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[Editor's Note: Ray Lee and I also prepared a letter of rebuttal to NATURE. We focused on Coltman et al.'s allegation that insufficient attention has been given to protection of male social structure by modern managers and the political nature of wildlife management in the USA. When we learned Dr. Geist's letter had been rejected, we didn't bother to submit ours. It was too long anyway. I've left it in the draft NATURE format. WEH]

UNDESIRABLE CONSEQUENCES OF UNQUALIFIED SPECULATION ON THE NEGATIVE EFFECTS OF TROPHY RAM HUNTING

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Status-enhancing, but highly speculative, publications such as Coltman *et al.*¹, may compromise wild sheep conservation. Such research communications encourage emotionally driven anti-hunters to contravene biologically sound management programs, particularly in the United States. Coltman *et al.*'s¹ letter grossly exaggerated hazards to wild sheep populations resulting from managed human harvests. Its secondary references to "sport harvesting" as "one of the most pervasive and potentially intrusive human activities that affect game mammal populations globally"², and the statement that "little attention has been paid to the potential evolutionary consequences, and hence the sustainability of harvest regimes"^{3,4} are incorrect and damagingly expansive. The letter reported larger-horned, larger-bodied rams sire more lambs than smaller individuals; and made much of the fact that human harvesters prefer the largest rams available. These findings are not new. Reproductive success was quantitatively linked to dominance three decades ago⁵. Modern "sport harvesting" management of wild mountain sheep has typically limited harvest to 3-10% of available rams for more than 40 years. In Alaska, the most prolific and harvest-friendly wild sheep jurisdiction in the world, harvest strategies have been specifically designed to foster social order among rams for almost 20 years⁶. Alternate rutting strategies among thinhorn sheep resulting from differing ram mortality levels were identified and factored into sheep harvest management in Alaska beginning in 1984^{7,8}. Coleman *et al.*'s failure to acknowledge these facts was compounded by sensationalized reporting of these non-revolutionary findings by the "NATURE Science Update" and the NATURE Publishing Group^{9,10}. Similar under-researched and over-sensationalized "scientific communications" are often used by animal rights groups and "anti-hunters" to orchestrate politically saleable, but biologically counter-productive 'corrections' in management programs through so called "citizen's initiatives" in the United States. These actions serve neither science, conservation, nor the managed species well in the longer run.

In 1971, Geist⁵ published quantitative behavioral studies linking reproductive privilege in mountain sheep rams to dominance. Many investigators considered this behavioral generality absolute and papers showing sub-dominant rams make significant genetic contributions have been well-noted. Using the same data as Coltman *et al.*¹ four of those co-authors reported subdominant rams have sired approximately 50% of the lambs on ram mountain over time¹¹. In that publication, our authors said,

These results suggest that young or small rams achieve mating success through alternative mating tactics that are less dependant on body and weapon size, such as coursing and blocking.¹¹

These findings do not appear to be congruent with the concern that "sport harvesting" management, as incorrectly represented by Coltman *et al.*¹ is a widespread cause of genetic deterioration in wild sheep. The earlier paper¹¹ interpreted the data as an adaptation to existing circumstances. We agree with that hypothesis.

Heimer⁷ discussed at least three alternate rutting strategies among wild sheep rams. These strategies function adaptively to set back behavioral selection for large horns, effectively increasing genetic diversity among wild sheep populations in times of population stress. The most complex, the “alpha ram,” strategy was identified by Hogg^{12,13}. When it is operative, ewes seek out unusually large dominant rams, while normal mature rams employ the more commonly observed coursing and blocking behaviors, attempting to sequester and mate with ewes as ewes seek the “alpha ram.” When “alpha rams” have been removed (either through “sport harvesting,” natural predation, or transplanting), the rutting strategy reverts to the more commonly understood “mature ram” or “normal” rutting strategy described in detail by Geist⁵. In cases where mature dominant rams were virtually absent, Heimer⁷ described the development of an “immature ram” strategy, demonstrated to lower lamb production compared with the other strategies. The “immature ram” strategy may result from causes other than “sport harvesting.” A current example is the scarcity of mature rams on some Alaska Dall sheep ranges resulting from consecutive-year recruitment failures associated with unfavorable weather events acting in concert with high lamb-predation (by coyotes as demonstrated in Alaska¹⁴). Significant winter wolf predation on adult sheep is also a contributing factor¹⁵.

Upon discovering the negative management consequences attending the “immature ram” strategy, managers in Alaska limited harvest to mature (Class IV) rams having complete full-curl horns, or a minimum age of 8 years, or with both horns broken by fighting⁸. Hence, the assertion that, “little attention has been paid to the potential evolutionary consequences, and hence the sustainability of harvest regimes” is demonstrably incorrect in the most sheep-rich and hunter-friendly jurisdiction in the world. The authors (and the *NATURE Publishing Group*'s) poorly researched indictment of “sport harvesting” and its management as unsustainable and having negative impacts on wild sheep genetics also betrays a distressing naivete with respect to the common management of bighorn ram harvests.

While regulations in some jurisdictions allow the harvest of “any ram” (designed to spare mature rams in harvested populations thus balancing ram age structures), the dominant practice is to limit harvests to biologically insignificant levels through the use of restricted entry permits. Even if every hunter were to succeed in taking a mature (or even a juvenile) ram, allowed harvests are predominantly limited to 3-10 percent of the available rams¹⁶. Only in exceptional circumstances, such as Ram Mountain, Alberta, is harvest allowed to exceed this level.

For decades, Ram Mountain has served as a “natural laboratory” and subjected to atypical population manipulations to test various hypotheses relating to mountain sheep management. Because of its isolation and unique population history, extension of Ram Mountain findings to the general case should be most judiciously applied. It wasn't in Coltman *et al.*¹ or the resulting popularized versions reported by *NATURE*^{8,9}.

First, it wasn't necessary to invoke genetic change to rationalize the observed decreases in horn and body size. These phenotypic effects are clearly explainable in non-genetic

terms (see earlier essays presented here). Additionally, the injudicious expansion of findings from Ram Mountain to wild sheep in general, not to mention diverse animal taxa, does conservation of mountain sheep a disservice.

The erroneous tarring of “sport harvesting” as harmful may lead to serious negative impacts on wild sheep conservation. In the United States of America (USA), management agency funds are generated through a self-imposed “sport harvester’s tax,” and conservation funding is dependant on the perceived social status of the conserved species. That is, conservation programs for highly valued species are well funded by the “owner/sport harvester/conservationists; unique to wildlife management in the USA. Primarily due to this novel public-trust ownership of wildlife and the accompanying tradition of use by a broad diversity of citizens through unrestricted licensing/participation, restoration of high-status species in the USA is a success unparalleled in human history¹⁷.

Surprisingly, wild sheep have not enjoyed historically high status with managing agencies so funding for wild sheep management has been traditionally minimal¹⁸. Hence, the managing agencies have not had great success in wild sheep restoration programs. Sheep “sport harvesters,” who place a high value on these species in spite of agency traditions, have seen to successes in restoration of wild sheep almost independently of public agency funding¹⁸.

These “sport harvesters” or “trophy hunters” operate primarily through the Foundation for North American Wild Sheep (FNAWS) by funding independent research and restoration projects as well as nascent agency programs. FNAWS has generated and spent funds approaching 30 million dollars over the last 27 year. Results have included a doubling of reported bighorn sheep numbers in North America¹⁹. Apparently unbeknownst to Coltman *et al.*¹, harvest from these restored populations is strictly regulated but nevertheless generates virtually all of the funding for wild sheep management and restoration in North America. Similar programs by other “trophy hunting” organizations such as the International Sheep Hunters Association (ISHA) support conservation of wild sheep worldwide.

In the USA, inaccurate or misleading indictment of sheep managers for alleged lack of concern regarding genetic (or overall population) health may have particularly deleterious effects. In the USA, many individual state constitutions allow citizens to enact legislation by popular vote without parliamentary discussion or amendment. This practice is becoming increasingly prevalent as animal rights groups seeking to outlaw, by emotional manipulation of the electorate, all animal uses they find philosophically objectionable. “Trophy hunting,” as negatively depicted by Coltman *et al.*¹, and the *NATURE Publishing Group* seems highly likely to become an attractive future issue for these interests.

The misapprehensions of Coltman *et al.*¹ regarding prevailing wild sheep management practices bespeak either inadequate scholarship or sympathy with a sociopolitical agenda that fosters a negative representation of “sport harvesters.” Alternately, in light of the

sensational, non-technical coverage afforded this letter, we suggest editors at *NATURE* may have used naïve authors to advance a similar sociopolitical agenda in the popular press. The authors' suggestions that harvests be limited to full-curl rams and their implication that harvests be kept sufficiently low to protect behavioral genetic selection would have been quite helpful and timely 25 years ago. Today they aren't.

While we applaud the innovative use of quantitative genetics in confirmation of field observations, such uses of these techniques should be clearly reported as such. We encourage the authors to read more widely in the management literature before aspiring to alter management.

¹Coltman, D. W. *et al.* Undesirable evolutionary consequences of trophy hunting. *Nature* **426**, 655-658 (2003)

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