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Feared Negative Effects of Publishing Data: A Rejoinder to Heimer et al.

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Abstract**:** The Proceedings of the 14th Symposium of the Northern Wild Sheep and Goat Council contained a 'compilation' by Wayne Heimer of critiques of a paper published by Coltman et al. (2003) in *Nature.* That 'compilation', published without giving us a chance to respond, refers to a 'sheep management community' including only those who do not agree with Coltman et al. (2003). It attempts to convey the impression that the paper was not based on empirical data and incorrectly claims that environmental effects on horn and body size were ignored. It uses the Boone and Crockett record book to argue that bighorn (*Ovis canadensis*) rams are increasing in size, ignoring the fact that only large rams make it to the record book and that the number of bighorn sheep has increased substantially over the last few decades. The paper by Geist in the 'compilation' does not critique Coltman et al. (2003). The compilation confuses management regimes at Ram Mountain and elsewhere and provides a data-free defense of the status quo in sheep management. We are confident most sheep managers are interested in our data and will consider their implications
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Most bighorn sheep (*Ovis canadensis*) hunting in Alberta involves an unlimited-entry 'trophy' hunt. Any resident can buy a sheep licence and the harvest is limited by the availability and accessibility of rams with horns describing 4/5 curl, reached by some rams at 4 yr of age and by many at 5 to 6 yr (Festa-Bianchet 1986, Jorgenson et al. 1993). Although it had long been assumed that larger-horned rams had higher fitness (Geist 1971), only recently data became available on mating success of bighorn rams (there are no published data on male mating success of any other mountain ungulate). Ram reproductive success was quantified in two populations in Alberta and one in Montana (Hogg and Forbes 1997, Coltman et al. 2002). While results confirm that large-horned males have high reproductive success, they reveal a strong interaction with age, so that only males at the top of the social hierarchy (typically aged 7 yr and older) benefit substantially from large horns. Other males rely on alternative mating strategies whose success is low and appears independent of horn size. That result confirms observations that rams employing alternative tactics rely mostly on speed, agility, and willingness to take risks, rather than combat with other rams (Hogg 1984;1988, Hogg and Forbes 1997). A ram with fast-growing horns will achieve high reproductive success if it survives to 6 to 7 yr (Coltman et al. 2002), but under unlimited-entry 4/5-curl regulations it may be harvested at 4 to 5 yr.

From those observations, and noting that ram horn length has a strong inheritable component (Coltman et al. 2005), one could predict that rams with slow-growing horns may be advantaged if their large-horned competitors were eliminated by sport hunting. That prediction led to a test based on information from pedigrees and calculation of breeding values for individual rams in the isolated population of Ram Mountain, Alberta (Jorgenson et al. 1998). Those empirical data confirmed artificial selection favouring small-horned rams (Coltman et al. 2003). More recent analyses suggest that systematic removal of high-quality individuals may lower the frequency of other fitness-enhancing traits, and possibly contribute to population stagnation (Coltman et al. 2005).

Until recently, the potential genetic effects of selective harvests figured more prominently in fisheries than in wildlife literature (Harris et al. 2002, Festa-Bianchet 2003). In the near future there should be more data available to assess what (if any) are the evolutionary impacts of sport harvest on wildlife.

Critiques of Coltman et al. (2003) were published in the 2004 Proceedings of the Northern Wild Sheep and Goat Council (Heimer 2004) as a ‘compilation’ that included personal attacks on the authors of the 2003 paper, who were not given the opportunity to defend themselves.

The apparent goal of the ‘compilation’ is set in the ‘Compiling author’s note and comment’, suggesting that the data in Coltman et al. (2003) should be ignored and attention should instead be focused on the ‘radical’ anti-hunting spin given to it by the ‘tabloid press’. The compilation appears to focus on two major critiques: It implies that Coltman et al. (2003) was based on computer simulations, not real data, and suggests that environmental effects were ignored in the analysis. Both claims are false.

Coltman et al. (2003) analyzed over 1000 horn and body measurements of 200 rams aged 2 to 4 yr and a population pedigree encompassing over 700 individuals, reaching back to 1971. Maternal linkages obtained through behavioural observations were supplemented using 20 microsatellite loci to identify 241 paternities and 31 clusters of paternal half-sibs, individuals sharing the same (but unknown) father. Data were analyzed using accepted statistical methods widely applied by quantitative geneticists in the domestic animal literature. Substantial effort was made to separate genetic and environmental causes of variation in horn and body size, again using accepted statistical methods. Coltman et al. (2003) specifically accounted for environmental effects by including the average mass of yearling ewes (that has a stronger correlation with lamb survival and ram horn growth than population density, presumably because it accounts directly for changes in resource availability).

'Breeding value' is the value of a phenotypic trait predicted to be expressed by the descendant of a particular individual. Breeding values are based on the performance of an individual's known relatives in pedigree. Animal scientists routinely use these techniques to select breeders for traits of commercial interest based on pedigree and performance data.

The first paper in the compilation series, by Michael and Margaret Frisina, reports that half of the bighorn rams in the Boone and Crockett Record Book scoring more than 200 points were shot between 1987 and 1997, that over half the top 100 rams were killed in the last 20 yr and that a new 'world record ram' was shot in Alberta in 2000. None of this is surprising. Many populations of bighorn sheep restored over the last few decades are expanding into unused habitat, where rapid horn growth is expected. There are a lot more bighorns today than 30 or 40 yr ago. In populations managed through a draw, the chances of a ram surviving to grow large horns presumably are higher than under unlimited-entry regulations. In addition to not accounting for the increase in sheep numbers, the use of a Record Book as a source of data assumes that reporting frequency does not change through time, and that 'record rams' are a random sample. At Ram Mountain, as ram horns became smaller through a combination of genetic and environmental effects, many rams never reached the 4/5-curl threshold (Jorgenson et al. 1998). These rams would not appear in records of shot animals, because it would be illegal to kill them. Data from harvested rams have many uses, but also several limitations (Martinez et al. 2005).

The 'Alberta record ram' was taken during a special hunt from a population that spends most of the regular hunting season in areas where hunting is not allowed. It illustrates the kind of rams that could be in Alberta if those with fast-growing horns were not selectively removed when aged 6 yr and younger.

The Frisinas state that Coltman et al. (2003) was not based on empirical data and that it did not account for environmental effects, two claims refuted above. They also claim our analyses did not account for the genetic contribution of mothers, yet Coltman et al. (2003) states that 709 maternities were used in pedigrees. The Frisinas provide a spirited defense of hunting, but we have no idea of what led them to suggest that our paper criticized successful sheep conservation programs.

Eric Rominger's paper, labeled a 'call to academic accountability', does not allow for the possibility that both genetic and environmental factors may affect horn growth. Festa-Bianchet et al. (2004) ascribed over two-thirds of the variance in body mass and annulus circumference to changes in resource availability and age. We stand by that result. Age and resource availability are important in determining horn size, but that does not imply that genotype has no role to play. As density on Ram Mountain declined, horn size of rams declined (Fig. 1, see also Fig. 2 in Coltman et al. 2003). Horn growth rates remained low despite the very low density of recent years. That is why instead of population density we accounted for yearly changes in resource availability by the average mass of yearling ewes in June.

Rominger's paper suggests that traits must be all-genetic or all-environmental. Our analysis partitioned environmental from genetic variance because both are important. We have now released sheep from an unselected population onto Ram Mountain and will monitor the growth of descendants with varying admixtures of 'local' and 'immigrant' genes. The importance of genetic rescue of stagnating, isolated populations was illustrated by an

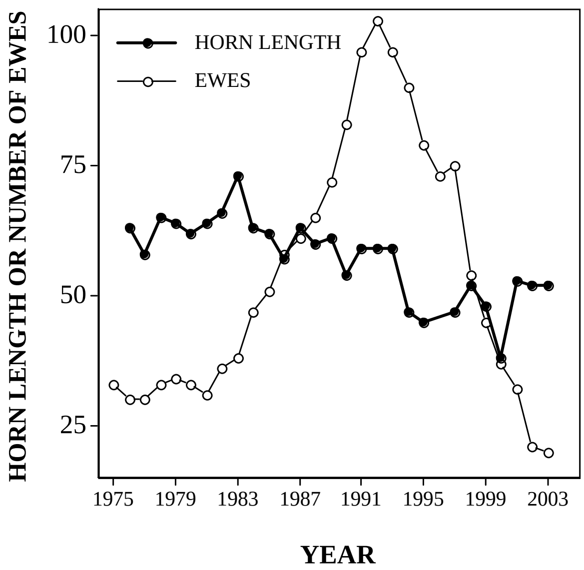

Figure 1. Average horn length of 4-yr-old bighorn sheep rams and number of ewes at Ram Mountain, Alberta, 1975 to 2003. Ram horn length continued to decrease after the number of ewes declined in 1995-2003.

elegant experiment in Montana (Hogg et al. 2006).

We find no need to issue an Errata/Corrigendum. Eric Rominger owes us an apology.

The paper by Val Geist is not a critique of our 2003 paper. Geist doubts that the decline in horn size is permanent but otherwise agrees with our conclusions. We don't know if the decline is permanent, but recent experimental work in fish suggests that overcoming the effects of artificial selection may be difficult (Walsh et al. 2006). Ram Mountain is an isolated population and some alleles present at the beginning of our study have now been lost (D. Coltman, unpublished data). There can be no evolution without genetic variability. After pointing out environmental effects on horn and antler growth (with which we are in agreement), Geist lists earlier examples of artificial selection on antler shape. In writing, Val Geist confirmed that he does not disagree with our 2003 paper. Why then is his paper in this 'compilation'?

The paper by Heimer and Lee includes offensive language and personal accusations. It claims that Coltman et al. (2003) compromised wild sheep conservation because it may be used as fuel for anti-hunting campaigns in the U.S. The result of this could be the loss of conservation funding coming from hunters and hunting organizations. Instead, we suggest that hunters and managers are interested in ensuring that trophy hunting regimes are sustainable. In many hunted deer, moose, reindeer, chamois, wild boar, pronghorn, black bear or sheep (adult males only in most cases) populations, most of which are managed sustainably, most adults die by getting shot (Festa-Bianchet 2003). Avoiding harvest could be a very strong selective pressure.

The same paragraph states that what we reported is not new because 'Reproductive success was quantitatively linked with dominance three decades ago'. The supporting citation is Geist (1971), which does not have data on paternity. Again, the interactions between dominance, horn growth, age, and mating strategy revealed by recent research (Hogg 1984;1988, Hogg and Forbes 1997, Coltman et al. 2002, Pelletier 2005, Pelletier and Festa-Bianchet 2006, Pelletier et al. 2006) are ignored. The relationship between either dominance or horn size and mating success is not linear.

Without citing a source, the next statement claims that only 3 to 10% of available rams are harvested in Alaska. Clearly, the lower the harvest rate, the lower the potential for artificial selective effects. What is meant by 'available rams' is important here. Most rams are not 'available' because they are not legal. The key question is what proportion of legal rams are taken. In the Yukon, with curl regulations similar to those in Alaska, approximately 37% of registered rams are shot the year they become legal, and about 72% within one year of reaching legal size (J. Carey, Yukon Environment, pers. comm.). That does not mean that the yearly harvest rate is 37% because it does not account for natural mortality, but it implies that the 3 to 10% figure may be an underestimate. Genetic consequences were observed at Ram Mountain with a harvest rate of ~35% of legal rams (Festa-Bianchet 1986) or about 5 to 8% of all rams.

The next section laments that papers by Heimer in the Northern Wild Sheep and Goat Council Proceedings are not given sufficient prominence. We strongly encourage those interested in sheep management to read all papers by Heimer as well as Whitten (2001).

Heimer and Lee argue that because 50% of lambs are not sired by dominant rams, selection against large horns cannot occur. Here they miss two points. First, the 50% of paternities by dominants typically belong to 2 to 3 rams each year, while the 50% by subordinates are shared by 10 or more individuals. That mating distribution implies a high potential for rapid selection for the genetic characteristics of the few highly successful rams. Second, as recognized by their own quote: "alternative mating tactics [are] less dependent on body and weapon size", horn size plays a limited role in the reproductive success of subordinate rams. Therefore, shooting a 6-yr-old with large horns ends its life before those horns helped achieve high mating success.

The final sentence is insulting and attempts to belittle people who have devoted a lifetime of effort to understanding the ecology and conservation of mountain ungulates.

Where do we go from here?

Ram Mountain is an isolated population that during our study fluctuated between 26 and 152 adults. It likely experienced genetic drift in addition to artificial selection, and is highly unlikely to receive immigrants from unhunted populations. Future research should focus on other possible genetic effects of trophy hunting, and on what management strategies can avoid artificial selection. Managers should be particularly concerned about the potential effects of selective hunting in small populations, including those recently established. Trophy hunting of mountain ungulates is a potential conservation tool for many species, particularly in Asia, that are threatened by habitat destruction, exotic disease, and poaching (Harris and Pletscher 2002). It is important not to perpetuate management strategies that select for small horns.

Full-curl regulations may decrease the selective effect of hunting by allowing some large-horned rams to survive to an age where large horns confer a high mating success. There may be differences in the determinants of mating success in bighorn and thinhorn (*Ovis dalli*) rams, and we do not know what level of selective harvest is tolerable before genetic consequences are generated. We suspect that a limit on the number of large-horned rams harvested (either through a draw or simply because of the inaccessibility of terrain) would decrease the selective effect of trophy hunting. Hence the urgent need to quantify harvest pressure in terms of the proportion of legal rams taken. We observed a selective effect with a 35% harvest of legal rams, therefore we recommend a lower harvest rate, but currently cannot suggest a more precise harvest goal. Finally, the potential role of protected areas as sources of unselected rams is worthy of investigation, for two reasons. It may dampen the selective effects of hunting, and it may lead to one-way gene flow out of protected areas, possibly decreasing effective population size inside those areas (Hogg 2000). There is much more to mountain ungulate conservation than trophy hunting. We are confident that managers will consider the potential implications of our work.

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