heritability of horn, tusk or antler size

Males become 'trophies' at a young age, before large horns, tusks or antlers increase their mating success

No or little compensatory growth: large-horned young males become large-horned mature males

Horn, tusk or antler size has a strong positive effect on male mating success

Males are gregarious: hunters can select the male with the largest horns, tusks or antlers in a group

Horns or tusks grow substantially over multiple years, with limited environmental effects on yearly growth

Horns, tusks or antlers subject to selective harvest in both sexes

Management

Legislated definition of minimum horn, tusk or antler size for males that can be harvested, based on shape, size, or number of tines

Intense selective pressure: no or very generous quotas, high proportion of trophy males are shot

Intense selective hunting persists over decades, affecting multiple generations

The hunt covers a large area, with spatially consistently high harvest pressure on 'trophy' males, so that genetic rescue is unlikely

Sources of unselected males for genetic rescue are unavailable or ineffective

Would-be genetic rescuers from protected areas are shot during the hunting season

size are changed by sport hunting. When more data become available, I expect there will be surprises. For example, preliminary data on white-tailed deer *Odocoileus virginianus* do not suggest a strong role of antler size on mating success (Sorin 2004), yet males clearly use antlers as weapons in contests for access to oestrous females. Limited data on Alpine ibex *Capra ibex* (Willisch et al. 2012) do not confirm the prediction, based on very high survival of males to age 10, that in this species mating success is heavily skewed towards older males (Toïgo et al. 2007).

In the absence of data on individual mating success, one can glean something about the relative role of horns, tusks or antlers from their age-specific growth patterns and the extent of compensatory growth. In species where horn, tusk or antler size is either known or suspected to be very important for male mating success, horns, tusks or antlers typically grow substantially over many years, for example, in mountain sheep, ibex and red deer (Festa-Bianchet 2012). For bovids in this category, compensatory horn growth is generally weak (Toïgo et al. 1999). In species where horn, tusk or antler size appears to play a lesser role, for example, chamois *Rupicapra rupicapra*, pronghorns, mountain goats and roe deer *Capreolus capreolus*, horns, tusks or antlers reach near-asymptotic size at 2–3 years (Festa-Bianchet 2012) and, for bovids, show substantial compensatory growth (Rughetti & Festa-Bianchet 2010). Therefore, I predict a stronger evolutionary effect of trophy hunting in the former group of species than in the latter. Finally, species in which both sexes grow horns, tusks or antlers that are the target of selective hunting may show faster evolutionary change than species where females are not selectively hunted. That may be the case, for example, for African elephants *Loxodonta africana* (Chiyo et al. 2015).

THE INTENSITY OF ARTIFICIAL SELECTIVE PRESSURE IS CRUCIAL

The key question here is how the relative chances of survival and reproduction vary according to horn, tusk or antler size, especially when selection through trophy hunting is countered by sexual selection favouring males with large horns, tusks or antlers. To estimate the strength of artificial selection, we must know the relative distribution of horn, tusk or antler size before and after the hunting season. Ideally, we also need to know how horn, tusk or antler size affects mating success among survivors. Simple measurements of hunting pressure on males do not allow the estimation of selective pressure. For example, in the Ram Mountain population of bighorn sheep from 1976 to 1994, the yearly harvest rate of 'legal' rams was 40%, but harvest of all adult rams was only 8%. Only males

aged 4 years and older, however, can have horns large enough to fit the legal definition, and rams with the largest horns become 'legal' at a younger age (Hengeveld & Festa-Bianchet 2011). The intense harvest pressure on 'legal' rams meant that, given natural mortality of about 15% (Bonenfant et al. 2009), a ram that was 'legal' at age 4 had a 91% chance of dying before the rut as a 7-year-old, when large horns actually increase mating success (Coltman et al. 2002) i.e. an exceptionally high selective pressure. Comparable data are rarely available for hunted ungulate populations. In the Yukon, Canada, a comparison of Dall's sheep rams classified during aerial surveys and reported as harvested suggested a 27% harvest rate for 'legal' rams (Loehr et al. 2010), again indicating very strong selective pressure. Claims that selective hunting cannot be a strong selective pressure based on harvest rate for all males, or even for the total population, are misleading.

HORN, TUSK OR ANTLER SIZE IS NOT CORRELATED WITH NATURAL MORTALITY

The suggestion that successful males with large horns, tusks or antlers suffer high natural mortality as a consequence of greater mating effort (Geist 1966), although solidly grounded in sexual selection theory, has received little empirical support. When hunting mortality is not considered, horn length has either no effect or a slight positive effect on the survival of adult males, with the possible exception of the very oldest males in some species (Bonenfant et al. 2009, Toïgo et al. 2013).

MANY FACTORS CAN CAUSE DECLINES IN HORN, TUSK OR ANTLER SIZE

Suppose that long-term monitoring revealed a decrease in horn, tusk or antler size in a hunted population, should managers immediately consider an evolutionary effect as the likely explanation? Certainly not. Plastic changes are much more rapid and more likely than evolutionary changes (Merilä & Hendry 2014). Environmental factors that can reduce horn, tusk or antler size include high population density, deteriorating habitat quality and availability, and adverse weather. For example, the recent sharp decline in mass of chamois in the Alps is probably due to climate change, and not due to selective harvest (Rughetti & Festa-Bianchet 2012). Evolution of smaller horns in response to intense trophy hunting has been clearly established for bighorn sheep at Ram Mountain, but even there, much of the observed decline in horn size was a plastic response to a doubling of population density (Pigeon et al. 2016). I am not aware of any evidence of harvest-induced evolutionary change in antler size, even in species such as red deer where mating

success is strongly affected by antler size. The size of red deer antlers, however, is highly dependent upon yearly environmental conditions, which may override the substantial genetic component of antler size (Kruuk et al. 2014). In addition, trophy red deer stags are often harvested at or after their peak breeding age (Rivrud et al. 2013), unlike bighorn sheep where the largest-horned males are shot before they become dominant rams. There may be a fundamental difference in susceptibility to hunter-induced evolution between cervids (and antilocaprids) and bovids (and pachyderms). Antlers and pronghorns are regrown every year, and are strongly affected by yearly environment (Foley et al. 2012). Horns and tusks, however, are permanent structures with only a relatively small amount of additional growth each year, so that year-to-year changes in resource availability may be less important drivers of horn than of antler size, and genetic effects may play a larger role on horn size than on antler size of mature males.

Changes in horn, tusk or antler size due to environment are likely to be more common than those induced by selective hunting, and they are easier to control by manipulating habitat or population density. Long-term declines in horn, tusk or antler size in the absence of changes in population density or habitat quality, and under strong selective hunting, however, can be attributed to hunter selection, especially when accompanied by evidence that males in areas not subject to the same level of selection do not show the same decline in horn, tusk or antler size. Such declines in horn size due to hunter selection are happening, for example, to two species of mountain sheep in Canada (Festa-Bianchet et al. 2014, Douhard et al. 2016).

ENVIRONMENTAL VARIABLES MUST BE ACCOUNTED FOR

Changes in population density and yearly weather fluctuations are regularly accounted for in analyses of hunter-induced selection (Pigeon et al. 2016). Climate change, however, poses a greater challenge. That is because both artificial selection and climate change may impose a directional pressure over time, making it difficult to distinguish their effects when the only data available are time series of horn, tusk or antler measurements, rather than direct measures of selection and evolution. The effects of climate change on horn, tusk or antler size vary depending upon several ecological variables. For example, climate warming in the Alps has been linked to increasing horn size in ibex (Büntgen et al. 2014) but decreasing body mass in chamois (Rughetti & Festa-Bianchet 2012). Yearly information on both weather and climate, including large-scale climate indices, can help sort out possible

environmental and selective effects, but availability of data from large protected areas to use as control would be preferable.

The gold standard for tests of hunter-induced evolution would be two nearby long-term monitoring programs of pedigreed populations, one protected and one subject to selective hunting, with accurate data on horn, tusk or antler size and individual reproductive success. That sort of study, regrettably, is unavailable. In the Ram Mountain study of bighorn sheep, a pedigreed population was monitored that was first subject to selective hunting, then released from that selective pressure through changes in hunting regulations (Pigeon et al. 2016). That is not as powerful as having a control population, but nevertheless the results indicate that the genetic decline in horn size stopped when the selective pressure was relaxed.

HARVEST DATA ARE BIASED BUT NOT USELESS

There are very few intensively monitored ungulate populations. Alternative sources of data include harvest records, especially if they also provide information on individual age and, for bovids, annual increments in horn size. That information is available, for example, for ibex in Switzerland, chamois in several European countries, and mountain sheep in British Columbia, Canada. Harvest data often provide a large sample size available over wide areas and collected for decades. These data, however, have several biases that must be accounted for, starting with regulations that direct the harvest to a specific phenotype. Rules on minimum size, minimum horn curl or number of tines lead to biased sampling by definition. For example, small-horned rams cannot be harvested under a minimum-curl definition. Data on harvested rams detected only half of the decline in horn length at Ram Mountain over 20 years (Pelletier et al. 2012). Trophy record books based on a very high minimum 'score' are nearly useless to monitor horn, tusk or antler size (Festa-Bianchet et al. 2015). Trophy shows that record 'the biggest each year' may not be quite as biased (Rivrud et al. 2013). Data on annual horn increments in bovids can help considerably in overcoming these biases and provide useful information for assessing the selective impacts of trophy hunting. For example, these measurements revealed that early horn growth was strongly correlated with age at harvest in two species of mountain sheep (Hengeveld & Festa-Bianchet 2011, Douhard et al. 2016). Stone's sheep *Ovis dalli stonei* rams harvested at 6–7 years of age had grown twice as much horn during their second and third year of life as those shot at 9–10 years (Douhard et al. 2016), demonstrating a very intense selective pressure against rams with fast-growing horns. Hunter preferences

are another source of bias, and are difficult to quantify (Mysterud et al. 2006). Even without horn-size limits, hunters in Switzerland shot ibex males with fast-growing horns at a younger age than males with slow-growing horns (Büntgen et al. 2014). In Spain, as horn growth of Iberian wild goats *Capra hispanica* decreased after intense selective harvests, hunters took males that were 4 years older on average, probably because the age at which horns were considered a 'trophy' increased over time as growth declined (Pérez et al. 2011).

LARGE PROTECTED AREAS MAY BE A SOURCE OF GENETIC RESCUE

Immigration of unselected males from protected areas may swamp the selective effects of harvest (Tenhumberg et al. 2004). Ungulate males may undertake breeding migrations over long distances, up to 80 km in bighorn sheep (Hogg 2000). Males from protected areas may benefit from moving to hunted areas where many of their competitors may have been shot, providing a source of unselected genes that could swamp the effects of selective hunting. The potential role of genetic rescue merits further study, but clearly it requires a source of unselected males, no barriers to movement and cessation of hunting before unselected males exit protected areas. For bighorn sheep in Alberta, Canada, evidence suggests that many would-be genetic rescuers are shot in late October as they exit National Parks (Pelletier et al. 2014), probably negating some or all of the potential genetic rescue. Habitat fragmentation and barriers to movements would also decrease the effectiveness of genetic rescue.

WHAT TO DO?

Wildlife managers have multiple options to decrease the potential for hunter-induced evolution (Table 1). One is to direct the harvest to post-breeding males. Another is to facilitate genetic rescue by establishing a network of large protected areas and ensuring that genetic rescuers are not shot. Of all the tools available to managers, however, clearly the easiest to implement is a reduction in harvest pressure, as recommended for heavily harvested fish (Uusi-Heikkilä et al. 2015). Evolutionarily sustainable trophy hunting is possible: low selective hunting pressure on Stone's sheep did not result in smaller horns (Douhard et al. 2016). Currently, the main obstacle to progress on this issue appears to be attitude: wildlife managers and hunters recognise the importance of population dynamics and habitat quality, but some appear to be reluctant to entertain the possibility that selective hunting may select.

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