



## Commentary

# Inefficiency of Evolutionarily Relevant Selection in Ungulate Trophy Hunting

JAMES R. HEFFELFINGER,<sup>1</sup> *Arizona Game and Fish Department, 5000 W. Carefree Highway, Phoenix, AZ 85086, USA*

**ABSTRACT** Differentially harvesting individual animals with specific traits has led some to argue that such selection can cause evolutionary change that may be detrimental to the species, especially if those traits are related positively to individual fitness. Most hunters are not selective in the type of animal they take, satisfied instead to harvest any legal animal. In a few exceptions, however, regulations may limit hunters to harvest animals of a minimum size or age regardless of their personal choice. Using information from a broad range of aquatic and terrestrial systems exposed to a myriad of potential and operational selective pressures, several authors have made expansive generalizations about selective harvest and its applicability to ungulates. Harvest-based selection can potentially be intensive enough to be relevant in an evolutionary sense, but phenotypic changes consistent with hunter selection are otherwise confounded with multiple environmental influences. Factors such as age, genetic contribution of females, nutrition, maternal effects, epigenetics, patterns of mating success, gene linkage, gene flow, refugia, date of birth, and other factors affecting selection interact with harvest to impede unidirectional evolution of a trait. The intensity of selection determines potential for evolutionary change in a meaningful temporal framework. Indeed, only under severe intensity, and strict selection on a trait, could human harvest prompt evolutionary changes in that trait. Broad generalizations across populations or ecological systems can yield erroneous extrapolations and inappropriate assumptions. Removal of males expressing a variety of horn or antler sizes, including some very large males, does not inevitably represent directional artificial selection unless the selective pressures are intensive enough to cause a unidirectional shift in allele frequencies that may act on some relevant life-history trait or process. Here I review the topic of harvest-based selection in male ungulates and discuss the inefficiency of trophy hunting in changing genetic expression of phenotype. © 2017 The Wildlife Society.

**KEY WORDS** evolutionary consequences, *Ovis canadensis*, phenotype, Ram Mountain, selection, trophy hunting.

North American wildlife conservation is built upon the foundation of habitat protection and scientifically regulated harvest, which has benefited many species of native wildlife, both hunted and non-hunted (Heffelfinger et al. 2013, Mahoney and Jackson 2013). What has become known as the North American Model of Wildlife Conservation has garnered worldwide recognition that regulated hunting can be a valuable tool for delivering conservation and promoting sustainable use of wildlife. At symposia in Europe and Africa, the importance of hunting to wildlife conservation has been reaffirmed repeatedly (Geist 2006, Mahoney 2009, Patterson 2009, Duda et al. 2010). Hunters have contributed billions of dollars, which supports conservation of wildlife in general, not just those that are hunted (Southwick and Allen 2010). The hunting community is the central pillar of the North American conservation paradigm, and is thus responsible for supporting a wide variety of conservation activities, which are highly valued by the broad public. Because of the role of

hunting in the broader scope of conservation, any negative implications related to the sustainability of harvest need to be investigated and explored as research priorities.

Most hunters are not selective in the type of animal they take, satisfied instead to simply harvest a legal animal (Responsive Management 2013). Trophy hunting in a general sense is a frequently misunderstood, and ill-defined, subset of hunting whereby hunters may choose an animal with large horns or antlers over others that are also legal to harvest. For a few species, in a subset of their range, harvest regulations may limit hunters to harvest animals of a minimum size or age regardless of personal choice. Differential harvest of individuals with specific traits has led some to argue that such selection can cause evolutionary change that may be detrimental to the species, especially if those traits are related to individual fitness (Coltman et al. 2003, Bonenfant et al. 2009, Darimont et al. 2009, Kuperinen and Festa-Bianchet 2016).

Care must be taken to not attribute phenotypic change to genetic selection based on simple correlation or assumed cause and effect. A classic paper by Gould and Lewontin (1979) cautioned against unsupported explanations for traits said to be under selection and challenged scientists to not

Received: 11 April 2017; Accepted: 10 August 2017

<sup>1</sup>E-mail: [jheffelfinger@azgfd.gov](mailto:jheffelfinger@azgfd.gov)

create stories that were plausible but lacked scientific support. Today the fields of domestic animal science and evolutionary biology are host to a great depth and breadth of literature on genetic selection (Montaldo 2001). The effectiveness of selection based on phenotype is a well-developed field of study with an extensive history of partitioning phenotypic variance ( $V_p$ ) into genetic variance ( $V_g$ ) and environmental variance ( $V_e$ ; stated simply as:  $V_p = V_g + V_e$ ; Falconer 1989). Studying populations of wild mammals presents challenges in rigorous experimental design, but biologists should strive to disentangle genetic from non-genetic effects.

Harvest-based selection can be intensive enough to be relevant in an evolutionary sense (Pigeon et al. 2016), but there is uncertainty whether the rate of change can be as high as sometimes reported (Coulson et al. 2017). Many of the oft-cited papers on this subject speculate that hunter selection of ungulates with larger horns or antlers is intensive enough to cause detrimental evolutionary change throughout mountain sheep range, or even all hunted mammals (Harris et al. 2002, Festa-Bianchet 2003, Stenseth and Dunlop 2009, Hedrick 2011, Festa-Bianchet et al. 2014). Authors of other published works compared different taxa, sometimes in different areas (Skogland 1989, Garel et al. 2007, Hengeveld and Festa-Bianchet 2011), or make management recommendations to alleviate detrimental evolutionary effects of trophy hunting on ungulates with no evidence it is actually occurring (Festa-Bianchet 2003, Myrsetrud and Bischof 2010, Pelletier et al. 2014, Kuparinen and Festa-Bianchet 2016).

Trait changes consistent with evolutionarily relevant hunter selection are often accompanied by confounding environmental influences (Coltman et al. 2003, Coltman 2008, Pérez et al. 2011, Pigeon et al. 2016). Clear evidence of negative evolutionary consequences of selective trophy harvest in ungulates is rare (Myrsetrud 2011, Kuparinen and Festa-Bianchet 2016). Other research has begun to emerge contradicting the assertion that trophy ungulate hunting is causing meaningful genetic and phenotypic changes in horn and antler size (Loehr et al. 2010, Rugghetti and Festa-Bianchet 2010, Monteith et al. 2013, Pelletier et al. 2014, Traill et al. 2014). Horn and antler growth are influenced by nutrition (French et al. 1956, Jorgenson et al. 1998, Lukefahr and Jacobson 1998, Festa-Bianchet et al. 2004), which can override selective effects of harvest (Kruuk et al. 2002, Schmidt et al. 2007). Here I review all relevant literature on selective harvest in male ungulates based on horn or antler size and highlight the importance of considering intensity of selection (Myrsetrud 2011, Kuparinen and Festa-Bianchet 2016) and nutritional effects on horn and antler growth before assuming selective harvest is responsible for observed trends.

## RELEVANT UNGULATE SELECTION LITERATURE

Out of concern for the effects of hunter selection, has grown a body of literature discussing the potential evolutionary impacts of selective harvest on ungulate species based on horn and antler sizes. The most recent interest in this topic

began when Coltman et al. (2003) analyzed bighorn sheep (*Ovis canadensis*) data from Ram Mountain, Alberta, Canada, and attributed a significant decline in horn size and body mass to genetic consequences of selective harvest of trophy males. This small (38 km<sup>2</sup>), isolated, bottlenecked population was regulated by a 4/5-curl harvest restriction with an unlimited number of hunters through 1996. This harvest system, atypical throughout the geographic range of mountain sheep, resulted in males with fast-growing horns being selectively removed at a higher rate. Because this population was isolated and fluctuated between 26 and 152 adults (8–61 M), the small effective population size likely allowed individuals (e.g., a productive small-horned male) to have a disproportionate influence on the analysis. Coltman et al. (2003) was widely reported in the popular press and gained broad notoriety in the media, and as such, reporters and researchers, generalized these effects to implicate trophy hunting as a ubiquitous force for degrading the genetic capacity for the growth of large horns and antlers.

Coltman et al. (2003) was subsequently criticized for analysis methods and inadequate consideration of nutritional and environmental influences that may have had much greater influence on the reduction in horn size (Heimer 2004, Postma 2006, Hadfield et al. 2010, Traill et al. 2014). Indeed, Coltman (2008) later acknowledged that the selective effect on the genetic contribution to horn size reduction could have been overestimated because they could not fully account for environmental effects due to changes in population density and nutrition. Additionally, the estimated breeding values in Coltman et al. (2003) were likely overestimated, exaggerating the amount of change due to genetics (Festa-Bianchet et al. 2014, Pigeon et al. 2016).

In further efforts to disentangle the genetic from environmental influences, Douhard et al. (2017) analyzed environmental variables and population density trends at Ram Mountain (1972–2013) and reported that population density was the major contributor to the variation in horn length (27%), explaining 3 times as much variance as the evolutionary effects of trophy hunter selection (9%). Subsequently, Coulson et al. (2017) showed the rate of phenotypic change attributed to trophy hunting by Coltman et al. (2003) and Pigeon et al. (2016) was 1–2 orders of magnitude faster than theoretically possible under standard assumptions of quantitative genetics. Our improved understanding of the minor role hunter selection made to changes reported by Coltman et al. (2003) is rarely reported in literature reviews on effects of selective harvest at Ram Mountain and elsewhere.

Pigeon et al. (2016) revisited the Ram Mountain data and addressed earlier criticisms related to analysis methods, genetic drift, and incorporating environmental factors. This analysis also benefitted from the inclusion of years after selective pressures were relaxed in the population. Although environmental factors were reported to be more important, Pigeon et al. (2016) confirmed earlier results of hunter selection contributing to a measurable decline in horn length, which subsequently increased 13% after intensive selection was relaxed (1997–present).

Using information from a broad range of aquatic and terrestrial systems exposed to a myriad of different types of potential and operational selective pressures, several authors have made expansive generalizations about the applicability to ungulates. Darimont et al. (2009) conducted a meta-analysis of 40 systems including 29 species in which humans participated as predators and reported extensive effects on morphology and reproductive biology of prey, including changes in body and horn size traits in 282 of 297 cases. However, of the 29 species analyzed, only 2 were ungulates and only 1 involved horns or antlers (Ram Mountain; Coltman et al. 2003). The second ungulate data source was a comparison of body size, fecundity, and mortality between Norwegian reindeer (*Rangifer tarandus tarandus*) and Canadian caribou (*R. t. caribou*, *R. t. groenlandicus*), speculating that selective harvest was the reason for smaller body size in Norwegian reindeer (Skogland 1989). A comparison of body size and demographics between different subspecies on different continents is not a valid test of the effects of trophy selectivity on ungulate horn and antler size, yet Darimont et al. (2009) is often cited as a useful contribution to this discussion. In a more expansive analysis focusing on exploitation rates, Darimont et al. (2015:859) include 399 species worldwide but express concerns for evolutionary consequences of “human preference for large ornaments” merely by citing Darimont et al. (2009).

Garel et al. (2007) is a commonly cited source for observed phenotypic horn size and shape changes due to selective trophy harvest in mouflon sheep (*Ovis* spp.). This study population consisted of a taxonomically and morphologically mixed group of mouflon translocated from  $\geq 3$  very different areas (Garel et al. 2005): Cadarache (a fenced nuclear research facility), Cambord (enclosed forest park), and Czechoslovakia. Mouflons from the latter 2 areas also contained an admixture of domestic sheep (*Ovis* sp.; Garel et al. 2005). The Cadarache mouflons are phenotypically similar to the canonical form from Corsica (wide flaring horns, *O. aries musimom*) and differ morphologically from the other hybrid stocks. An analysis of horn measurements during 2 periods (1977–1984 and 1996–2002) revealed a reduction in size and shift in horn morphology they attributed to the selective harvest of the canonical horn morph. Selective removal of one taxonomically different phenotype causing a shift in average overall horn morphology is a poor surrogate analysis for trophy selection influencing evolution in a single taxon. Concomitant with this shift to a greater proportion of smaller, hybrid mouflon was a dramatic degradation of habitat that also caused a reduction in height at shoulder, and lamb and adult body mass (Garel et al. 2007).

Far better would be to test potential evolutionary effects of selective harvest on a single taxon in the same or similar vegetation associations and environmental conditions. Hengeveld and Festa-Bianchet (2011) compared 2 different subspecies of bighorn sheep (*O. canadensis canadensis*, *O. c. californiana*) in different areas of British Columbia and concluded that differential selective pressures from trophy hunting contributed to a decline in age-specific horn

size where one subspecies was harvested under 3/4-curl regulations. There are many known and unknown environmental factors that differ between these taxa and areas that could confound such comparisons, seriously limiting inferences about the evolutionary effects of selective harvest in a single taxon.

In a similar comparison, Douhard et al. (2016) used harvested Stone sheep (*O. dalli stonei*) measurements from nearly 4 decades to compare trends in age-specific horn size and availability of legal males between 2 adjacent areas with differing hunter densities. The intensity of selection was not known in this case, but they documented smaller horns and fewer males in the area with higher hunter density and speculated that at least some of the difference was attributed to the undesirable effects of hunter selection (Douhard et al. 2016). The controversy continues, as does scientific inquiry, but much of the speculative discourse on potential negative evolutionary consequences of harvest-based selection has lacked detailed discussion of what is actually needed to cause changes on an evolutionary scale.

## FOUNDATIONS OF SELECTION-BASED EVOLUTIONARY CHANGE

Humans have the potential to alter the gene pool anytime they influence what animals are available to do the breeding for the next generation. This includes human activities such as selectively harvesting trophy males, culling undesirable animals, establishing harvest restrictions based on horn or antler size, and translocations. For a trait to be subjected to evolutionary change, it must be variable, heritable, and intensively selected in a sustained way free from significant interference and counterbalancing selection (Falconer 1989). Some or all of these requirements are frequently assumed or extrapolated from other taxa or populations when discussing potential effects of selective harvest on ungulates.

We know secondary sexual characteristics are variable in male bovids and cervids. Estimates vary regarding the degree to which horns and antlers are heritable in different species (Williams et al. 1994, Lukefahr and Jacobson 1998, Kruuk et al. 2002, Michel et al. 2016a), but in general we know size and shape of horns and antlers are heritable enough for intensive selection to act on them (Lockwood et al. 2007). Selection in some cases may be intensive enough to cause genotypic and phenotypic changes to the population, or so light and sporadic that it is not measurable or meaningful from an evolutionary perspective. The degree to which a trait is heritable is critical to the issue of the effectiveness of selection on a phenotypic trait such as horn or antler size. The question is not whether hunters can be agents of selection, it is the intensity of overall unidirectional selection that is the fulcrum upon which this whole issue balances.

In captivity, managers have been able to make dramatic changes to cervid antler size in herds maintained within small enclosures where managers had complete control of selection (Lockwood et al. 2007). Stedman (1998) referred to this concept as the Corral to County Continuum. In other words, what you can accomplish in a controlled corral (captivity) you may not be able to apply to an entire county to produce the

same treatment. This concept applies equally to intentional management actions, such as culling or predator control, as it does to unintentional impacts such as selective harvest. In free-ranging wild populations there are many obstacles that impede, counterbalance, or dilute the intensity of harvest-based selection from becoming evolutionarily relevant.

## OBSTACLES TO EVOLUTIONARY CHANGE THROUGH TROPHY SELECTION

Many factors interfere with hunters exerting evolutionarily relevant selection and each one must be considered on a population-by-population basis. A broad generalization across many populations, or many ecological systems (Darimont et al. 2009, 2015), creates erroneous extrapolations and inappropriate assumptions in other poorly studied systems. In small, captive populations, managers have control over most variables and can effectively practice intensive selection. Regardless of demonstrated selection-induced phenotypic changes in captivity, there are many obstacles to applying this level of intensive selective pressures in wild, free-ranging populations (Webb et al. 2012, Demarais et al. 2016). These obstacles work to dilute, counterbalance, and interfere with the selective pressures generated by hunter selectivity. Understanding harvest-based selection warrants full consideration of the inefficiency of selection.

### Low Proportion of Trophy Hunters

Horn- and antler-based harvest restrictions make up a minority of regulatory harvest scenarios throughout the range of hunted ungulates. Assertions that legal restrictions are imposing widespread selective forces throughout many ungulate populations are unfounded. Liberal definitions of what constitutes a legal animal is the norm and the hunter is free to choose which animal they harvest. That is not to say there is no intensive selection occurring because of regulatory restrictions, only that it is uncommon and limited to localized parts of a species' range, and then mostly in North American mountain sheep.

The general inferences derived from the results at Ram Mountain (Coltman et al. 2003, Darimont et al. 2009, Douhard et al. 2016, Kuparinen and Festa-Bianchet 2016, Pigeon et al. 2016) have created a misconception that trophy hunters are ubiquitous, selecting genetically superior specimens in most populations and imposing a detrimental footprint on the evolutionary trajectory of horned and antlered ungulates. Human dimensions surveys do not support these broad extrapolations. Data collected by social scientists consistently show that for a vast majority of hunters, harvesting a trophy animal is not important. In a survey of active hunters, only 1–3% said that the lack of trophy game took away from their enjoyment of hunting (Duda et al. 2010:65). Trophy hunting is the most important reason for hunting for only 1% of hunters throughout the United States (Responsive Management 2013). North American hunters consistently prioritize their desires in descending order as getting a chance to go hunting, seeing legal animals, harvesting any animal, and then harvesting a

trophy (Duda et al. 2010). Repeated surveys asking hunters their primary motivations for hunting shows that obtaining meat is increasingly important, as is spending time with friends and family and being closer to nature (Duda et al. 2010:71, Responsive Management 2013).

For the relatively few who are selecting trophy animals, the perception of what constitutes a trophy is a matter of personal opinion. One hunter may be very satisfied with a trophy animal that another hunter has already passed up in their search for one larger. If one hunter's trophy is another's reject, it becomes difficult to assess the genetic effect of removing this nebulous entity collectively called a trophy.

### Age

In free-ranging populations without the benefit of a known pedigree, it is difficult to differentiate whether the size of an individual's horns or antlers reflect superior genetics or simply advanced age (Brown et al. 2010, Hewitt et al. 2014). Hunters deciding whether to harvest an animal may not know if they are selecting a mature cervid with below-average antlers, or a young male with great potential for large antlers later in life. Likewise, in the absence of harvest restrictions, sheep hunters harvesting the largest males are often taking the oldest in the population and not exerting a strong unidirectional selection against males with superior genetic potential (Frisina and Frisina 2012). Declines in horn and antler size often reflect a declining male age composition in hunted populations (Schmidt et al. 2007, Monteith et al. 2013, Rivrud et al. 2013). Except in limited cases, trophy hunters do not impose intensive selection by removing the largest males in each age class but rather the largest they are able to harvest during the hunting season, during daylight hours, in the areas they are allowed to hunt, and on the days they are afield. The inability to disentangle age and genetic potential for horn and antler growth in most free-ranging ungulate populations represents yet another obstacle to selection efficiency.

### Genetic Contribution of Females

Female cervids contribute at least as much to the antler size and shape of their male offspring as do the sires (Lockwood et al. 2007, Webb et al. 2012). Similar relationships have been demonstrated in bovids, such as successful efforts to identify male cattle with greater genetic potential for milk production in their female offspring (Georges et al. 1995). Experiments in captivity have shown that white-tailed deer (*Odocoileus virginianus*) fawns born from the same female, but sired by different males, often have antler conformations similar to each other. Even wild ungulate male:female ratios of 1:2 or 1:3 means that 66–75% of the population is comprised of females that cannot be subjected to selective pressures related to horn or antler quality in the wild. In some captive studies, researchers removed females from the breeding experiments if they produced  $\geq 2$  male offspring with only 2 antler points (Lockwood et al. 2007). This was used to show that selection can work under the most controlled and optimistic scenarios in captivity. In the wild, it would be very difficult to induce a genetically based evolutionary response in horn and antler size through

incomplete selection acting on only 25–34% of the potential breeders and no control over which animals breed (Webb et al. 2012).

### Nutrition

Biologists know that horn, antler, and pronghorn (*Antilocapra americana*) development is heavily influenced by nutrition in ungulates, including mountain sheep (Jorgenson et al. 1998, Coltman 2008, Pigeon et al. 2016), elk (*Cervus canadensis*), red deer (*Cervus elaphus*; Wang et al. 1999, Kruuk et al. 2002), deer (French et al. 1956, Brown 1990, Lockwood et al. 2007, Foley et al. 2012, Michel et al. 2016b), pronghorn (O’Gara 1990, 2004), and caribou (Cronin et al. 2003, Mahoney et al. 2011). Substandard and variable nutrition, caused by weather patterns, independent habitat degradation, or the density-dependent effects of high population density, results in animals not expressing their genetic potential for horn or antler size. Because body growth and maintenance takes priority over the growth of secondary sexual characteristics, ungulate weaponry can be substantially reduced by dietary restrictions. Further, this phenotypic plasticity is more common in antlers because they are lost and regrown each year (Festa-Bianchet 2016).

Early studies underestimated the contribution that environmental effects (primarily nutrition) made to observed declines in horn size in mountain sheep (Coltman et al. 2003). More recent work is shedding much needed clarity even for the Ram Mountain population, which has been the centerpiece to which nearly all related publications refer when speculating on the widespread effects of selective harvest on ungulates (Coltman 2008, Loehr et al. 2010, Pigeon et al. 2016, Douhard et al. 2017).

Any selection based on the size of an animal’s horns or antlers will be confounded by variations in nutrition. During a year of exceptional nutrition, a cervid with below average genetic potential for antler size might fit many hunters’ criteria as a harvestable trophy and be removed from the population. Obviously, the strong effects of nutritionally influenced phenotypic plasticity erodes the ability of hunters to cause evolutionarily significant declines in a population’s future genetic potential for large horns or antlers.

### Maternal Effect

In addition to the direct effect of genetics and nutrition on the physical appearance of offspring, there is another non-genetic influence on their health, survival, and ultimate phenotype, including horn and antler size. Maternal effect is a phenomenon where the environmental conditions affecting the mother before, during, and immediately after gestation also shapes the future phenotype of her offspring independent of their genotype (Bernardo 1996; Monteith et al. 2009, 2017; Michel et al. 2016a,b). Monteith et al. (2009) housed white-tailed deer from western and eastern South Dakota together to test the influence of intergenerational maternal effects. The western phenotype is 29% smaller than the eastern phenotype. These original source animals and their offspring were provided feed *ad libitum* throughout the study. The first-generation offspring born to well-fed small phenotype dams reached 30% larger body mass than their

parents and had significantly larger antlers. The second-generation small phenotype offspring, the product of unlimited maternal and grandmaternal nutrition, approached the size of the larger phenotype. This is relevant to any analysis of phenotype-based selection because this maternal effect can be positive or negative and influence phenotypic characters of the offspring through adulthood and even on to future generations (Kirkpatrick and Lande 1989, 1992; Mech et al. 1991). Maternal effects can accelerate, slow, or counterbalance the effects of selection and thereby interfere with expected evolutionary change (Kirkpatrick and Lande 1989, 1992; Bernardo 1996).

The potential intergenerational maternal effects on an individual means that its phenotype is a product of environmental influences, its genotype, and also the phenotype of its ancestors. Obviously, this complexity makes it difficult for simple selection for or against a particular trait to alter the average phenotype in a wild population.

### Epigenetics

We normally think of genetically based phenotypic change in terms of simple Mendelian genetics governed by hardwired genetic code. It is becoming increasingly evident that the expression of genotype is not that simple (Nijland et al. 2008, Triantaphyllopoulos et al. 2016). Without changes to the DNA sequence, environmental influences such as nutrition, stress, or disease can alter the way genes are expressed resulting in more than one phenotype (Quarta et al. 2016). This source of variation in phenotype can occur through several different chemical pathways at the molecular level that subsequently influence development of physical characteristics or behaviors. These different phenotypes are heritable even though they are derived solely from changes in gene expression with no alteration of the DNA sequence (Triantaphyllopoulos et al. 2016). For example, Dalgaard et al. (2016) identified 2 diverse phenotypes in mice (*Mus musculus*) epigenetically inherited in non-Mendelian fashion. Despite dedicated attempts to cross-breed them, they were unsuccessful in disrupting the persistence of 2 phenotypes. We are just beginning to learn about how much natural phenotypic plasticity in wildlife is due to these epigenetic effects.

Epigenetics results in a disconnect between an individual’s genotype and phenotype and thus adds another level of complexity to evaluating the effects of selection on heritable genetic traits. If direct environmental stressors can alter heritable phenotypic expression without changing genotype, it has the potential to provide a pathway for evolutionary change that is partially independent of selection acting on genotype alone (Bossdorf et al. 2008). Harvest-based selection for a particular phenotype is diluted to an unknown degree by epigenetic effects that interfere with the traditional view of selection acting directly on an individual’s genome.

### Patterns of Mating Success

Although mature animals do a disproportionate amount of the mating (McCullough 1979), information is now emerging from bovids and cervids that subordinate males are more successful in fathering offspring than previously

thought (Hogg and Forbes 1997, Coltman et al. 2002, Sorin 2004, DeYoung et al. 2009). DeYoung et al. (2009) investigated patterns of male white-tailed deer mating success with genetic paternity testing and reported 30–33% of the white-tailed deer fawns on 3 study areas were sired by physically immature 1.5- and 2.5-year-old males. The remainder were sired by males  $\geq 3.5$  years old. In addition, multiple paternity occurred in 24% of compound ( $>1$  fawn) litters (DeYoung et al. 2002).

Likewise in mountain sheep, a microsatellite DNA analysis of 2 populations revealed 44% of bighorn lambs sampled were fathered by subordinate males that were able to gain access to estrus females in the presence of a mature dominant male (Hogg and Forbes 1997). Coltman et al. (2002) also report approximately 50% of the lambs born on Ram Mountain 1995–2000 were sired by younger males. These patterns of mating may not be ubiquitous throughout all ungulates but provide examples of mating systems that are more complex than the simple assumption that a few dominant males sire most of the annual recruitment. This reality illustrates another reason why it is difficult for hunters to cause evolutionary change in phenotype at the population level even if they are selecting the largest male available to them during the season.

### Gene Linkage

When genes reside close to one another on the same chromosome they do not assort independently so genes linked in this manner are inherited together more often than not (Pierce 2005). This means that selection acting strongly on a particular gene also will affect the evolutionary trajectory of other genes linked to it. If a gene related to inferior horn or antler growth is linked to one that increases survival, these traits will be inherited together more than expected. For example, alleles for larger horn size in Soay sheep (*Ovis aries*) increased reproductive success, whereas alleles for the smaller horn size were associated with increased survival, thereby maintaining the smaller phenotypes through gene linkage (Johnston et al. 2013). This means intensive harvest-based selection acting on horn or antler size in ungulates may affect survival or other traits related to fitness in a positive or negative way. Linked genes present another obstacle interfering with the genetic and phenotypic consequences of selective harvest for horn or antler size.

### Gene Flow and Refugia

If harvest-based selection against large horns and antlers were intensive enough to be evolutionarily relevant, population immigration and emigration with areas not under similar selection would lessen its effects (Festa-Bianchet 2016). Although there are exceptions (Ram Mountain; Coltman et al. 2003), most ungulate populations are not isolated from genetic exchange. Cervid distribution is generally more spatially homogenous than mountain sheep, but even seemingly separate mountain sheep populations exchange genes with one another (Schwartz et al. 1986, Hogg 2000), which results in retention of genetic diversity and counters the effects of random genetic drift and accumulation of deleterious alleles. Metapopulation dynamics helps to retain genetic diversity

throughout and dilutes selection applied to a subpopulation. Even hunted subpopulations often contain refugial areas that are unhunted or difficult to access because of the road network, terrain, or vegetation. The extent and presence of these *de facto* refuges vary considerably, but even a small amount of gene flow among lightly or unhunted areas or subpopulations (Pelletier et al. 2014) is sufficient to swamp the effects of selective harvest (Slatkin 1987, Hendry et al. 2001).

### Date of Birth

The relative birth date (i.e., earlier or later in the summer) of neonate ungulates can have an effect on the development of horns (Pérez-Barbería et al. 1996) and antlers (Gray et al. 2002, Michel et al. 2016a) during the following year. Gray et al. (2002) reported early born white-tailed deer fawns had greater mainbeam length and circumference, higher body mass, and more antler points than other fawns born later. This effect could reflect the advantage of a higher nutritional plane earlier in the summer, or simply that early born individuals have more time to acquire nutrients to satisfy priority body growth in their first year. Hewitt et al. (2014) reported that antler size in yearling males predicts future antler size. If late birth date masks a male's true genetic potential, this adds yet another obstacle to selection. Even for those areas with harvest restrictions based on the antler size of young males, hunter selection would not efficiently act on individuals with superior genetic potential because of the limited genetic effect on phenotype given the strong environmental (birth date) effect.

### Other Selective Pressures

In most populations, early mortality factors take more than half of the neonate cohort each year (Linnell et al. 1995). Additionally, collisions with automobiles, falls, predation, disease, malnutrition, and accidents remove a large number of adult ungulates annually. These neonate and adult losses are likely to be unrelated to the individuals' future genetic potential for horn or antler size. Many of these sources of mortality independently represent selection based on a variety of different physical or behavioral traits. Some individuals may be genetically predisposed or immune to certain diseases. For example, some individual deer appear to have a genotype that offers delayed progress or reduced susceptibility to chronic wasting disease (Robinson et al. 2012b) and the frequency of some of these genotypes is increasing in the population because selection is intensive enough to drive an evolutionary change, albeit unrelated to harvest (Robinson et al. 2012a). Any source of mortality that is removing individuals from the population at random or for reasons uncorrelated with horn or antler size serves to dilute any harvest-based selection for those traits.

## DISCUSSION

Selective harvest selects, but that does not mean the selection is intensive enough to affect future population genotypes or phenotypes to a measurable or meaningful degree in the evolutionary context. Removal of males expressing a variety of horn and antler sizes, including some very large males, does not inevitably represent directional artificial selection

unless the selective pressures are intensive enough to cause a unidirectional shift in phenotype or allele frequencies that may act on some relevant life-history trait or process. The crux of this issue is the intensity of selection on a moderate to highly heritable trait with evolutionary consequences (Myserud 2011, Festa-Bianchet 2016, Kupařinen and Festa-Bianchet 2016).

There are jurisdictions with harvest restrictions that are based on horn and antler size (Wallingford et al. 2017). The extent to which these restrictions contribute to evolutionarily relevant selection depends on the local age-specific horn or antler size in relation to the restrictions (Strickland and Demarais 2000, Coltman et al. 2003, Jones et al. 2010). Additionally, it depends on the intensity of selection for those phenotypic traits and the influence of the multitude of factors that may obstruct a unidirectional evolutionary effect. As noted above, many things interfere and complicate the concept of human harvest genetically altering average horn or antler size in ungulates. The way in which these factors represent obstacles and confounding influences is not trivial to our understanding of human-mediated evolutionary change. A greater focus in the future on disentangling these factors from harvest-based selection will help to guide the discussion in a more productive direction.

Although some are expressing concern over hunter-induced evolutionary change in horn and antler size, others are actively building deer management plans to do just that. In some states (e.g., Texas) there is widespread acceptance of the concept of culling males thought to show genetically inferior antler growth from the herd in an attempt to improve overall genetic potential for future antler size. Early research in captivity showed that you can improve the average antler development through time by culling if you have complete control over which males breed, which females breed, and the nutrition of the herd (Lockwood et al. 2007). These conditions are never met in a wild population so it is unclear how this information from captivity relates to wild, free-ranging populations. Webb et al. (2012) used quantitative genetic models to predict the effects of an intensive selection scenario favoring males with larger age-specific antlers by removing those with smaller antlers. They failed to achieve the success in the wild that has been seen in captivity despite selectively removing 28–56% of the smallest antlered males each year. Webb et al. (2012) concluded that even their intensive selection was inefficient to change population-level genetic characteristics related to antler size.

In captivity, intense selective pressures can be brought to bear on a group of animals (as done with domestic animals for millennia), but the genetic dynamics of a wild population are also reacting to an array of competing, compounding, and correlated selective pressures. Selection applied to captive populations cannot be reproduced in large free-ranging herds (Stedman 1998, Webb et al. 2012, Demarais et al. 2016). Accordingly, it is inappropriate to extrapolate unreplicated research findings from a small, unique, and isolated population such as Ram Mountain across diverse regulatory, geographic, demographic, and taxonomic boundaries.

Coltman et al. (2003) highlighted concern in the Ram Mountain population for an evolutionary response to trophy hunting, which was later confirmed by Pigeon et al. (2016). Although later work on this population showed reduction in horn size was more related to environmental influences than selection (Coltman 2008, Festa-Bianchet 2016, Pigeon et al. 2016), this elicited intense interest in this phenomenon through the conservation community. Unfortunately, many subsequent papers cited the results from Ram Mountain and then relied on an international body of literature across unrelated taxa to speculate trophy hunting was likely causing negative evolutionary consequences for horned and antlered ungulates in general (Allendorf et al. 2008; Bischof et al. 2008; Fenberg and Roy 2008; Allendorf and Hard 2009; Darimont et al. 2009, 2015).

## MANAGEMENT IMPLICATIONS

In a majority of cases, ungulate populations are not being subjected to selective harvest intensive enough to have an evolutionary effect on overall genotypes or phenotypes. The antlers of cervids and pronghorns of antilocaprids are shed and regrown each year and thus more affected by environmental variation than the horns of bovids, especially in mature males (Festa-Bianchet 2016). Festa-Bianchet (2016:3) stated he was “... 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.”

Some studies have called for dramatic changes in harvest management to alleviate the negative effects of selective harvest on ungulates without actually demonstrating any evolutionarily relevant artificial selection (Bischof et al. 2008, Fenberg and Roy 2008, Myserud and Bischof 2010, Myserud 2011, Pelletier et al. 2014). This *non sequitur* only confuses this already-complex topic. Likewise, criticisms implying managers or hunters are either uninformed or obstinately reluctant to adopt good science (Festa-Bianchet 2016, Kupařinen and Festa-Bianchet 2016), reduces the discussion to an overly simplistic and inaccurate depiction of the issue. In reality, managers want to base conservation efforts on credible and reliable knowledge that applies to the populations for which they are responsible. Inappropriate extrapolations from data collected from somewhat unique populations under uncommon regulatory scenarios provides a reasonable basis for the resistance to broad sweeping renovations of harvest management paradigms. Considering the current human footprint on our environment, it is unreasonable to expect our harvest of wildlife, which funds a massive conservation effort, leaves absolutely no demographic or genetic trace of exploitation. What matters is that our management is not harmful in the long term and continues to be sustainable.

The scientific community is aware at this point of the potential effects of intensive harvest-based selection on ungulates. Future work should focus on generating and analyzing original datasets rather than conducting meta-analyses that are of little conservation value at finer geographic or taxonomic scales. Identifying where and

when selective harvest pressures are evolutionarily relevant is important so managers can address those cases. Research should continue in more geographic areas and more ungulate species but with the full inclusion of all sources of potential trait variation to advance our understanding of harvest selectivity on evolutionary processes. In the interim, restraint should be exercised in calling for management changes by extrapolating from relatively unique and isolated populations, single genera, or uncommon harvest paradigms to more diverse units of conservation.

## ACKNOWLEDGMENTS

Thanks to V. C. Bleich, R. T. Bowyer, R. W. DeYoung, V. Geist, P. R. Krausman, R. A. Long, T. LaSharr, and K. L. Monteith for their thoughtful discussions of the ideas presented in this manuscript. Thanks to M. A. Cronin, R. W. DeYoung, and S. L. Webb for excellent comments that improved the manuscript. Funding provided by the Federal Aid in Wildlife Restoration Act (Pittman-Robertson).

## LITERATURE CITED

- Allendorf, F. W., P. R. England, G. Luikart, P. A. Ritchie, and N. Ryman. 2008. Genetic effects of harvest on wild animal populations. *Trends in Ecology and Evolution* 23:327–337.
- Allendorf, F. W., and J. J. Hard. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proceedings of the National Academy of Sciences* 106:9987–9994.
- Bernardo, J. 1996. Maternal effects in animal ecology. *American Zoologist* 36:83–105.
- Bischof, R., A. Mysterud, and J. E. Swenson. 2008. Should hunting mortality mimic the patterns of natural mortality? *Biology Letters* 4:307–310.
- Bonenfant, C., F. Pelletier, M. Garel, and P. Bergeron. 2009. Age-dependent relationship between horn growth and survival in wild sheep. *Journal of Animal Ecology* 78:161–171.
- Bosssdorf, O., C. L. Richards, and M. Pigliucci. 2008. Epigenetics for ecologists. *Ecology Letters* 11:106–115.
- Brown, R. D. 1990. Nutrition and antler development. Pages 426–441 in G. A. Bubenik and A. B. Bubenik, editors. *Horns, pronghorns, and antlers*. Springer-Verlag, New York, New York, USA.
- Brown, D. E., W. C. Keebler, and C. D. Mitchell. 2010. Hunting and trophy horn size in male pronghorn. *Proceedings Pronghorn Workshop* 24:30–45.
- Coltman, D. W. 2008. Molecular ecological approaches to studying the evolutionary impacts of selective harvesting in wildlife. *Molecular Ecology* 16:221–235.
- Coltman, D. W., M. Festa-Bianchet, J. T. Jorgenson, and C. Strobeck. 2002. Age-dependent sexual selection in bighorn rams. *Proceedings of the Royal Society B: Biological Sciences* 269:165–172.
- Coltman, D. W., P. O'Donoghue, J. T. Jorgenson, J. T. Hogg, C. Strobeck, and M. Festa Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting. *Nature* 426:655–658.
- Coulson, T., S. Schindler, L. Traill, and B. Kendall. 2017. Predicting the evolutionary consequences of trophy hunting on a quantitative trait. *Journal of Wildlife Management* 81:in press. Doi: 10.1002/jwmg.21261
- Cronin, M. A., S. P. Haskell, and W. B. Ballard. 2003. The frequency of antlerless female caribou and reindeer in Alaska. *Rangifer* 23:67–70.
- Dalgaard, K., K. Landgraf, S. Heyne, A. Lempradl, J. Longinotto, K. Gossens, M. Ruf, M. Orthofer, R. Strogantsev, M. Selvaraj, T. Tsai-Hsiu Lu, E. Casas, R. Teperino, M. Azim Surani, I. Zvetkova, D. Rimmington, Y. C. Loraine Tung, B. Lam, R. Larder, G. S. H. Yeo, S. O'Rahilly, T. Vavouri, E. Whitelaw, J. M. Penninger, T. Jenuwein, C. Cheung, A. C. Ferguson-Smith, A. P. Coll, A. Korner, and J. A. Pospisilik. 2016. Trim28 haploinsufficiency triggers bi-stable epigenetic obesity. *Cell* 164:353–364.
- Darimont, C. T., S. M. Carlson, M. T. Kinnison, P. C. Paquet, T. E. Reimchen, and C. C. Wilmsers. 2009. Human predators outpace other agents of trait change in the wild. *Proceedings of the National Academy of Sciences* 106:952–954.
- Darimont, C. T., C. H. Fox, H. M. Bryan, and T. E. Reimchen. 2015. The unique ecology of human predators. *Science* 349:858.
- Demarais, S., B. K. Strickland, S. L. Webb, T. Smith, and C. McDonald. 2016. Simulated effects of releasing pen-raised deer into the wild to alter population-level antler size. *Wildlife Society Bulletin* 40:41–49.
- DeYoung, R. W., S. Demarais, K. L. Gee, R. L. Honeycutt, M. W. Hellickson, and R. A. Gonzales. 2009. Molecular evaluation of the white-tailed deer (*Odocoileus virginianus*) mating system. *Journal of Mammalogy* 90:946–953.
- DeYoung, R. W., S. Demarais, R. A. Gonzales, R. L. Honeycutt, and K. L. Gee. 2002. Multiple paternity in white-tailed deer (*Odocoileus virginianus*) revealed by DNA microsatellites. *Journal of Mammalogy* 83:884–892.
- Douhard, M., M. Festa-Bianchet, F. Pelletier, J.-M. Gaillard, and C. Bonenfant. 2016. Changes in horn size of Stone's sheep over four decades correlate with trophy hunting pressure. *Ecological Applications* 26:309–321.
- Douhard, M., G. Pigeon, M. Festa-Bianchet, D. W. Coltman, S. Guillemette, and F. Pelletier. 2017. Environmental and evolutionary effects on horn growth of male bighorn sheep. *Oikos* 126:1071–1227.
- Duda, M. D., M. F. Jones, and A. Criscione. 2010. *The sportsman's voice*. Venture, State College, Pennsylvania, USA.
- Falconer, D. S. 1989. *Introduction to quantitative genetics*, Third edition. John Wiley and Sons, New York, New York, USA.
- Fenberg, P. B., and K. Roy. 2008. Ecological and evolutionary consequences of size-selective harvesting: How much do we know? *Molecular Ecology* 17:209–220.
- Festa-Bianchet, M. 2003. Exploitative wildlife management as a selective pressure for the life history evolution of large mammals. Pages 191–207 in M. Festa-Bianchet and M. Apollonio, editors. *Animal behavior and wildlife conservation*. Island Press, Washington, D.C., USA.
- Festa-Bianchet, M. 2016. When does selective hunting select, how can we tell, and what should we do about it? *Mammal Review* 47:76–81.
- Festa-Bianchet, M., D. W. Coltman, L. Turelli, and J. T. Jorgenson. 2004. Relative allocation to horn and body growth in bighorn rams varies with resource availability. *Behavioral Ecology* 15:305–312.
- Festa-Bianchet, M., F. Pelletier, J. T. Jorgenson, C. Feder, and A. Hubbs. 2014. Decrease in horn size and increase in age of trophy sheep in Alberta over 37 years. *Journal of Wildlife Management* 78:133–141.
- Foley, A. M., R. W. DeYoung, S. D. Lukefahr, J. S. Lewis, D. G. Hewitt, M. W. Hellickson, D. A. Draeger, and C. A. DeYoung. 2012. Repeatability of antler characteristics in mature white-tailed deer in south Texas: consequences of environmental effects. *Journal of Mammalogy* 93:1149–1157.
- French, C. E., L. C. McEwen, N. D. Magruder, R. H. Ingram, and R. W. Swift. 1956. Nutrient requirements for growth and antler development in the white-tailed deer. *Journal of Wildlife Management* 20:221–232.
- Frisina, M. R., and R. M. Frisina. 2012. Influence of trophy harvest on the population age structure of argali (*Ovis ammon*) in Mongolia. *Journal of the Bombay Natural History Society* 109:173–176.
- Garel, M., J.-M. Cugnasse, J.-M. Gaillard, A. Loison, P. Gibert, P. Duvre, and D. Dubray. 2005. Reproductive output of female mouflon (*Ovis gmelini musimon* 3 *Ovis* sp.): a comparative analysis. *Journal of Zoology* 266:65–71.
- Garel, M., J.-M. Cugnasse, D. Maillard, J.-M. Gaillard, A. J. M. Hewison, and D. Dubray. 2007. Selective harvesting and habitat loss produce long-term life history changes in a mouflon population. *Ecological Applications* 17:1607–1618.
- Geist, V. 2006. The North American Model of Wildlife Conservation: a means of creating wealth and protecting public health while generating biodiversity. Pages 285–293 in D. M. Lavigne, editor. *Gaining ground: in pursuit of ecological sustainability*. International Fund for Animal Welfare, University of Limerick, Limerick, Ireland.
- Georges, M., D. Nielsen, M. Mackinnon, A. Mishra, R. Okimoto, A. T. Pasquino, L. S. Sargeant, A. Sorensen, M. R. Steele, X. Zhao, J. E. Womack, and I. Hoeschele. 1995. Mapping quantitative trait loci controlling milk production in dairy cattle by exploiting progeny testing. *Genetics* 139:907–920.



- Gould, S. J., and R. C. Lewontin. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London B* 205:581–598.
- Gray, W. N., H. S. S. Ditchkoff, M. K. Causey, and C. W. Cook. 2002. The yearling disadvantage in Alabama deer: effect of birth date on development. *Proceedings of the Southeastern Association of Fish and Wildlife Agencies* 56:255–264.
- Hadfield, J. D., A. J. Wilson, D. Garant, B. C. Sheldon, and L. E. B. Kruuk. 2010. The misuse of BLUP in ecology and evolution. *American Naturalist* 175:116–125.
- Harris, R. B., W. A. Wall, and F. W. Allendorf. 2002. Genetic consequences of hunting: what do we know and what should we do? *Wildlife Society Bulletin* 30:634–643.
- Hedrick, P. W. 2011. Rapid decrease in horn size of bighorn sheep: environmental decline, inbreeding depression, or evolutionary response to trophy hunting? *Journal of Heredity* 102:770–781.
- Heffelfinger, J. R., V. Geist, and W. Wishart. 2013. The role of hunting in North American Wildlife Conservation. *International Journal of Environmental Studies* 70:399–413.
- Heimer, W. E. 2004. Inferred negative effect of “trophy hunting” in Alberta: the great Ram Mountain/Nature controversy. *Proceedings of the Northern Wild Sheep and Goat Council* 14:193–210.
- Hendry, A. P., T. Day, and E. B. Taylor. 2001. Population mixing and the adaptive divergence of quantitative traits in discrete populations: a theoretical framework for empirical tests. *Evolution* 55:459–466.
- Hengeveld, P. E., and M. Festa-Bianchet. 2011. Harvest regulations and artificial selection on horn size in male bighorn sheep. *Journal of Wildlife Management* 75:189–197.
- Hewitt, D. G., M. W. Hellickson, J. S. Lewis, D. B. Wester, and F. C. Bryant. 2014. Age-related patterns of antler development in free-ranging white-tailed deer. *Journal of Wildlife Management* 78:976–984.
- Hogg, J. T. 2000. Mating systems and conservation at large spatial scales. Pages 214–252 in M. Apollonio, M. Festa-Bianchet, D. Mainardi, editors. *Vertebrate mating systems*. World Scientific, Singapore.
- Hogg, J. T., and S. H. Forbes. 1997. Mating in bighorn sheep: frequent male reproduction via a high-risk “unconventional” tactic. *Behavioral Ecology and Sociobiology* 41:33–48.
- Johnston, S. E., J. Gratten, C. Berenos, J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and J. Slate. 2013. Life history trade-offs at a single locus maintain sexually-selected genetic variation. *Nature* 502:93–93.
- Jones, P. D., B. K. Strickland, S. Demarais, B. J. Rude, S. L. Edwards, and J. P. Muir. 2010. Soils and forage quality as predictors of white-tailed deer *Odocoileus virginianus* morphometrics. *Wildlife Biology* 16:430–439.
- Jorgenson, J. T., M. Festa-Bianchet, and W. D. Wishart. 1998. Effects of population density on horn development in bighorn rams. *Journal of Wildlife Management* 62:1011–1020.
- Kirkpatrick, M., and R. Lande. 1989. The evolution of maternal characters. *Evolution* 43:485–503.
- Kirkpatrick, M., and R. Lande. 1992. The evolution of maternal characters: Errata. *Evolution* 46:284.
- Kruuk, L. E. B., J. Slate, J. M. Pemberton, S. Brotherstone, F. Guinness, and T. Clutton Brock. 2002. Antler size in red deer: heritability and selection but no evolution. *Evolution* 56:1683–1695.
- Kuparinen, A., and M. Festa-Bianchet. 2016. Harvest-induced evolution: insights from aquatic and terrestrial systems. *Philosophical Transactions of the Royal Society B* 372:20160036. Doi:10.1098/rstb.2016.0036
- Linnell, J. D. C., R. Aanes, and R. Andersen. 1995. Who killed bambi? The role of predation in the neonatal mortality of temperate ungulates. *Wildlife Biology* 1:209–223.
- Lockwood, M. A., D. B. Frels, Jr., W. E. Armstrong, E. Fuchs, and D. E. Harmel. 2007. Genetic and environmental interaction in white-tailed deer. *Journal of Wildlife Management* 71:2732–2735.
- Loehr, J., J. Carey, R. B. O'Hara, and D. S. Hik. 2010. The role of phenotypic plasticity in responses of hunted thinhorn sheep ram horn growth to changing climate conditions. *Journal of Evolutionary Biology* 23:783–790.
- Lukefahr, S. D., and H. A. Jacobson. 1998. Variance component analysis and heritability of antler traits in white-tailed deer. *Journal of Wildlife Management* 62:252–268.
- Mahoney, S. P. 2009. Recreational hunting and sustainable wildlife use in North America. Pages 266–281 in B. Dickson, J. Hutton, and W. M. Adams, editors. *Recreational hunting, conservation and rural livelihoods: science and practice*. Blackwell, Chichester, West Sussex, United Kingdom.
- Mahoney, S. P., and J. J. Jackson. 2013. Enshrining hunting as a foundation for conservation – the North American Model. *International Journal of Environmental Studies* 70:448–459.
- Mahoney, S. P., J. N. Weir, G. Luther, J. A. Schaefer, and S. F. Morrison. 2011. Morphological change in Newfoundland caribou: effects of abundance and climate. *Rangifer* 31:21–34.
- McCullough, D. R. 1979. *The George Reserve deer herd: population ecology of a K-selected species*. University of Michigan Press, Ann Arbor, USA.
- Mech, L. D., M. E. Nelson, and R. E. McRoberts. 1991. Effects of maternal and grandmaternal nutrition on deer mass and vulnerability to wolf predation. *Journal of Mammalogy* 72:146–151.
- Michel, E. S., S. Demarais, B. K. Strickland, T. Smith, and C. M. Dacus. 2016a. Antler characteristics are highly heritable but influenced by maternal factors. *Journal of Wildlife Management* 80:1420–1426.
- Michel, E. S., E. B. Flinn, S. Demarais, B. K. Strickland, G. Wang, and C. M. Dacus. 2016b. Improved nutrition cues switch from efficiency to luxury phenotypes for a long-lived ungulate. *Ecology and Evolution* 6:7276–7285.
- Montaldo, H. 2001. Genotype by environment interactions in livestock breeding programs: a review. *Interciencia* 26:229–235.
- Monteith, K. L., R. A. Long, V. C. Bleich, J. R. Heffelfinger, P. R. Krausman, and R. T. Bowyer. 2013. Effects of harvest, culture, and climate on trends in size of horn-like structures in trophy ungulates. *Wildlife Monographs* 183:1–28.
- Monteith, K. L., R. A. Long, T. R. Stephenson, V. C. Bleich, R. T. Bowyer, and T. N. LaSharr. 2017. Horn size and nutrition in mountain sheep: can ewe handle the truth? *Journal of Wildlife Management* 81:in press.
- Monteith, K. L., L. E. Schmitz, J. A. Jenks, J. A. Delger, and R. T. Bowyer. 2009. Growth of male white-tailed deer: consequences of maternal effects. *Journal of Mammalogy* 90:651–660.
- Mysterud, A. 2011. Selective harvesting of large mammals: how often does it result in directional selection? *Journal of Animal Ecology* 48:827–834.
- Mysterud, A., and R. Bischof. 2010. Can compensatory culling offset undesirable evolutionary consequences of trophy hunting? *Journal of Animal Ecology* 79:148–160.
- Nijland, M. J., S. P. Ford, and P. W. Nathanielsz. 2008. Prenatal origins of adult disease. *Current Opinion in Obstetrics and Gynecology* 20:132–138.
- O'Gara, B. W. 1990. The pronghorn (*Antilocapra americana*). Pages 231–264 in G. A. Bubenik and A. B. Bubenik, editors. *Horns, pronghorns, and antlers*. Springer-Verlag, New York, New York, USA.
- O'Gara, B. W. 2004. Physical characteristics. Pages 109–143 in B. W. O'Gara, and J. D. Yoakum, editors. *Pronghorn ecology and management*. University of Colorado Press, Boulder, USA.
- Patterson, R. 2009. Executive summary. Pages 391–392 in *World symposium: ecologic and economic benefits of hunting*. World Forum on the Future of Sport Shooting Activities, Windhoek, Namibia.
- Pelletier, F., M. Festa-Bianchet, J. T. Jorgenson, C. Feder, and A. Hubbs. 2014. Can phenotypic rescue from harvest refuges buffer wild sheep from selective hunting? *Ecology and Evolution* 4:3375–3382.
- Pérez, J. M., E. Serrano, M. González-Candela, L. León-Vizcaino, G. G. Barberá, M. A. Simón, P. Fandos, J. E. Granados, R. C. Soriguer, and M. Festa-Bianchet. 2011. Reduced horn size in two wild trophy-hunted species of Caprinae. *Wildlife Biology* 17:102–112.
- Pérez-Barbería, F. J., L. Robles, and C. Nore. 1996. Horn growth pattern in Cantabrian chamois *Rupicapra pyrenaica parva*: influence of sex, location and phenology. *Acta Theriologica* 41:83–92.
- Pierce, B. A. 2005. *Genetics: a conceptual approach*. Second edition. W. H. Freeman, New York, New York, USA.
- Pigeon, G., M. Festa-Bianchet, D. W. Coltman, and F. Pelletier. 2016. Intense selective hunting leads to artificial evolution in horn size. *Evolutionary Applications* 9:521–530.
- Postma, E. 2006. Implications of the difference between true and predicted breeding values for the study of natural selection and micro-evolution. *Journal of Evolutionary Biology* 19:309–320.
- Quarta, C., R. Schneider, and M. H. Tscho. 2016. Epigenetic on/off switches for obesity. *Cell* 164:341–342.
- Responsive Management. 2013. *Nationwide survey of hunters regarding participation in and motivations for hunting*. Responsive Management, Harrisonburg, Virginia, USA.

- Rivrud, I. M., K. Sonkoly, R. Lehocski, S. Csányi, G. O. Storvik, and A. Mysterud. 2013. Hunter selection and long-term trend (1881–2008) of red deer trophy sizes in Hungary. *Journal of Applied Ecology* 50:168–180.
- Robinson, S. J., M. D. Samuel, C. J. Johnson, D. I. McKenzie, and M. Adams. 2012a. Emerging prion disease drives host selection in a wildlife population. *Ecological Applications* 22:1050–1059.
- Robinson, S. J., M. D. Samuel, K. I. O'Rourke, and C. J. Johnson. 2012b. The role of genetics in chronic wasting disease of North American cervids. *Prion* 6:1–10.
- Rughetti, M., and M. Festa-Bianchet. 2010. Compensatory growth limits opportunities for artificial selection in alpine chamois. *Journal of Wildlife Management* 74:1024–1029.
- Schmidt, J. I., J. M. Ver Hoef, and R. T. Bowyer. 2007. Antler size of Alaskan moose *Alces alces gigas*: effects of population density, hunter harvest and use of guides. *Wildlife Biology* 13:53–65.
- Schwartz, O. A., V. C. Bleich, and S. A. Holl. 1986. Genetics and the conservation of mountain sheep *Ovis canadensis nelsoni*. *Biological Conservation* 37:179–190.
- Skogland, T. 1989. Natural selection of wild reindeer life history traits by food limitation and predation. *Oikos* 55:101–110.
- Slatkin, M. 1987. Gene flow and the geographic structure of natural populations. *Science* 236:787–792.
- Sorin, A. B. 2004. Paternity assignment for white-tailed deer (*Odocoileus virginianus*): mating across age classes and multiple paternity. *Journal of Mammalogy* 85:356–362.
- Southwick, R., and T. Allen. 2010. Expenditures, economic impacts and conservation contributions of hunters in the United States. Pages 308–313 in *World symposium: ecologic and economic benefits of hunting*. World Forum on the Future of Sport Shooting Activities, Windhoek, Namibia.
- Stedman, S. W. 1998. One manager's perspective on culling. Pages 94–96 in D. Rollins, editor. *The role of genetics in white-tailed deer management*. Proceedings of a Symposium, Texas Agricultural Extension Service, Texas A&M University, College Station, USA.
- Stenseth, N. H., and E. S. Dunlop. 2009. Evolution: unnatural selection. *Nature* 457:803–804.
- Strickland, B. K., and S. Demarais. 2000. Age and regional differences in antlers and mass of white-tailed deer. *Journal of Wildlife Management* 64:903–911.
- Trall, L. W., S. Schindler, and T. Coulson. 2014. Demography, not inheritance, drives phenotypic change in hunted bighorn sheep. *Proceedings of the National Academy of Sciences* 111:13223–13228.
- Triantaphyllopoulos, K. A., I. Ikonopoulou, and A. J. Bannister. 2016. Epigenetics and inheritance of phenotype variation in livestock. *Epigenetics & Chromatin* 9:31. Doi: 10.1186/s13072-016-0081-5.
- Wallingford, B. D., D. R. Diefenbach, E. S. Long, C. S. Rosenberry, and G. L. Alt. 2017. Biological and social outcomes of antler point restriction harvest regulations for white-tailed deer. *Wildlife Monographs* 196:1–26.
- Wang, Z., R. C. Yang, L. A. Goonewardene, and C. Huedepohl. 1999. Genetic analysis of velvet antler yield in farmed elk (*Cervus elaphus*). *Canadian Journal of Animal Science* 79:569–571.
- Webb, S. L., S. Demarais, B. K. Strickland, R. W. DeYoung, B. P. Kinghorn, and K. Gee. 2012. Effects of selective harvest on antler size in white-tailed deer: a modeling approach. *Journal of Wildlife Management* 76:48–56.
- Williams, J. D., W. F. Krueger, and D. H. Harmel. 1994. Heritability for antler characteristics and body weight in yearling white-tailed deer. *Heredity* 73:78–83.

Associate Editor: Mark Boyce.