Age-related Horn Growth, Mating Tactics, and Vulnerability to Harvest: Why Horn Curl Limits may Select for Small Horns in Bighorn Sheep

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Abstract: Male bighorn sheep (*Ovis canadensis*) complete about 80% of horn growth by age 5, yet horn size appears to play little or no role in their mating success until they are 6-8 yr old. Only the most dominant rams, typically 8 yr and older, can tend estrous ewes. Subordinate rams use alternative mating tactics whose success appears independent of their horn size. Rams with fast-growing horns may become 'legal' to harvest a few years before those large horns lead to higher mating success. If hunting pressure is high, rams with rapidly growing horns will have lower lifetime mating success than rams with slow-growing horns that do not become legal until an older age. Because ram horn size is inheritable, harvest of rams with rapidly growing horns may favor genetically small-horned rams. We documented this phenomenon at Ram Mountain, where rams with horns of 4/5 curl or greater were 'legal' and hunting by Alberta residents was unrestricted, leading to an average harvest rate of about 30% of 'legal' rams. Because traits that affect horn size in rams are genetically correlated with fitness-related traits in ewes, selective hunting may have affected the demographic performance of the population. The selective effects of trophy hunting should increase with hunting pressure and decrease with immigration of rams from protected areas.

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In most of their range outside protected areas, bighorn sheep (*Ovis canadensis*) are managed based on a horn curl limit, so that only rams whose horns exceed a minimum size can be legally harvested. Although in many States horn curl limits are associated with a limited number of permits, until recently in much of Alberta or British Columbia any resident could purchase a trophy sheep license and hunt in all or most of his or her province. Harvest was only limited by the availability of ‘legal’ rams or by the difficulty of access (Festa-Bianchet 1989).

Sport hunting plays an important role in the conservation of mountain sheep in North America (Geist 1994) and, increasingly, large mammals elsewhere (Leader-Williams et al. 2001). Very large sums are expended by tourist hunters who seek large-horned rams, providing recreational opportunities and the possibility, sometimes realized, of using funds generated through hunting for conservation and management (Erickson 1988, Harris and Pletscher 2002). Because of hunting regulations and hunter preference, however, the survival of large-horned rams may be lower than that of small-horned ones, particularly if harvest rates are high. There are many examples of harvest-induced changes in the morphology and life history of exploited species (Hartl et al. 1991, Rijnsdorp 1993, Jachmann et al. 1995, Ericsson et al. 2001, Harris et al. 2002, Festa-Bianchet 2003, Swenson 2003, Olsen et al. 2004, Walsh et al. 2006) and it is important for managers to know whether selective harvest of large-horned rams could lead to artificial selection favouring genetically small-horned rams.

Coltman et al. (2003) reported that in one population of bighorn sheep, 30 yr of unlimited-entry harvest of rams with horns describing at least 4/5 of a curl led to a decrease in breeding values (the genetic component of a trait, estimated from a pedigree analysis and trait measurements of related individuals) for both horn length and body mass. That paper stimulated much interest on the potential evolutionary consequences of sport harvest. Increasingly, evidence is accumulating that sport hunting has selective effects on morphology and life history (Martinez et al. 2005, Zedrosser 2006, Garel et al. 2007). A few people, however, appeared not to understand the paper, feared its consequences for a cherished status quo, and questioned its motivations (Heimer and Lee 2004). Because of the importance of the potential evolutionary consequences of trophy hunting on mountain sheep, and because of misinterpretations of Coltman et al. (2003) disseminated in various outlets, we provide a brief summary of published evidence that selective hunting of bighorn rams may have a selective effect. We also explore some of the management actions that may exacerbate or attenuate artificial selection through trophy hunting.

Horn size is inheritable

Horn or antler size of many ungulates is affected by non-genetic characteristics, including age, population density, habitat and soil quality, and weather conditions (Bunnell 1978, Hoefs 1984, Wehausen 1989, Jorgenson et al. 1993, Fandos 1995, Hoefs and Nowlan 1997, Jorgenson et al. 1998, Toïgo et al. 1999, Festa-Bianchet et al. 2000; 2004, Mysterud et al. 2005). Horn and antler size, however, are also dependent on genotype (Stewart and Butts 1982, Fitzsimmon et al. 1995, Lukefahr and Jacobson 1998, Wehausen and Ramey 2000, Kruuk et al. 2002, Coltman et al. 2003). In bighorn sheep at Ram Mountain, Alberta, both horn size and body mass have a strong inheritable component (Réale et al. 1999, Coltman et al. 2003; 2005). Once environmental variables and age are controlled, the sons of large-horned rams tend to have larger horns than the sons of small-horned rams (Coltman et al. 2005).

Horn growth is rapid early in life

Much of the growth in horn length in bighorn rams takes place during the first five years of life (Jorgenson et al. 1998). Under a 4/5-curl regulation some rams can reach 'legal' horn size at 4 or 5 yr, and exceptionally at 3 yr (Festa-Bianchet 1986;1989, Jorgenson et al. 1993).

Horn size affects mating success only for dominant rams

Based on behavioural observations and visual estimations of horn size, Geist (1971) concluded that large-horned rams had higher mating success than small-horned ones. Subsequently, several distinct mating tactics used by bighorn males, which to some extent depend on horn size were identified (Hogg 1984;1988). Although a relationship existed between horn size and mating success was long assumed, only molecular techniques can quantify the reproductive success of bighorn rams. Male reproductive success has been measured in 3 populations of bighorn sheep: Sheep River and Ram Mountain in Alberta, and the introduced National Bison Range population in Montana (Hogg and Forbes 1997, Hogg 2000, Coltman et al. 2002; 2003; 2005, Hogg et al. 2006). Those results confirm that the largest-horned (or heaviest, or most dominant) rams, that can defend estrous ewes, have a much higher reproductive success than other rams. Analyses of paternity success also reveal that other rams father lambs by using alternative mating tactics, as suggested by Hogg (1984). Importantly, however, the mating success of rams using alternative tactics is not dependent on horn size, possibly because direct competition plays a limited role in their copulatory success. Only for males that have achieved high dominance status, typically those in the top 2-4 places in the social hierarchy, do individual characteristics such as dominance, body mass, and horn size play an important role in mating success (Hogg and Forbes 1997, Coltman et al. 2002). Because rams grow in both horn size and mass with age, depending on population age structure the top spots in the hierarchy are typically occupied by rams aged 7 yr and older (Hogg and Forbes 1997, Coltman et al. 2002). For the (mostly younger) rams lower in the hierarchy, horn size affects social status but has a limited if any effect on their mating success.

Rams with fast-growing horns reach 'legal' status years before they reach the top of the dominance hierarchy.

Rams in Alberta rams with rapidly growing horns can be 'legal' at 4 yr but do not reach the top of the dominance hierarchy for another 2-4 yr (Pelletier and Festa-Bianchet 2006). Those rams can be harvested at 4 or 5 yr (Festa-Bianchet et al. 2004), while rams whose horns become 'legal' at a later age (or never) have a higher life expectancy and presumably a higher probability of reaching the top dominance ranks. It should be pointed out that records of harvested rams rarely include 'illegal' rams, and therefore provide a biased impression of age-specific horn size, as the fastest-growing rams are shot at younger ages. With the 30% harvest rate of legal rams typical of Ram Mountain added to natural age-specific mortality, a ram legal at age 4 yr has about a 15% chance of surviving to rut at age 7 yr, while a ram not legal until 8 yr (that only faces natural mortality) has about a 64% chance of surviving over the same period (Jorgenson et al. 1997, Loison et al. 1999). Recent research on both bighorn sheep and Alpine ibex (*Capra ibex*) casts doubt over the hypothesis that horn growth is negatively correlated with longevity in either species (Geist 1966; 1971). Instead, the relationship appears to be positive, as one may expect if large-horned males were high-quality individuals (von Hardenberg et al. 2004, Pelletier et al. 2006). Consequently, if rams with fast-growing horns were not harvested at 4 to 6 yr of age, their survival to the age where large horns make a strong positive contribution to reproductive success may well be higher than the average for all rams (Coltman et al. 2003). Interestingly, Geist (1966) compared horn length of rams that died at 7 to 11 yr and 12 yr and older, yet his data frequently are cited to support the selective killing of 4- and 5-yr-old rams with rapid horn growth. None of Geist's work supports the contention of higher mortality at 4 to 6 yr for rams with large horns.

Selective hunting selects

Coltman et al. (2003) showed that over 30 yr of unlimited-entry harvest of 4/5-curl rams, the average breeding value for horn and body size (two traits that are genetically correlated (Coltman et al. 2005)) declined. Rams on the mountain now have horns both phenotypically and genotypically smaller than those of rams on the mountain 5 sheep generations ago. That conclusion was based on the analysis of pedigrees established over 30 yr and included over 700 marked sheep and hundreds of horn measurements. Mother-lamb links established by behavioural observations were supplemented by 241 paternity links established through 20 microsatellite loci, in addition to several paternal half-sibships where individuals were inferred to share a father although that father was not sampled. In that study, some rams with genetically and phenotypically small horns achieved high social status and high reproductive success because their horns never became 'legal' and they survived past 10 yr. Fast-growing rams became 'legal' several years before their large horns could confer to them a high reproductive success. Most of those fast-growing rams were shot at a young age, leading to negative correlations between horn length breeding value and both longevity and known lifetime reproductive success. In unhunted populations, those correlations would presumably be positive.

Management strategies

Sport hunting is a valuable conservation tool (Geist 1994, Leader-Williams et al. 2001, Harris and Pletscher 2002, Festa-Bianchet 2003) and it is a manager's responsibility to ensure that harvest strategies are sustainable, both on a demographic and evolutionary basis. We must consider what can lead to artificial selection and what management strategies can avoid or at least limit artificial selection, bearing in mind that, inevitably, any hunting strategy will lead to some effect, either ecological or evolutionary, on the hunted population.

Clearly, the major factors that affect the intensity of artificial selection through hunting include the definition of 'legal ram', the possibility of immigration from unhunted (and therefore unselected) populations, and the intensity of harvest on 'legal' rams. Ram Mountain is an isolated population that is unlikely to obtain any 'genetic rescue' (Hogg et al. 2006) from sheep originating in protected areas, but most other sheep populations in Alberta could receive immigrant rams from the national parks during the rut (Hogg 2000). Protected areas may therefore play a key role on a management strategy at the landscape level. The 4/5-curl definition used at Ram Mountain until 1996 led to fast-growing rams being selectively removed before they could benefit from their large horns by achieving high social status. The move to a 'full-curl' regulation in 1997 may have come too late for this population, but it has now been implemented in some parts of Alberta and is used in most of British Columbia. Because some large rams never fit the definition of full curl, and others may reach it after obtaining a mating benefit from large horns, a definition of 'legal' ram as 'full' rather than '4/5' curl may lessen the selective effect of hunting. Whether that is the case or not remains to be seen. Finally, the unlimited-entry management used in most of Alberta makes a complete kill of all rams in the year they become legal a possibility, particularly in areas with easy motorized access. At both Ram Mountain (with relatively difficult access) and Sheep River (where the easily accessible part of the range used by rams is protected from hunting), harvest rate of 'legal' rams was about 30% (Festa-Bianchet 1986), but it may be much higher in other areas. Unfortunately, information on the harvest rate of 'legal' rams is seldom available for other areas. A greater effort to estimate harvest rates of 'harvestable' (*i.e.* legal) rams is required.

A management scheme involving a limited number of permits, distributed through a draw, would decrease the intensity of artificial selection by allowing some large-horned rams to survive to rut as mature rams. The difficulties involved in estimating hunter success under a draw system, and in estimating the available number of mature rams, however, cannot be underestimated. A conservative management strategy is called for. It will likely involve a lower rate of harvest than what was applied in Alberta under the unlimited-entry 4/5-curl rule, and lead to a much larger proportion of rams dying of natural death rather than from sport harvest.

We found a decrease in the genetic component of horn length, but the definition of what can and cannot be shot relies on both horn length and shape. Depending on horn shape, different rams may attain 'legal' status with horns of different length. Further investigation of the possible selective effects of hunting should concentrate more directly on some measurement of horn shape that makes rams either 'legal' or more attractive as trophies (Garel et al. 2007).

Management of bighorn sheep has never been easy. The identification of possible selective effects of trophy hunting presents managers and hunters interested in the conservation of mountain sheep with an additional challenge. We fully expect them to rise to that challenge.

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