

Seventh World Mountain Ungulate Conference, Bozeman, Montana

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On 10-13 September 2019, more than 150 of the world's leading ungulate biologists gathered in Bozeman, Montana, to participate in the 7th World Mountain Ungulate Conference, which was hosted by the Wild Sheep Foundation (WSF) and the Safari Club International Foundation. Scientists from ≥ 14 countries were in attendance, including some from as far away as central Asia. This was the first time this international conference has been held in North America and Kurt Alt, of WSF, largely was responsible for the organization and success of the meeting. Funds provided by WSF and the Safari Club International Foundation also were instrumental in supporting travel costs for many of the attendees. In addition, the Conference was endorsed by the International Union for the Conservation of Nature (IUCN) Caprinae Specialist Group and the IUCN Species Survival Commission.

Scientists actively working in California were involved, either directly or indirectly, in 7 of the presentations on the biology, ecology, or conservation of North American wild sheep. Topics ranged from the evolutionary history of Stone's sheep to the constraints that legislated wilderness has imposed on efforts to conserve mountain ungulates in the American southwest, and just about everything in between. Appearing below are abstracts of papers either presented by scientists working in California, or on subjects having their genesis there and to which scientists from California have contributed. I have listed the senior author of each paper, followed parenthetically by the name(s) of collaborator(s) from California, and the total number of additional coauthors, an approach was dictated by space limitations. Abstracts appear below in the relative order in which they were presented during the Conference.

Wehausen, J. D. (C. W. Epps + 1). Insights into the evolutionary history of North American wild sheep from analyses of skull shape and mitochondrial DNA sequence data.

We use results of analyses of cranial shape as a reflection of geographic patterns of nuclear DNA and compare those with analyses >5000 base pairs of DNA sequence data from 6 mitochondrial genes to elucidate important events in the evolution of North American wild sheep. Our results indicate that these sheep have a considerably more complex evolutionary history than previously thought, involving two colonizations of North America and a number of hybridization events between species and subspecies. These hybridization events result in a phenomenon known as cytonuclear genomic dissociation, where nuclear and mitochondrial DNA exhibit independent evolutionary histories. Bighorn sheep trace their ancestry to the first colonization of North America, with descendants from that colonization still present in the Brooks Range of Alaska and detectable via mitochondrial haplotypes. Dall's sheep stem from a second colonization with subsequent hybridization with the northern ancestors of bighorn sheep. Stone's sheep result from a northward colonization by Rocky Mountain bighorn, followed by hybridization with Dall's sheep.

Denryter, K. (T. R. Stephenson + 1). Plasticity in migratory behaviors of male bighorn sheep.

Migration is an evolutionary adaptation to seasonal environments that is functionally important to demography of populations. Among north-temperate ungulates, migratory behaviors of males are poorly understood compared to females. Our objectives were to better understand migratory flexibility of males and determine if there was an energetic underpinning for migration. We fit models of elevation migration to GPS locations of male Sierra Nevada bighorn sheep—a federally endangered subspecies—to categorize migratory behaviors (and created a continuous index of migration to quantify intermediate migratory behaviors) and assessed relations between body fat and migratory strategy. Migration was the predominant migratory strategy of male Sierra bighorn followed by residency. Within migrants, 12 made multiple round-trip movements between seasonal ranges, whereas 15 residents wintered high, but moved down in elevation for ≤ 30 days in late spring–early summer. Among 69 potential strategy-switching events (i.e., males tracked for ≥ 2 years), 7 switches occurred. Mean body fat levels of resident males in autumn and spring were slightly greater than those of migratory males in autumn. Our results indicate that migratory strategies of males were less flexible than females and energetics underpinned migration. Our continuous metric of migration has utility in analyses of survival and other management questions because it accommodates the spectrum of migratory behaviors exhibited by ungulates, rather than forcing individuals into a false dichotomy of migratory behaviors. Results from our work exemplify the importance of accounting for unique physiology and behavior of male ungulates in their conservation and management.

LaSharr, T. N. (V. C. Bleich + 14). Horn size of mountain sheep: are current harvest practices evolutionary sustainable?

The influence of human harvest on evolution of secondary sexual characteristics has implications for sustainable management of wildlife populations. The evolutionary consequences of selectively removing males with large horns or antlers from ungulate populations has been a topic of heightened concern in recent years. harvest can affect size of horn-like structures in two ways: 1) shifting age structure toward younger age classes, which can reduce the mean size of horn-like structures; or 2) selecting against genes that produce large, fast-growing males. We evaluated effects of age, climatic and forage conditions, and metrics of harvest on horn size of mountain sheep (*Ovis canadensis* ssp.) in 72 hunt areas across North America from 1981 to 2016. In 50% of hunt areas, changes in mean horn size during the study period were related to changes in age structure of harvested sheep. environmental conditions explained directional changes in horn growth in 28% of hunt areas, while revealing directional change in growth in 7% that did not exhibit change before accounting for environment. After accounting for age and environment, horn size of mountain sheep was either stable or increasing in the majority (~78%) of hunt areas. Age-specific horn size declined in 44% of hunt areas where harvest was regulated solely by morphological criteria, which supports the notion that harvest practices that are simultaneously selective and intensive may lead to evolutionary changes in horn size. nevertheless, evolutionary consequences are not a foregone conclusion in the face of selective harvest; over half of the hunt areas with highly selective and intensive harvest did not exhibit age-specific declines in horn size. Our results demonstrate that while harvest regimes are an important consideration, horn growth of harvested male mountain sheep

has remained largely stable, indicating that evolutionary changes are an unlikely consequence of harvest in most of North America.

Monteith, K. L. (T. R. Stephenson, V. C. Bleich + 3). Horn size and nutrition in mountain sheep: can ewe handle the truth?

Horns, antlers, and other horn-like structures are products of sexual selection, confer reproductive advantages, and are heritable and honest indicators of individual quality. In addition, horns and antlers garner societal interest that, when combined with the powerful motivation to acquire trophy animals, likely has spawned a growing hornographic culture fixated on males with exceptional horn-like structures. Intensive harvest of large, fast-growing males may have deleterious effects on the very trait being sought, which has led to considerable controversy in the popular and scientific literature over the past 2 decades. Mountain sheep, possibly the only large ungulate in North America managed almost exclusively as trophy species, embody this controversy because of the emphasis on managing for large males. That controversy has led to polarizing views among scientists and stakeholders as to how mountain sheep should be managed. Our goal was to discuss the relative contributions of the key ecological and intrinsic factors that influence horn growth, how those factors might interact with harvest strategies, and identify what determinants of horn size are most amenable to management and most effective in achieving desired outcomes. Given the hyperbole surrounding trophy management and big horns, we suggest the importance of females in the management of bighorn sheep has been largely forgotten. Females play a critically important role, not just as the reproductive segment of the population responsible for producing young, but because maternal condition can produce life-long effects of on size and growth of males (via maternal effects); and additionally abundance of females, in turn, affects nutritional limitation within populations through density-dependent feedbacks. Ultimately, we call for greater recognition of the pervasive role of the ewe—and other female ungulates—in the production of large males and in contributions to population performance; and accordingly, that they be better integrated into harvest and management programs.

Stephenson, T. R. (D. R. German + 7). Linking population performance to nutritional condition in bighorn sheep.

Bighorn sheep can live in extremely harsh environments and subsist on submaintenance diets for much of the year. Under these conditions, energy stored as body fat serves as an essential reserve for supplementing dietary intake to meet metabolic demands of survival and reproduction. We developed equations to predict ingesta-free body fat in bighorn sheep using ultrasonography and condition scores in vivo and carcass measurements post-mortem. We then used in vivo equations to investigate the relationships between body fat, pregnancy, over-winter survival, and population growth in free-ranging bighorn sheep in California and Nevada. Among 11 subpopulations that included alpine winter residents and migrants, mean ingesta-free body fat of lactating adult females during autumn varied between 8.8 and 15.0%; mean body fat for non-lactating adult females during autumn ranged from 16.4 to 20.9%. In adult females, ingesta-free body fat >7.7% during January (early in second trimester) corresponded with a >90% probability of pregnancy and ingesta-free body fat > 13.5% during autumn predicted a probability of overwinter survival >90%. Mean ingesta-free body fat of lactating females in autumn predicted

the rate of population increase over the subsequent year in bighorn subpopulations that wintered in alpine landscapes. Bighorn sheep with ingesta-free body fat levels of 26% and living in alpine environments possess energy reserves sufficient to survive at resting metabolic rate for 83 days on fat reserves alone. We demonstrated that nutritional condition can be a significant mechanism driving demography in bighorn sheep and characterizes the nutritional value of their occupied ranges. Mountain seep are capital survivors in addition to being capital breeders, and because they inhabit landscapes with extreme seasonal forage scarcity they are fat reserve obligates. Quantifying nutritional condition is essential for understanding the quality of habitats, how it drives demography, and the proximity of a population to carrying capacity.

Rominger, E. M. (J. D. Wehausen + 6). Puma as a predator of mountain ungulates in North America.

Following the extirpation of wolves in the western United States in the early 1900s, the formerly subordinate puma became the dominant predator of adult mountain ungulates in many ecosystems south of resident wolves. In the absence of wolves, the realized niche of puma has expanded and puma are documented to be a primary predator of North American mountain ungulates including bighorn sheep, mountain goats, woodland caribou, mule deer, and elk. Puma caused annual mortality rates in excess of 0.25 have been reported for all these species. The ecological shift of the apex predator guild from a coursing canid predator to a stalking felid predator has caused the decline of some mountain ungulate populations and contributed to listing as endangered species for Selkirk woodland caribou, Sierra Nevada bighorn sheep, peninsular bighorn sheep, and New Mexico desert bighorn sheep. The role of apparent competition has been documented for all of these endangered populations whereby the ability of puma to prey-switch from more numerous sympatric ungulates, primarily deer and/or domestic cattle contributes to declining populations of the rarer mountain ungulate. It is hypothesized that some North American mountain ungulates have fallen into an ecological trap following the expansion of the realized ecological niche of pumas. The current facilitation of wolf recovery in many western states may have profound effects on the persistence of puma as a dominant predator in North American mountain ungulate communities.

Bleich, V. C. Mountain ungulates, conservation challenges, and American wilderness legislation.

Wilderness management objectives and wildlife conservation objectives often conflict with each other, despite conservation being one of six basic reasons for which wilderness is established. Many wilderness areas established by the United States Congress appear to have been the result of political or societal desires, but were designated in the absence of critical ecological thought, a problem that appears to be on an upward trend. In an era of increasing anthropogenic impacts to wildlife populations and to wildlife habitat outside of legislated wilderness, those ostensibly "pristine" areas in and of themselves will become less and less effective as conservation tools, particularly for large vagile mammals, among which are the three species of mountain ungulates native to North America. Impacts occurring outside of wilderness areas have ramifications for wide-ranging animals that use those areas during portions of their annual cycles, thereby affecting wilderness character. Similarly, impacts occurring inside of designated wilderness also have ramifications for large, vagile mammals that also utilize lands

proximal to those 'pristine' lands. There is a need to re-ignite the debate over the value of wilderness as a wildlife conservation strategy, as well as in the context of its societal role. It is essential that wildlife populations and wildlife conservation objectives be elevated to the same level of value that is accorded solitude and other less tangible or subjective attributes of wilderness.

Dr. Vern Bleich worked for the California Department of Fish and Game for 35 years. He has relocated to North Dakota, but remains active in research and conservation of bighorn sheep and other large mammals occupying the arid lands of the southwestern United States. Vern can be contacted at vcbleich@gmail.com.