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Running header: Hunting and evolution

Hunting and evolution: theory, evidence, and unknowns

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Intense selective harvest of large mammals who carry the largest weapons may lead to an evolutionary shrinkage of those weapons. Currently, evidence suggesting evolutionary effects of harvest is limited to a few species of bovidae and only one study has obtained data indicating a genetic effect. To have an evolutionary impact, harvest must be intense, persistent over time, similar over a large area without an effective source of unselected immigrants, and remove large individuals before they have a chance to breed. Many current harvest schemes do not fulfill all of these requirements, and they are unlikely to cause evolution. Before changes in weapon size over time are attributed to evolution, potential environmental sources of change, mainly density and climate, must be considered. We suggest that the role of weapon size in determining reproductive success, especially in interaction with male age, will determine whether or not intensive selective harvests may have evolutionary consequences. Age at harvest is a very important variable to consider. Changes in age structure over time may reveal underlying changes in harvest pressure or selectivity. A lack of data hampers our ability to assess the potential evolutionary effects of selective hunting. We provide a list of research hypotheses required to advance our ability to assess the evolutionary sustainability of current management practices.

Key words: antlers, evolution, horns, large herbivores, long-term monitoring, selective harvest, selective hunting, ungulates, wildlife management

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Hunting is an important component of many conservation programs and can provide economic and social incentives to encourage support for wildlife conservation (Di Minin et al. 2016, Wanger et al. 2017). Recreational hunting also provides important revenue for rural communities (Olaussen & Mysterud 2012). For many populations of large mammals, hunting is the most important source of adult mortality. For some ungulate (Langvatn & Loison 1999, Pac & White 2007, Kvalnes et al. 2016) and carnivore (Whitman et al. 2004, Bischof et al. 2008, Cooley et al. 2009) populations, more than 50% of adult male mortality is through hunting. In these heavily harvested populations, avoiding hunting mortality is a major determinant of individual fitness (Zedrosser et al. 2013). If hunting mortality is not random with respect to traits that have an heritable component, selective hunting could lead to evolution. That expectation is justified by basic evolutionary theory: offspring resemble their parents in traits that are at least partly controlled by genes, traits vary among individuals, and some individuals with specific traits have higher fitness. If these conditions are met, evolution is expected, irrespective of whether selection is natural or artificial (Endler 1986). Yet, this issue is controversial.

The possibility that intense selective hunting may lead to evolutionary changes in the size of horns, tusks or antlers (henceforth referred to as 'weapons') is disputed by some hunting groups, wildlife managers and scientists (Boyce & Krausman 2018). Wildlife management must rely on the best available science, even if that requires changing some long-established practices or challenges preconceptions. Here, we argue that many current hunting management systems likely have no detectable evolutionary impacts on weapon size or shape. Results suggesting evolution of smaller horn size of male bighorn sheep (*Ovis canadensis*) due to selective hunting (Pigeon et al. 2016), and model simulations underlying the possible effects of a covariance between trophy size and fitness (Knell & Martinez-Ruiz 2017) have been misrepresented in popular media, making hunting appear to have a much stronger evolutionary effect than what is supported by data. Another reason for the controversial nature of this subject is the difficulty of distinguishing evolution from phenotypic plasticity. That is a key issue that we address in this review, by considering the assumptions of the hypothesis that intense selective hunting leads to evolution and by critically examining the evidence provided by attempts to test that hypothesis.

Hunting practices are very diverse. The most selective types are trophy hunting and cases where selection is imposed by regulations. For example, in many jurisdictions in North America, harvest male deer whose antlers have fewer than a specified number of tines is illegal. When hunting is for meat or recreation, however, it is less selective (Mysterud 2011) and regulations sometimes include quotas for specific sex-age classes (Büntgen et al. 2018). The main characteristics of large mammals that affect vulnerability to hunting are behavior (Leclerc et al. 2017) and morphology (Festa-Bianchet 2017). Recent, elevated interest in behaviors that affect hunting mortality has included circadian activity, movement rates, habitat selection and timing of migration (Ciuti et al. 2012, Lone et al. 2015, Rivrud et al. 2016). If those behaviors are heritable, they could potentially evolve. In fishes, evidence suggests that behaviors have evolved that decrease capture by anglers (Andersen et al. 2018). So far, however, no study has directly addressed the links between behavioral differences, heritability and evolutionary changes possibly induced by hunting (Leclerc et al. 2017). Therefore, we focus our review on harvests based on morphological traits.

Intense harvesting could have evolutionary effects on life-history strategies simply by lowering population density (Engen et al. 2014) or by changing age-specific mortality rates (Proaktor et al. 2007). While there is abundant evidence of harvest-induced life-history evolution in fishes (Kuparinen & Festa-Bianchet 2017), evidence in mammals is very limited (Gamelon et al. 2011, Zedrosser et al. 2011, Kvalnes et al. 2016). We suggest three non-exclusive reasons for this taxonomic difference. One, hunting pressure may be insufficient to lead to measurable evolution. Two, many of the predicted life-history changes, such as earlier primiparity, faster juvenile growth rate, increased maternal care, larger litter size and shorter interlitter intervals are the same as those expected through plasticity, simply because by lowering population density harvest may increase resource abundance. Three, unlike most mammals, most fishes have indeterminate growth and an exponential relationship between female body size and egg production. In the absence of fishing mortality, fish may allocate resources to growth rather than reproduction until they reach a substantial size (Hutchings 2009). Although fecundity increases with female size also in terrestrial mammals, that increase is not as strong as in many fishes (Kuparinen & Festa-Bianchet 2017). Therefore, in mammals selective pressure to delay primiparity is weaker, even in the absence of harvests, as the potential gain in fertility with increased age and body growth would be much less than in fish. Even though hunting can have substantial effects on life expectancy (Bischof et al. 2018), its scope to select for changes in mammal life-history traits may be limited. Therefore, we will not consider the selective effects of lowering population density through harvest or the possible effects of harvest on life-history.

THE POTENTIAL FOR SELECTIVE HUNTING TO CAUSE MICROEVOLUTION

Many ecological and management variables can affect the potential for evolutionary change in large mammals subject to selective hunting (Festa-Bianchet 2017). The most important is the strength of selection against males with large weapons. That strength would ideally be measured through the selection differential and selection gradient associated with weapon size over an episode of selection (Arnold & Wade 1984, Kingsolver et al. 2012). Those estimates require measurements of harvested and non-harvested individuals, which are generally not available. Alternative estimates of the strength of selection include the relationship between weapon size and probability of harvest, or the relative harvest rate of males with large and small weapons. Again, however, these estimates are difficult to obtain if all only data on harvested animals are available.

Festa-Bianchet (2017) suggested that selective hunting is most likely to lead to evolution of smaller weapons when weapon size has an important genetic component, harvest probability is strongly related to weapon size, weapon size does not exhibit compensatory growth, males with large weapons are harvested before they reproduce, harvest of young males with large weapons is intense and persistent over both time and space, and unselected breeders do not immigrate from protected areas. Finally, hunter selection is likely more effective on gregarious than on solitary animals, because a hunter can easily compare weapon sizes of multiple males in a group (Mysterud 2011). Nearly all of these variables can be affected by regulations, providing opportunities to limit or to eliminate harvest-induced evolutionary change.

Selection would be stronger if it affected both sexes but in most species only males are hunted selectively, reducing the strength of selection by half (Kardos et al. 2018). For populations with highly polygynous mating systems, removal of a few very dominant males could have major effects on the distribution of reproductive success. For example, in fallow deer (*Dama dama*), the most successful male can account for over half the copulations (Apollonio et al. 1989a), and removal of only 1-2 dominant males can drastically alter the distribution of reproductive success (Apollonio et al. 1989b). Similarly, in black bears (*Ursus americanus*) paternities are monopolize by a few large males (Kovach & Powell 2003).

WHEN ARE SELECTIVE HARVESTS LIKELY TO LEAD TO EVOLUTION?

To have an evolutionary impact, selective hunting must meet several conditions. Most importantly, the trait selected by hunters must be heritable. Horns and antlers have the typical heritability of physical traits in mammals: 20-40% of their variability, after considering the effects of age, is heritable (Table 1). The number of species with information on weapon heritability in the wild, however, is very small.

Even if weapon size is heritable, selective hunting of males with large weapons will not lead to evolution of smaller weapons unless the artificial selective pressure is stronger than sexual selection favoring large weapons. Artificial selection is strongest when it occurs before males with large weapons have a chance to breed, as in mountain sheep (*Ovis* spp.; (Festa-Bianchet et al. 2014). The selective impact of hunting is weak if unselected males immigrate from protected areas and bred successfully, as suggested by a simulation of size-selective harvest of kangaroos (*Macropus* spp.) (Tenhumberg et al. 2004). Finally, the artificial selective pressure must be consistent over a large area and over multiple generations (Festa-Bianchet 2017). Here, we will focus on what we know about the strength and persistence of artificial selection through hunting.

Data on paternity adequate to estimate the relative role of weapon size on variability in male reproductive success exist for only a few species of large mammals (Festa-Bianchet 2012). Those data suggest that weapon size plays a weak role in reproductive success for animals whose weapons grow rapidly to near an asymptote during the first few years of life. Males in these species often fight by stabbing, as opposed to species where males grow large weapons over multiple years and fight by clashing or pushing. In the former group, contests depend more on strength and agility than on weapon size, while in the second group weapon size may play a direct role in winning interactions. For example, weapon size has a weaker correlation with reproductive success in roe deer (*Capreolus capreolus*) (Vanpé et al. 2010), mountain goats (*Oreamnos americanus*) (Mainguy et al. 2009), chamois (*Rupicapra rupicapra*) (Corlatti et al. 2015) and white-tailed deer (*Odocoileus virginianus*) (DeYoung et al. 2009) than in bighorn sheep (Martin et al. 2016) or red deer (*Cervus elaphus*) (Kruuk et al. 2002). Hunter-induced evolution of small weapons is more likely in the latter group because removal of males with the largest weapons will affect the redistribution of mating success among survivors. For example, if a hunter shot the largest-horned mountain goat among 10 competing males, on average 10% of the available paternities will be redistributed among survivors, because mating success is mostly independent of horn size in mountain goat males (Mainguy et al. 2009). If the dominant individual within a group of 10 competing bighorn rams is shot, up to 35% of paternities will be redistributed among survivors (Hogg & Forbes 1997). The possible implications for artificial selection on the distribution of male mating success in relation to weapon size are a fruitful area for future investigation.

GENETIC ARCHITECTURE OF HORNS AND ANTLERS

Evolutionary change is expected to be slow and selection inefficient on polygenic traits, especially when complicated by genetic covariations (Morrissey et al. 2012b). Detection of evolutionary change in nature is notoriously complex (Pujol et al. 2018). For example, the horns of feral sheep have a simple genetic architecture: presence or near-absence of horns is controlled by a single locus, which also accounts for all known genetic variability in horn length for rams with normal horns (Johnston et al. 2013). We do not know of any examples of simple genetic architecture for horns or antlers of wild ungulates. Domestic sheep, including Soay sheep, reveal a strong genomic signature of artificial selection against horns (Kijas et al. 2012) and the genetic architecture of their horns may not be comparable to that of wild ungulates. For bighorn sheep, in contrast, horn size appears to be polygenic and, so far, no loci have been clearly linked to horn size (Miller et al. 2018). Therefore, based on their apparently complex genetic architecture, one does not expect rapid or drastic effects of artificial selection on horn size of wild sheep unless selective pressures are very strong.

WHAT DOES THE RAM MOUNTAIN RESEARCH SHOW?

To date, the only genetic evidence for a microevolutionary change in weapon size induced by selective hunting is from a study of bighorn sheep in Alberta, Canada (Coltman et al. 2003, Pigeon et al. 2016). Until 1996, Bighorn sheep on Ram Mountain experienced quota-free hunting of rams with horns describing at least 4/5 of a curl, regulations typical for most of Alberta, with a harvest rate of about 40% for 'legal' rams (Festa-Bianchet et al. 2014). The definition of 'legal' ram changed to 'full-curl' in 1996 and the hunt was closed in 2011. Coltman et al. (2003) used the Animal Model (Kruuk 2004) to calculate the breeding values of horn length in rams. A breeding value is an estimate of the total additive effect of genes on a phenotypic trait. Individuals with positive breeding values for a given trait are expected to have offspring whose trait is genetically larger than the population mean. Coltman et al. (2003) reported a decrease in breeding value for horn size for cohorts born between 1967 and 2002. They did not explicitly attribute a proportion of the decrease in horn length to genetic change, although a genetic decrease of about 2.25 cm can be estimated from their Fig. 3 (Pelletier & Coltman 2018). Attention to the total phenotypic change shown in Fig. 2 of Coltman et al. (2003) contributed to the misconception that much of the overall decrease in horn length of about 20 cm was attributed to microevolution (Coulson et al. 2018).

Subsequent criticisms of applications of the Animal Model to wild populations outlined the importance of better accounting for environmental effects and errors in the estimates of breeding values, in addition to emphasizing the possible role of genetic drift (Postma 2006, Hadfield et al. 2009). These criticisms were incorporated by Pigeon et al. (2016), who considered phenotypic and genetic changes in horn length for cohorts born until and after 1996, when selective hunting essentially stopped. A decrease of about 2.6 cm was attributed to evolutionary change, or 17% of the overall phenotypic decrease in horn length over 23 years of hunting. For a young adult ram, that small effect would decrease the probability of being 'legal' from 38% to 24% (Festa-Bianchet et al. 2014). With a 40% harvest rate of legal rams, that would lower the risk of harvest by more than a third and would have substantial fitness consequences. The decrease in breeding value stopped but was not reversed during the subsequent 16 years through 2011 with little or no hunting. The 2.6 cm change occurred over just 3.3 generations. Consequently, decreases of similar magnitude reported for harvested rams under quota-free selective harvest over 4.1 (Hengeveld & Festa-Bianchet 2011) or 5.3 (Festa-Bianchet et al. 2014, Douhard et al. 2016b) generations are quantitatively consistent with evolutionary changes in horn size.

DO OTHER STUDIES OF HUNTED UNGULATES SUGGEST AN EVOLUTIONARY EFFECT?

Decreases in horn size consistent with hunter-induced microevolution have been reported for five species of mountain ungulates (Garel et al. 2007, Hengeveld & Festa-Bianchet 2011, Pérez et al. 2011, Festa-Bianchet et al. 2014) but those studies relied on time series of harvested animals, could not estimate the relative contribution of genetic and plastic changes and did not monitor control, unhunted areas. Douhard et al. (2016) found that horn size of harvested Stone's sheep (*Ovis dalli stonei*) decreased in an area with heavy hunting pressure but showed no decrease in an area where hunting pressure was lower over the same period of time.

Few studies of other ungulates have attempted to test for a potential evolutionary change in weapon size or for another phenotypic change consistent with hunting-induced evolution. Therefore, the evidence for or against harvest-induced microevolutionary change is limited. Rivrud et al. (2013) found no long-term decreases in red deer antler size in Hungary. Red deer management in Hungary, and in central Europe in general, does not strongly select against large-antlered males and includes culling of males with small antlers, which could compensate for a possible evolutionary effect of trophy hunting (Mysterud & Bischof 2010). Decreases in both horn length and mass have been reported for hunted populations of chamois (Rughetti & Festa-Bianchet 2012, Mason et al. 2014, Corlatti et al. 2017) but those decreases appear more likely due to climate change than to selective hunting. Horn size appears to play a limited role in chamois male mating success (Corlatti et al. 2015). An analysis of 3 species of African antelope within the same hunting area provided inconsistent results, with horn size increasing over time in one species and decreasing in another (Crosmary et al. 2013). Intense poaching pressure may have selected for smaller tusks in African elephants (*Loxodonta africana*) (Chiyo et al. 2015), but age was not directly included in the analysis and the case for evolutionary change is weakened by the lack of clear evidence that poachers spare elephants with smaller tusks.

Lockwood et al. (2007) reported that very intense artificial selection favoring males with large antlers had strong effects on antler phenotype of captive white-tailed deer over about 4 generations. Their experiment led to an increase of about 90% in trophy score, while the proportion of yearling males with 8 or more antler points increased from 3 to 48%. It is unclear, however, how this artificial selective regime may compare with hunter selection because most regulations protect small males, not large ones. For the same species, a simulation study (Webb et al. 2012) suggested that selective hunting of males with small antlers would have a limited effect, because it could only affect the phenotypic distribution of males that survived to mate and not of those that actually mated. In white-tailed deer, antler size does not appear to plays an overwhelming role in male mating success (DeYoung et al. 2009, Foley et al. 2018). Therefore, hunter-induced evolution is expected to be weak for this species, because even if hunters exerted a strong selection against large-antlered bucks, hunting mortality would not lead to a strong redistribution of male mating success.

HOW TO MEASURE EVOLUTION IN WEAPON SIZE IN THE WILD

To conclude that a change in weapon size is a result of selective hunting, one has to demonstrate that it is genetic and therefore heritable, not simply a plastic response to environmental changes, and that it is caused by the mortality pattern imposed by hunting. For example, Pigeon et al. (2016) showed that intense selective hunting of bighorn rams led to the change in the breeding value of horn length predicted by the secondary theorem of selection

(Morrissey et al. 2012a), which states that evolutionary change is determined by the genetic correlation between a trait and fitness. Pigeon et al. (2016) reported an additive genetic covariance between horn length and fitness of bighorn rams measured as relative longevity, and found that the breeding values of horn length decreased as predicted by the relationship of horn length and relative longevity. Rams with longer horns died young because they were shot. Ideally, one should also show that genes that control weapon size have changed in frequency (Table 2). So far, no studies have linked changes in weapon size to changes in gene frequency.

Studies of possible evolutionary effects of hunting based on time series without genetic data must include in analyses several possible non-genetic sources of variation in weapon size, such as weather (Douhard et al. 2017), age, and population density (Jorgenson et al. 1998). It is also important to account for local conditions or for differences in the geographical origin of samples, as many local variables can affect weapon development. Climate change may induce a directional change that could be erroneously assigned to artificial selection. Recent studies of both ibex (*Capra ibex*) (Büntgen et al. 2014) and chamois (Rughetti & Festa-Bianchet 2012, Mason et al. 2014, Corlatti et al. 2017) showed effects of climate change on horn size or body mass. With warming temperatures, chamois appear to be shrinking. Without a consideration of changes in climate, smaller size could be attributed to selective hunting in this species, whose biology makes an evolutionary effect of hunting unlikely (Rughetti & Festa-Bianchet 2010). On the contrary, ibex horns appear to grow faster with warmer climate, similar to the positive effect of warm springs reported for bighorn sheep horns (Douhard et al. 2017). In bighorn sheep, climate change may partially compensate a possible hunting-induced decrease in horn size (Festa-Bianchet et al. 2014).

Many jurisdictions have accumulated decades of measurements of weapons of thousands of harvested animals. Those time series are valuable to test the possible effects of selective harvest on microevolution of weapon size and shape, especially if data were collected while hunting regulations or harvest pressure changed over time or space, providing a quasi-experimental system (Pac & White 2007). The analysis of such data, however, must take into account that harvested animals are not a random sample of the population. These biases include hunter preferences and hunting regulations. For example, Pelletier et al. (2012) showed that only half the decrease in horn length of bighorn sheep at Ram Mountain could be detected by an analysis of harvested rams, as it is illegal to harvest small-horned rams.

Age at harvest is often available for some bovids, where age can be estimated reliably by counting horn annuli. Age can also be estimated from cementum annuli in teeth, which is a more laborious and expensive technique, so precise data on age are less readily available in species that do not form horn annuli. With intense harvests and no evolutionary response in weapon growth, average age may decrease over time (Schindler et al. 2017), leading to the appearance of a decrease in weapon size if age at harvest is ignored. Record books of the very largest trophies are a tempting source of data as they extend back over a century (Monteith et al. 2013). When entries in these books are based on a minimum 'score', however, they report a truncated distribution and are less likely to detect decreases (Festa-Bianchet et al. 2015). Trophy shows, such as those typical of central Europe, may be more useful if they report the entire harvest or the 'largest' animals shot in any one year, so they would reflect temporal changes in the upper tail of the distribution of weapon size (Rivrud et al. 2013).

WHAT DO WE KNOW ABOUT HUNTER SELECTIVITY?

Selective hunting can be forced by regulations or can emerge through social preferences (Mysterud 2011). Regulations that establish a minimum weapon size or a minimum number of tines for males that can be harvested are commonly used in North America, while in Europe regulations can be complex, establishing quotas by age class or according to various classes of weapon size (Büntgen et al. 2017). Minimum-size limits are widely used for North American wild sheep. In this case, hunter selection is mandatory, as small-horned males cannot be shot. Harvest of wild cervids in North America is often restricted by a minimum number of tines (Wallingford et al. 2017). Because of variability in the number of tines in young males, however, many have suggested that this strategy is counterproductive. Regulations that only allow the harvest of young deer with well-developed antlers may favor small-antlered males. For example, Thelen (1991) used simulations to suggest that elk (*Cervus canadensis*) hunting regulations that impose a minimum number of tines may select for fewer tines, assuming some heritability of tine number. Under these regulations, young males with multi-branched antlers would be at greater risk of harvest before they could mate. Strickland et al. (2001) found that restricting harvest to white-tailed deer with a minimum of 4 tines led to a decrease in antler size of males aged 2 or 3 years, especially in areas where environmental conditions favored the development of larger antlers and many males had 4 tines at young ages. In these situations, hunter selectivity is defined by regulations. The question is whether or not the intensity of selective harvest is sufficient to have evolutionary consequences. A first step to assessing evolutionary potential would be to estimate the probability of harvest for animals with varying antler size. That information is not available: we were unable to locate any studies that examined the harvest rate for deer with different types of antlers.

For bovids that form a distinct horn growth annulus every year, one way to assess hunter selectivity is to compare early horn growth with age at harvest. If hunters select males with rapidly-growing horns, males with slow-growing horns should live longer, and therefore early horn growth should decrease with age at harvest. That pattern has been confirmed for all species and subspecies of wild sheep in Canada: bighorn (Hengeveld and Festa-Bianchet 2011), Stone's (Douhard et al. 2016) and Dall (Loehr et al. 2006). These effects can be substantial: for Stone's sheep rams in British Columbia, each additional 10 cm of horn growth during the second and third year of life reduced age at harvest by 0.6 to 0.8 years depending on hunting pressure. Under high hunting pressure, rams shot at 10 years of age and older had grown less than a third as much horn at 2 and 3 years of age than those shot at 7 years or younger (Douhard et al. 2016). For bighorn rams in south-central British Columbia, the negative relationship between early horn growth and age at harvest was affected by regulations: when hunters could only take full-curl rams, growth during the second and third year of life decreased by 32% from rams shot at 4 years (47 cm) to rams shot at 9 years (32 cm). When hunters could take any ram, the corresponding decrease in early growth was only about 8% (Hengeveld and Festa-Bianchet 2011). A similar analysis for female chamois, however, found no evidence of selection against individuals with rapidly-growing horns (Rughetti & Festa-Bianchet 2011). In another study of chamois, Corlatti et al. (2017) found that early horn growth had strong effects on age at harvest for both sexes where hunters faced few restrictions or age preferences. Effects were weak for males in an area in Austria where hunters mostly harvested old males, and nonexistent for females in an area in Italy with restrictions on harvesting lactating females. Therefore, both hunting regulations and hunter preferences can play a role in selective harvests. Loehr et al. (2006) attributed the decrease in early horn growth with age at harvest of Dall sheep rams to high natural mortality of males with rapidly-growing horns, induced by greater reproductive effort. Individual-based studies, however, found no or little support for the hypothesis (Geist 1966) that rapid horn growth increases natural mortality in wild sheep and goats (Bonenfant et al. 2009, Toïgo et al. 2013).

Where hunter selectivity is regulated, what is the harvest rate for 'legal' males? This is rarely known, but in some cases selective pressures can be very strong. At Ram Mountain, the harvest rate of 'legal' rams was about 40% (Coltman et al. 2003). The resulting negative selective pressure on rams with rapid early horn growth was comparable to the artificial selective pressures faced by domestic animals. For example, a ram legal to harvest at age 4 had about an 8% chance of surviving to rut as a 7-year-old, combining harvest and age-specific natural survival (Loison et al. 1999). A ram that did not become legal until 8 years of age or older, and faced natural mortality only, had about a 60% chance of surviving to rut at age 7. Loehr et al. (2006) estimated a 27% harvest rate of 'legal' Dall's rams in the Yukon. With that harvest rate, assuming the same age-specific mortality rates as bighorn sheep, a ram legal at age 5 (4-year-olds are unlikely to reach the full-curl definition) would have a 27% chance to survive to rut at age 7, compared to a 69% chance for a ram that was illegal to harvest. Again, these are not trivial differences, and suggest strong selection.

A recent study of ibex in Switzerland found that although hunters preferred to take males with long horns, selection was very weak and did not result in a temporal change in horn size (Büntgen et al. 2018). Ibex in Switzerland are hunted with age-specific quotas, and hunters are penalized if they harvest a male outside the assigned narrow age class. Those regulations substantially limit the potential for selective hunting, with the exception of males in the oldest age class (11 years and older), which have likely had a chance to reproduce. Male ibex shot at 5-

7 years of age, for example, had horns that were only 5-17 mm (1-3%) longer than those grown by the same age by males harvested at an older age (Büntgen et al. 2018). That compares with a 70% difference in early horn growth according to age at harvest for Stone's sheep rams in Canada (Douhard et al. 2016b).

When it is not dictated by regulations, hunter selectivity appears mostly affected by perceived opportunities to obtain a large trophy. For roe deer, Ramanzin and Sturaro (2014) found a 10% decrease in antler size and an increase in the proportion of yearlings shot over the course of the hunting season, suggesting that hunters were less selective as residual hunting opportunities decreased. That effect, however, was only evident where average antler size was small. Where roe deer had larger antlers, fewer yearlings were shot and there was no temporal trend in antler size over the hunting season, presumably because more males with large antlers were available. Another study of roe deer also suggested that the largest males were shot early in the season (Mysterud et al. 2006) and found that, when date and habitat were considered, foreign hunters shot larger-antlered deer. Local hunters avoided taking large trophies, as substantial revenue was obtained by charging foreigners a fee that increases with antler size. The practice of charging fees proportional to trophy 'score' is prevalent in Europe but not in North America, creating an important socio-economic difference between the two continents. In Spain, trophy stalking of the largest red deer males took place before other, less selective types of hunting, again suggesting that selectivity decreases over the hunting season (Martinez et al. 2005).

Age is an important factor affecting weapon size of many species and the studies we cite had measures of age that ranged from nonexistent to very accurate (Supplementary Data S1). Generally, age estimates were more reliable for bovids that form annual horn growth rings and for cervids for which a measurement of tooth cementum annuli was available. A few studies had accurate age estimates because they monitored animals from birth (Supplementary Data S1).

Many other factors likely affect hunter selectivity but few have been measured. These include distance from roads, perceived competition with other hunters, previous experience and many cultural aspects that vary according to species hunted and local traditions (Milner et al. 2006, Mysterud 2011). While we know rather little about hunter selectivity, in some populations male harvest rates are very high (Table 3). Males aged 4 years and older often constitute less than 10% of the harvest of adult males, suggesting a very short lifespan for males that survive to 1 year of age (Langvatn & Loison 1999, Biederbeck et al. 2001, Mysterud et al. 2001, Mysterud et al. 2005). High harvest rates have two consequences: male fitness is likely mostly determined by the ability to survive 1 or 2 hunting seasons and any heritable trait that favored survival during the hunting season would be selected strongly.

DISCUSSION

We suggest that the possible evolutionary effects of selective hunting are worthy of research and attention by managers. Empirical evidence of artificial evolution is currently restricted to mountain ungulates, with 1 study providing genetic evidence of a 2.6 cm reduction in horn length over 3 generations (Pigeon et al. 2016) and 5 analyses of harvested males providing evidence consistent with evolutionary changes caused by intensive, selective hunting (Garel et al. 2007, Hengeveld & Festa-Bianchet 2011, Pérez et al. 2011, Festa-Bianchet et al. 2014, Douhard et al. 2016b). In contrast, no clear evidence exists of evolutionary changes in antler size of cervids, despite very intense harvest in many populations. Our ability to assess the potential for evolutionary impacts of hunting, however, is limited by the lack of long-term monitoring programs of harvested populations and of data on the strength of selection.

Important knowledge gaps exist about the age-specific relationship between weapon size and mating success in large mammals and about how this relationship may change as the age structure (or weapon-size structure) of a population is altered by harvests. Evolution is dependent on phenotype-specific reproductive success, yet very little is known about how the phenotype-specific reproductive success of males changes under different harvest schemes. Most data on male mating success in ungulates come from unhunted populations but most populations are hunted, and often have substantially altered male age structures. Relationships between weapon size and age-specific male reproductive success differ among species. Therefore, results from, for example, mountain sheep, cannot be applied to species with different mating systems and different relationships among male weapon size, age, and reproductive success. We propose a testable hypothesis: evolutionary changes caused by selective hunting are proportional to the strength of the relationship between weapon size and male reproductive success. We call for long-term studies of marked individuals in hunted populations of ungulates. Advances in genomics (Huisman et al. 2016) may allow examination of changes in genetic composition to look for evidence of selection (Kardos et al. 2015) without a need to assemble pedigrees. Genomics could also enable a better understanding of how genetic architecture constrains evolutionary changes under harvest pressure. Most ungulate populations are hunted but nearly all long-term, individual-based studies are on unhunted populations (Festa-Bianchet et al. 2017). We do not know how much their results are applicable to hunted populations.

Another useful way to approach this issue is through controlled experiments or quasi-experiments. For wild ungulates, experiments can be approximated by cooperating with game management agencies to examine the consequences of different harvest regimes. Researchers could take advantage of opportunities when changes in regulations are due to changing management aims rather than for research per see, forming quasi-experimental approaches. These analyses must accommodate possible temporal changes in age structure, environmental quality, population density and other characteristics that can affect weapon size, in addition to possible biases through hunter selectivity. Preferably, they should also monitor target genes that are linked to the traits of interest, though in some cases numerous genes are involved in controlling trait size (Miller et al. 2018). Comparisons of time series under different management regimes and hunting rates would benefit from the inclusion of a 'control' population in a protected area with no hunting. The latter, however, must be sufficiently distant from hunted populations to avoid possible selective effects if males regularly travel to nearby hunted areas. For example in late October in Alberta, many bighorn rams are likely shot as they come out of National Parks (Pelletier et al. 2014). The genetic consequences of the selective harvest of 'park' rams for populations that mostly live inside National Park are unknown.

The possibility that immigration from protected areas may provide a genetic rescue for populations subject to intense selective hunting is also worthy of additional investigation. A measurement of gene flow is required to test the hypothesis that protected areas provide unselected immigrants to hunted areas. That test could involve monitoring of marked individuals and analyses of genetic samples from hairs or feces. In addition to providing an estimate of the possibility of genetic rescue, that research would be of substantial interest for the management of protected areas, for at least 2 reasons. One, it may quantify what proportion of adult males from supposedly protected populations are at risk of harvest in nearby hunted areas (Loveridge et al. 2007). Two, gene flow may be mostly from protected to hunted areas. That would occur if males exiting protected areas were to enjoy high reproductive success by rutting where many of their potential competitors had been shot (Hogg 2000). Surviving males moving from hunted to protected areas, however, may encounter greater competition. If that were true, 1-way gene flow could eventually depauperate genetic diversity in protected areas.

Where hunting has been demonstrated to cause the evolution of decreased weapon size, we suggest that managers should consider that effect when setting hunting regulations. We suspect most managers and hunters are interested in wildlife management that is both ecologically and evolutionarily sustainable. Hunting-induced evolution cannot be remedied quickly, because selective pressures favoring large weapons are likely to be weaker than the artificial selective pressure that may have caused them to shrink (Walsh et al. 2006, Pigeon et al. 2016). Possible solutions include a reduction in harvest intensity (Kuparinen & Festa-Bianchet 2017), shifting the harvest to males in age classes that likely have already reproduced, and favoring genetic rescue from protected areas. The evolutionary effects of selective hunting should be considered also because of their possible impact on population dynamics. That possibility rests largely on the assumption of a genetic correlation between fitness and male trophy size. While theory shows that such a correlation could have important consequences for population dynamics (Knell & Martinez-Ruiz 2017), evidence supporting it in large mammals is limited so far. That is partly because this subject has received little attention, making it another area ripe for additional investigation (Table 4). Positive genetic correlation between paternal horn size and fitness-related traits in both sexes have been reported in bighorn sheep (Coltman et al. 2005), while paternal effects on offspring fitness, sometimes varying according to offspring sex, have been shown in bighorn sheep, mountain goats and red deer (Foerster et al. 2007, Mainguy et al. 2009, Douhard et al. 2016a).

The potential role of hunting in conservation, with some conditions, has been endorsed by the IUCN (2012). Sustainability is a fundamental principle underlying any harvest. Clearly, if intense selective hunting had consequences for fitness and population dynamics beyond just some evolutionary shrinking of weapons, it would be a more serious conservation issue (Knell & Martinez-Ruiz 2017). Our review highlights the current limitations of the empirical evidence and suggest new research towards determining whether harvesting practices are evolutionary sustainable (Ashley et al. 2003) and not just ecologically sustainable.

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Table 1 Heritability estimates for horns and antlers of wild ungulates.

Species	Trait	Heritability	Reference
Bighorn sheep	horn length	0.397 (0.203-0.534)[1]	Pigeon et al. 2016
	horn base	0.250 (0.119-0.413)[1]	
Feral sheep	horn length	0.301 ± 0.039 SE	Johnston et al. 2013
	horn base	0.414 ± 0.041 SE	
Red deer	antler mass	0.33 ± 0.12 SE	Kruuk et al. 2002
White-tailed deer	antler mass 1 yr	0.09 ± 0.14 SE[2]	Lukefahr and Jacobson 1988
	antler mass 2 yr	0.26 ± 0.19 SE[2]	
	antler mass 3 yr+	0.43 ± 0.16 SE	
White-tailed deer	antler length	0.45 (0.22-0.71)[1]	Michel et al. 2016
	antler mass	0.33 (0.09-0.59)[1]	
	antler base	0.42 (0.11-0.69)[1]	

1. Bayesian credible interval
2. Not statistically significant

Table 2 Decreasing standards of evidence to support the contention that selective hunting affects the evolution of weapon size in ungulates.

1. Experimental manipulation with identified genes that affect horn/antler size, and evidence of changes in both gene frequency and trait size after manipulation (no studies so far)
2. Experimental manipulation over time with multiple, replicated populations, including an unhunted control, and quantitative genetics methods to monitor changes in Breeding Value for weapon size (no studies so far)
3. Quasi-experimental manipulation of selective pressure over time of a single populations and quantitative genetics methods to monitor changes in Breeding Value for weapon size (Ram Mountain bighorn sheep)
4. Long-term monitoring of populations with different levels of selective hunting (Stone sheep in Northern BC; bighorn sheep comparing Interior vs Rocky Mountain of BC)
5. Long-term monitoring correlating changes in horn/antler size with selective harvest pressure, accounting for environmental variability (Evidence consistent with evolution: Alberta bighorn sheep, Spanish ibex, Aoudad in Spain, mouflons in France. Evidence not consistent with evolutionary change: red deer in Hungary, Alpine ibex in Switzerland)

Table 3. Examples of high annual harvest rates of adult male ungulates.

Species	Country	Harvest	Reference
White-tailed deer	USA	36-69% of males aged 2+ years	Norton et al. 2011
White-tailed deer	USA	63% of males aged 2+ years[a]	Wallingford et al. 2017
Mule deer	USA	60% of males aged 2+ years[b]	Pac and White 2007
Red deer	Norway	42% of males aged 2+ years	Langvatn and Loison 1999
Moose	Norway	33% of males aged 1+ years	Kvalnes et al. 2016
Moose	Norway	43% of males aged 2+ years	Solberg et al. 2000
Wild boar	France	70% of males aged 2+ years	Toïgo et al. 2008

[a] Cases with minimum antler point or horn size restrictions

[b] late-season prohibition on males with more than 2 points.

Table 4. Examples of data requirements and research initiatives needed to elucidate when, why and how selective hunting may lead to undesirable evolutionary consequences.

Hunter selectivity: what is the difference in trait distribution (weapon size, age, interaction between age and weapon size) between the overall population and harvested individuals?

Harvest pressure: what proportion of males in different age classes are harvested? When regulations specify which individuals can be harvested, for example based on horn size or number of tines, what is the harvest rate of those individuals?

Genetic changes: how does the distribution of genotypes vary with hunting pressure, and is there evidence of hunting-induced selection at the genomic level?

Fitness effects of large horns/antlers: how strong is it, and does it vary with male age? Does the relationship between weapon size and fitness change as selective harvest alters the distribution of weapon sizes?

Mating system: what are the effects on mating system and on the distribution of male mating success of removing a certain proportion of males with the largest weapons?

Rescue effect: What proportion of the harvest is made up of males born in protected areas? What is the range of a possible genetic rescue, and how does it degrade with distance from protected areas? Is gene flow unidirectional from protected to hunted areas, and does that decrease genetic variability in protected areas?

Population dynamics consequences: are there genetic correlations between weapon size and fitness-related traits, in both sexes? Do these affect population growth? Are there possible nongenetic paternal effects related to weapon size or male age?

Supplementary Data S1. Information on age available from the studies cited in the paper. Age is indicated as Actual when the paper provides information on estimated age in years, otherwise the age classes considered are listed (Juv = young of the year; Yrlg = yearling; 2Yr = 2-year-old; Ad = adult). The aging method reported in the paper is listed. When the method is listed as 'unclear', it is possible that it had been explained in an earlier publication, but we found no mention of how age was estimated. 'Birth' refers to studies where animals were of known age because they were first marked in their first 2 years of age, usually as juveniles. 'Teeth' refers to tooth eruption or wear, 'Cementum' to cementum annuli in teeth, annuli-H to horn growth rings. 'Size' refers to studies where animals were assigned to age classes based on body or weapon size. We do not list repeated studies of the same population.

Species	Age	Method	Reference
Ovis aries	Actual	Birth	Johnston et al. 2013
Ovis canadensis	Actual	Birth	Pigeon et al. 2016
	Actual	Annuli-H	Festa-Bianchet et al. 2014
	Actual	Birth	Hogg and Forbes 1997
	Actual	Annuli-H	Hengeveld & Festa-Bianchet 2011
	Actual	Annuli-H	Geist 1966
Ovis dalli	Actual	Annuli-H	Douhard et al. 2016b
	Actual	Annuli-H	Loher et al. 2006
Ovis gmelini	Actual	Annuli-H	Garel et al. 2007
Capra hispanica	Actual	Annuli-H	Pérez et al. 2011
Capra ibex	Actual	Annuli-H	Büntgen et al. 2018
	Actual	Annuli-H	Toïgo et al. 2013
Ammotragus lervia	Actual	Annuli-H	Pérez et al. 2011
Oreamnos americanus	Actual	Birth, annuli-H	Mainguy et al. 2009
Rupicapra rupicapra	Actual	Annuli-H	Corlatti et al. 2015
	Actual	Annuli-H	Rughetti & Festa-Bianchet 2012
	Actual	Annuli-H	Mason et al. 2014
	Actual	Annuli-H	Corlatti et al. 2017
Aepyceros melampus	Actual	Teeth	Crosmary et al. 2013
Tragelaphus strepsiceros	Actual	Teeth	Crosmary et al. 2013
Hippotragus niger	Actual	Teeth	Crosmary et al. 2013

Alces alces	Actual	Unclear	Kvalnes et al. 2016
	Actual	Cementum	Solberg et al. 2000
	Actual	Cementum	Mysterud et al. 2005
Dama dama	Ad	Size	Apollonio et al. 1989a
Capreolus capreolus	Actual	Birth	Vanpé et al. 2010
	Yrlg, 2Yr, Ad	Teeth	Ramanzin & Sturaro 2014
	Actual	Teeth	Mysterud 2006
Odocoileus virginianus	Yrlg, 2Yr, Ad	Teeth	De Young et al. 2009
	Actual	Birth[a]	Lockwood et al. 2007
	Yrlg, Ad	Birth, teeth	Wallingford et al. 2017
	Yrlg, 2Yr, 3Yr,Ad	Birth[a]	Strickland et al. 2001
	Yrlg, 2Yr, Ad	Birth[a]	Lukefahr & Jacobson 1988
	Yrlg, Ad	Unclear	Norton et al. 2012
Odocoileus hemionus	Juv, Yrlg, Ad	Cementum	Pac & White 2007
Cervus elaphus	Actual	Birth	Kruuk et al. 2002
	Adult	Size	Rivrud et al. 2013
	Actual	Cementum	Martinez et al. 2005
	Juv, Ad	Unclear	Milner et al. 2006
	Juv, Yrlg, Ad	Birth	Langvatn & Loison 1999
Cervus canadensis	Yrlg, 2Yr, 3Yr,Ad	Cementum	Biederbeck et al. 2001
Loxodonta africana	Approx[b]	Size, teeth	Chyo et al. 2015
Sus scrofa	Juv, Yrlg, Ad	Birth	Gamelon et al 2011
	Juv, Yrlg, Ad	Teeth	Toïgo et al. 2008
Ursus arctos	Actual	Birth, Cementum	Zedrosser et al 2011
Various	Ad	Size	Monteith et al. 2013

Notes

[a] Captive animals

[b] Shoulder height was used as a proxy of age