WAYNE HEIMER - A WORKING HYPOTHESIS FOR THINHORN SHEEP MANAGEMENT

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Abstract: Thinhorn sheep come in two colors. The white, or Dall sheep (*Ovis dalli dalli*) inhabit more northern, predominantly alpine ecosystems. The colored Stone's sheep (*Ovis dalli stonei*) distributions are more southerly, and while typically alpine, often include forested ecosystems. Modern, management-relevant research on Stone's sheep has been limited to behavioral study while a fairly extensive body of data is available for the varied management-relevant aspects of Dall sheep biology. Hence, a generalized working hypothesis for thinhorn sheep management must presently rely on presumably common biology applied from the more intensively studied, Dall sheep. Both *dalli* subspecies are similar to the thinhorn Asiatic snow sheep (*Ovis nivicola*) in body and horn size/conformation. Both North American forms have 54 chromosomes, and presumably common ontogeny. Even though Dall lambs are born gray, soon to turn white, mid-term fetuses exhibit pelage coloration and markings similar to adult pigmented sheep.

Distribution, abundance, and population strategies: Distribution of both *dalli* subspecies is determined by geologic factors (most directly influenced by glacial retreat) driven by macro-geography which subsequently defines local climate. In concert with weather, geography determines distribution and abundance by producing habitats of varying size and suitability for both subspecies. Habitat stability in turn defines seasonal home ranges and apparent fidelity to these ranges. Home range size in Dall sheep is a function of habitat structure which determines quality of essential habitat components such as forage and escape terrain. Better habitats correlate with smaller home ranges that support higher population densities where high range fidelity dominates distribution. Because of these relationships and adaptations to stable climax habitats, thinhorn sheep appear at the more extremely k-selected end of the ungulate population strategy spectrum. Twinning is unknown, and population growth appears dominated by environmental resistance from weather and predation influences. Density-dependent nutritional limitations have never been demonstrated for thinhorn sheep, probably because winter food quality is so low that every thinhorn sheep population may be considered "at or above nutritional carrying capacity" each winter regardless of population size.

Predation and harvest management: Predation, by both human and other carnivorous predators, is the most important management-relevant component of environmental resistance, if for no other reason than it is the most management-alterable influence on thinhorn sheep population growth and size. Detailed description of canid predation effects on thinhorn sheep population dynamics is lacking, and opinion on its importance is divided. However, experience managing harvest by humans has shown mature rams constitute the only clear harvestable surplus from thinhorn populations in intact ecosystems. Ewe harvests by human hunters are generally considered additive to other mortality factors. In contrast with thinhorn management, ewe harvests are commonly applied to bighorn populations to check population growth or reduce population size where predators are a lesser factor. Consistent with the behavioral data from Stone's and bighorn sheep, Dall ram harvests resulting in the virtual absence of socially dominant mature rams have been causatively associated with lowered ovulation rate, rare successful consecutive-year lamb production, frequent alternate-year breeding by ewes, and compromised juvenile ram survival. If population maintenance or growth is a management goal for thinhorn sheep, harvest by humans should be limited to mature rams.

Disease: Throughout their distribution, thinhorn sheep are presently free of exotic diseases carried by domestic livestock. Consequently, disease-related mortality is not a significant factor in their management. However, preliminary *in vitro* macrophage toxicity studies suggest thinhorns may be more susceptible to *Pasteurella* cytotoxins than bighorns. Penning of healthy domestic sheep with Dall sheep resulted in *Pasteurella* pneumonia among the Dalls. All necessary steps to prevent introduction of exotic diseases, particularly those associated with domestic sheep should be taken. Legislative action excluding domestic sheep from Dall sheep ranges holds the greatest promise.

Parasites: Parasites of Dall sheep have been cataloged, and are of academic interest. Presently, parasites are not considered alterable factors in thinhorn management.

Disturbance: Although both Dall and Stone's sheep appear, in specific instances, to have survived notable local disturbances (probably because of their seasonal range loyalty and ability to habituate), common sense dictates managers should mitigate disturbance to thinhorn sheep to the maximum extent.

Data for the above synoptic statements will be introduced and discussed. Adherence to the established and rationally deduced biology of thinhorn sheep, educating the publics involved with thinhorn sheep, and empowering those publics to participate in thinhorn sheep policy development and management are identified as the basis of successful thinhorn management.

Development of a synoptic working hypothesis for thinhorn sheep is a challenging task because of the disparity of research emphasis the *dalli* subspecies have received. In his early behavioral work, Geist (1971) focused heavily on Stone's sheep. Unfortunately, subsequent specific studies of Stone's sheep autecology have been scarce. In contrast, work on Dall sheep has focused on varying, and more directly management-applicable aspects of their biology. As a result, I shall proceed under the assumption that while there may be differences (primarily related to habitat), the subspecies are sufficiently similar that producing a generalized working management hypothesis for thinhorn sheep will produce a net management benefit.

Before beginning, I should briefly review several relevant considerations of the working hypothesis concept I first articulated (Heimer 1988). Consistent with the definition of a working management hypothesis, this one will be a synthesis of all the information which can be brought to bear on thinhorn sheep management. Hence, it will include refereed, "white" literature, less formally reviewed "gray" literature, unpublished data, local knowledge, and personal observations of those inti-

mately familiar with thinhorn sheep. These data will be interpreted within the context of traditional ungulate management theory as tempered by application of evolutionary principles of specific adaptation to environment.

Readers should be aware that my bias lies toward setting aside the generalities of conventional ungulate management when they cannot be rationalized with successful adaptations or specific data at hand. I hold this view because my experience indicates a higher probability of management success attends basing decisions on data which reveal thinhorn autecology rationalized by the evolutionary adaptation model. I prefer this to applying generalized ungulate models derived primarily from successionally-adapted cervids inhabiting lower latitude, temperate ecosystems where non-human predators are virtually absent. Virtually all thinhorn sheep populations exist in what I call intact ecosystems, where predators exist at natural or augmented densities.

Synthesis of a working management hypothesis under these conditions requires a manager's (with due respect to our gambling-state meeting venue)

"knowing what to throw away, and knowing what to keep." For this reason, I suggest formulation of working management hypotheses will be most productively deferred to biologists with extensive practical research and management experience.

This said, it should be emphasized that the working management hypothesis should not be considered a definitive statement of the natural history of Dall or Stone's sheep. Instead, it is intended to be a framework to guide policy makers, planners, and managers within the "envelope" of thinhorn sheep biology and adaptation. The working hypothesis should be continually subject to testing and modification as new knowledge emerges. It is unlikely the hypothesis will ever be validated as "objective truth," but if continually tested and refined, it should increase the probability of successful management.

STRUCTURAL COMPONENTS OF A THINHORN SHEEP WORKING MANAGEMENT HYPOTHESIS:

Successful management results from maintenance or enhancement of thinhorn sheep populations in their existing pristine habitats. Production of human benefits from these managed populations has been the traditional "common currency" of North American wildlife management, and sustained or enhanced benefits will be the cumulative result of management decisions which positively affect population size, growth rate, trend, and human uses of thinhorn sheep.

Because protection of thinhorn habitats is basic to management success, I shall begin with a discussion of the effects of habitat macrostructure on distribution and abundance, and link them to the suite of adaptations to environment which have made thinhorn sheep successful to date. Once this physio-geographic framework for understanding thinhorn biology and adaptation has been presented, I shall discuss more management-alterable components of thinhorn autecology. These will include management of human harvest and predation, disease prevention, and human disturbance management.

Habitat, distribution, abundance, and population strategy: At the outset, it should be noted, that interpretation and synthesis of observations which contribute to this rationalization of thinhorn biology hang less upon data gathered in controlled experiments than on thoughtful *post hoc* rationalizations for "the way things are." This is necessary because gathering objective experimental data to test hypotheses explaining what happened in geologic time and sheep evolution is impossible. The best we can do is to infer from the biological and geologic records and principles of natural selection, "why" things are the way they are. Our implicit assumption in this approach is that the inferred adaptations, which have obviously served sheep well throughout time, are still management-relevant. As stated above, my experience suggests greater management success will result from this approach coupled with specific management-relevant research than applying generalized ungulate models. Certainly sheep are ungulates, but their particular adaptations set them apart from classic "ungulate biology."

It is biologically axiomatic that animal adaptations are responses to environmental factors. This cause-and-effect relationship is particularly apparent among thinhorn sheep, which are outstanding examples of adaptation to their northern environments. The major components of thinhorn sheep biology, ranging from geographic distribution through physiological and behavioral adaptations, are readily rationalized as adaptations to stable, high latitude alpine environments. These postglacial habitats and their impacts on selection for specific adaptations were first specifically related to mountain sheep (Geist 1971), and have been conceptually expanded by Geist (1975, 1978).

Along with the glaciated mountainous country they inhabit, climate is an obvious environmental factor driving adaptation in thinhorn sheep. Climate is, of course, a function of geography, and by interpreting thinhorn biology through geography and its effects on terrain, weather, and plant communities, the most basic clues to understanding the "why questions" of thinhorn biology begin to emerge.

Thinhorn sheep distribution and abundance result from the interaction of habitat suitability and environmental resistance. While these terms are certainly linked, I suggest it is profitable to consider them separately.

Throughout their distribution, thinhorn sheep are limited to areas of relatively light snowfall. As a general rule, mean annual snowfalls exceeding 70 inches (178cm) preclude Dall sheep survival (Heimer and Smith, 1975). Simply put, thinhorn sheep don't live where normal snow accumulation is deeper than the length of their legs (Heimer in Toweill and Geist 1999). This limits their distribution to areas of continental or mitigated marine climate. Winter nutritional constraints and predation appear to render thinhorn population density under pristine conditions a moot point as data from Dall sheep demonstrate.

Although mean snow depth, through limitation of sheep movement and food availability, is clearly the deciding factor between suitable and unsuitable habitats, other climatic factors influence Dall sheep abundance and home range size within their distribution (Heimer et al. 1994). Within areas of generally tolerable mean snowfall, some habitats are prime, while others are barely habitable (Heimer 1995a).

These differences result from macro-habitat structure and the effect local topography has on prevailing weather. During winter, the major food source for Dall sheep is dried, frozen forage made available by winds which remove snow from standing grasses and sedges. Nevertheless, Dall sheep have varied diets throughout their distribution (compare Hoefs 1979 with Heimer 1983). These winter forages are uniformly low in available nutrients throughout Dall sheep distribution, and weight losses approaching 10% over winter are typical of Dall sheep (Nichols 1972, Heimer 1983). In the 1983 comparative study, there was no measurable difference in sheep body composition (percent fat, bone, protein, and water in ewe carcasses) or winter food quality between a high-density population with poor lamb production and low individual growth performance and a low-density population

with outstanding lamb production and high individual growth performance. Subsequently, I argued (Heimer 1992) individual Dall sheep welfare should be considered independent of Dall sheep population density because low winter food quality is such a severe nutritional bottleneck that the number of sheep competing for this low quality forage is typically irrelevant. Hence, differences in population quality and performance are unlikely to be functions of density-dependent nutritional constraints (Heimer 1980a, Heimer and Watson 1986a).

Prime thinhorn habitats not only have limited snowfall, but consistent cold, dry winter winds which remove snow from the surplus of low-quality forage. For Dall sheep, better habitats are typically found on the "precipitation shadowed" sides of relatively narrow mountain ranges which lie across the paths traced by ocean-generated winter storms as they move inland. The best of prime habitats are found on the "lee sides" of these mountain ranges adjacent to low passes identified as wind channels (F. Mauer, USFWS sheep specialist, pers. commun.), which accelerate surface winds and consistently remove snow from Dall sheep winter forage. The better habitats also consist of relatively long straight drainages which allow density-driven (catabatic) winds to consistently remove accumulated dry snow from ridges along the major drainages in the absence of major frontal movements (Heimer et al. 1994). Prime habitats contain extensive climax vegetative communities of suitable plants which are consistently available to Dall sheep for winter nutritional sustenance. In prime habitats, Dall sheep home ranges are small and predictable (Heimer et al. 1994). In contrast, where habitats are not "prime," Dall sheep have adapted by having larger and hence less predictable home ranges (Heimer et al. 1994). The validity of applying these inferences from geography and weather to distribution and abundance of Stone's sheep is uncertain.

In spite of variations in home range size resulting from habitat "primeness," thinhorn sheep demonstrate characteristics most biologists (inferred from the *post hoc* rationalizations discussed above)

consider adaptations to stable habitats with a relatively high cumulative environmental resistance. These characteristics differentiate mountain sheep from other North American ungulates, and successful sheep management requires an elevated appreciation of these adaptations as management-relevant constraints. The classic assumptions upon which successful deer management rests are questionably relevant to sheep management in general (Heimer 1992, 1998) and highly suspect in thinhorn sheep management, which is invariably practiced in intact ecosystems where predators are often a major component of environmental resistance (Heimer 1996).

Thinhorn adaptations to a consistent winter nutritional bottleneck based on climax plant communities include low ewe fecundity. Twinning is unknown, and delayed breeding by first-estrous ewes mediated through a rigid social hierarchy among rams is a fact of life in minimally disturbed populations (predicted by Geist 1971, inferred by Nichols 1978, and confirmed by Heimer and Watson 1986a, 1986b,1990).

The most striking difference between "deer" and "sheep" management is based on differences in the adaptive biology of both groups. While the deer family is adapted to seral plant communities, and thrives as vegetative succession following disturbance of climax plant communities follows its natural course, Dall sheep adaptations are to a stable food source (the climax plant community). Seral-adapted species (such as the deer family) show nutrition-mediated high frequencies of multiple birth and early breeding by females when early successional stages produce nutritional abundance. In contrast, Dall sheep never produce multiple births, and early breeding has been linked directly to the absence of mature rams--not nutritional abundance.

Here, it should be noted that thinhorn responses to their seasonally pulsed nutrition/growth cycle differ from the contemporary Alaskan interpretation of summer drought effects on caribou cow nutrition and fecundity (Valkenburg 1997). Sexual maturity among yearling caribou and ovulation by mature cows appear exquisitely susceptible to nutritional constraints. Only on unusually high planes of nutrition do female caribou yearlings ovulate, breed, and conceive. Similarly, caribou cows appear at risk of reaching sufficient body mass to successfully reproduce if summer nutrition is compromised. In contrast, all 18-month old Dall ewes appear to ovulate. The sample size of 18-month old Dall sheep ovaries actually examined approached 50, but has no variance. The documented number of Dall ewes which have delivered lambs at 24 months runs into the hundreds. It contains yearlings covering the nutritional spectrum from those fed high quality food, *ad libitum*, in zoos (Heimer and Watson 1986a), through less luxurious diets in game farms (Hoefs 1979), descending the nutritional quality ladder to high-density populations showing low lamb production ratios and low individual growth (yet where documented lamb production by two-year old ewes averaged 25 percent over an eight-year period). The Dall yearling ewe sample also included individuals from low-density populations where, even though lamb production ratios were high and individual growth was outstanding, lamb production by two- year old ewes which would have bread as yearlings (at 18 months) was virtually absent (Heimer and Watson 1986a and Heimer and Watson-Keller, unpublished data). Additionally, Egorov (1967 cited in Hoefs 1979) reported yearling snow sheep ewes in Yakutia. are capable of breeding.

Since all yearling Dall ewes apparently ovulate, it would appear that low body weight due to poor summer nutrition is not as robust an explanation for variations in lamb production in Dall sheep as for calf production in cervid species. Thinhorn sheep may simply be more highly adapted to climax habitats than caribou.

An additional adaptation imputed by Geist (1975) and Toweill and Geist (1999) is learning ability inferred from brain size and behavior among mountain sheep. Learning ability appears to be expressed in high fidelity to seasonal ranges.

These adaptations, coupled with the longevity and

documented age-specific mortality patterns of among Dall ewes (Heimer and Watson-Keller unpublished data) may render interpretation of population size fluctuations in thinhorn sheep problematic for managers (Watson and Heimer 1984). Gathering data on internal population dynamics (Heimer 1994) holds potential for alleviating this problem.

Planners often push sheep managers to identify the critical thinhorn habitats considered most necessary to survival and welfare. Just as seasonal home ranges vary with geography-driven habitat stability, differing populations of thinhorn sheep are likely to show variability in apparent critical seasonal ranges. Some may rut, lamb, use mineral licks, and rear young within a small geographic radius while others travel significant distances between separate regions supporting these activities. For thinhorn sheep to survive as viable populations capable of providing human benefits, all components of their habitats must remain suitable for sheep uses.

Summary: Because of their adaptations to seasonally pulsed nutrition, particularly the winter food quality bottleneck, managers should not anticipate major increases in reproduction or individual growth to attend lowered population densities among thinhorn sheep. There is no doubt thinhorn sheep will do better if fed better. Similarly there is every reason to believe thinhorn sheep are biologically capable of the "compound interest effect" demonstrated for bighorn sheep by Wishart et al. (1998, and bighorn working hypothesis this conference). An instance where unusually low environmental resistance due to favorable weather and low predation has resulted in explosive thinhorn population growth resulting in classic density-dependent nutritional constraints has yet to be documented using modern methods. If it is to be seen among thinhorns in intact, pristine ecosystems Wishart's "compounding effect" will have to result from lowered mortality rather than increased reproduction.

Human harvest management and predation: If thinhorn sheep exist in intact, pristine ecosystems

and the adaptations discussed above limit potential for managers to increase populations through conventional habitat augmentations or growth rates through population density reductions, the remaining possibility for management success must lie in limiting mortality. Thinhorn sheep mortality sources can be divided into human-caused mortality (primarily hunting) and predation by other animals such as wolves, coyotes, bears, and eagles. The majority of management effort has gone to control human-induced mortality.

Human harvest management: A brief review of wild sheep history in North America indicates that after the decline of North American mountain sheep which accompanied the settlement of the American west (Buechner 1960), enlightened approaches to management of wild mountain sheep (typically the total protection from hunting attending the emergence of modern wildlife management) eventually brought many populations back to huntable numbers (Trefethen 1975, Hoefs 1985). Contributing to this recovery was coincidence (from 1930 to the mid-1960s) with the all-time North American low in wolf, coyote, cougar, grizzly bear, and golden eagle abundance. That is, environmental resistance to population growth was suppressed more than at any other time in American history.

As sheep populations returned to viability, managers sought a balance between protection and use. This meant allowing for harvest, either by hunting or transplant, within the limits of biological safety and herd growth. The need to assure continued herd recovery and health was easily understood. Likewise, appreciation of benefits attending maximal hunter use (license and tag fee revenues, and development of guiding and outfitting industries) was growing.

Demarchi's (1978) review of hunting regulations across North America shows the most common attempt to balance herd growth with maximized hunter use was limitation of harvest to surplus males (rams). Historically rams which could be harvested without compromising lamb production were defined as surplus. The intuitive conclusion

of most managers was that harvesting rams at the youngest acceptable age (before natural mortality removed them from the shootable population) would produce the maximum sustainable harvest. The youngest acceptable age was defined as the age at 3/4 curl horn development. Defining legally harvestable rams by degree of horn curl made sense because ram horns grow throughout life and generally describe a full circle (full curl) at maturity. This attempt to limit harvest to mature rams appears to have been designed either to protect younger rams from harvest, or assure larger horns on harvested rams. Its rationale has apparently been lost in history. Interestingly, the 3/4 curl rule (established in 1930) was a data-free assumption which antedated the first sheep mortality study (Murie 1944) by 14 years. Nevertheless, it dominated sheep harvest management for almost half a century.

Among thinhorns, rams have been shown to reach 3/4 curl horn size (Geist's Class III, 1968) at the approximate age of 5.5 years (Heimer and Smith 1975), well after they develop the capacity to sire offspring, usually at 18 months of age (Nichols 1978). In the absence of mature rams, juvenile rams participate actively in breeding activities (Nichols 1978, Heimer and Watson 1986a). Consequently, even total harvest of all rams down to 3/4 curl or 5.5 years of age does not preclude lamb production. For this reason the harmful effects of Dall ram overharvest were overlooked until the late 1980s.

As increasing hunter interest during the late 1960s and 1970s drove Dall ram harvest pressure upward in Alaska, accessible populations were harvested to the legal 3/4 curl limit (Heimer 1980b). That is, virtually every legal 3/4 curl ram in these populations was harvested each year. Subsequent field research where marked ewe reproductive success was monitored over the course of about 20 years revealed consecutive-year reproduction was rare in these populations (Heimer 1978). A high percentage of ewes (almost 25 percent) bred at 18 months of age, ewes maintained lambs on milk throughout winter rather than weaning in October, and ovulation rate was low. The cumulative effect was an

alternate-year reproductive success syndrome (Heimer and Watson 1990). Nutritional and body composition studies (Heimer 1983) showed no difference between populations exhibiting the alternate-year syndrome and comparable populations where consecutive-year reproductive success was high (but yearling ewe breeding was virtually absent (Heimer and Watson 1986a). The obvious difference between these radically different populations was mature ram presence, which was linked with overall higher ram abundance. Subsequent adjustment of harvest regimes from a lower legal limit of 3/4 curl upward to 7/8 curl eliminated the alternate-year reproductive syndrome among ewes (Heimer and Watson 1990), but did not result in the anticipated increase in ram harvests.

Subsequent analysis of marked sublegal ram survivorship from the poor quality population indicated harvests were compromised because physically and socially immature rams were paying the mortality cost of dominance beginning at age three instead of at social and physical maturity at age eight (Heimer and Watson 1986b). That is, mortality rates among marked sublegal rams equaled those calculated by Deevey (1947) from Murie's (1944) age distribution at death. The difference was that, in the absence of dominant rams, the accelerated mortality portion of Deevey's survivorship curve began at age three instead of age eight. These findings were consistent with predictions from Geist (1971 and pers. commun.). Increasing the legal horn size minimum from 7/8 to full curl resulted in highly significant (mean 35 percent increase, $p < 0.001$) increases in realized harvests from this population (Heimer and Watson 1990).

With the exception of the divided Northwest Territories, thinhorn sheep are now harvested at legal minimums defined as full-curl throughout their distribution. The extent of actual horn development differs between Alaska and the Canadian jurisdictions (Heimer 1990, Barichello and Carey 1990, Case 1990, A. Veitch pers commun.), but intent is to restrict non-subsistence hunting to mature rams.

Summary: Mature rams are the only clearly surplus animals in thinhorn populations. Harvest by humans should be limited to fully mature rams if population maintenance and maximized human benefit are management goals.

Subsistence hunting of thinhorn sheep is a relatively recent recurrence (Heimer 1998). Man has "always" used thinhorn sheep for food as necessity demanded or opportunity occurred. Most accounts emphasize that sheep were considered a specialty food item or "back up" for use when other resources, e.g. caribou, failed (Campbell 1974). Economy of effort dominated these human enterprises, so the most available sheep were harvested. Hence, it is presumed the historic harvest focused on the more abundant and approachable ewes. This presumption has been validated as contemporary subsistence harvest data show a selection for ewes (Heimer 1998). Historically, human use of sheep for food was practiced sparingly by small populations of humans using primitive technology, and was probably not a significant factor in overall thinhorn population dynamics.

Due to its formal recognition, increased subsistence user populations, and advances in harvest technologies, subsistence hunting is now practiced by a greatly increased human population using advanced technologies. As such, this use poses the real possibility of local population extirpation, with some extirpations being matters of recent historical record (see Heimer 1998 for a review). Most thinhorn subsistence harvests are only loosely monitored, and provide large bag limits which may be taken during extended seasons (Heimer 1998). These factors have made management of subsistence thinhorn harvests an issue of some concern among managers. The concern results from disagreement on whether there is a harvestable surplus of ewes from thinhorn sheep populations.

One school of thought argues that Dall sheep are ungulates, and must therefore be subject to general principles of ungulate management. These principles are dominated by the assumption that ungulate populations grow until limited by their density at carrying capacity (Heimer 1992). Simply put, this assumption predicts that populations below carrying capacity will grow (by producing "surplus individuals") until they become sufficiently dense that productivity declines due to nutritional limitations. When this happens, recruitment declines, the population ceases to grow, may decline somewhat, and then appear stable in numbers (Caughley 1970). In populations at carrying capacity, theory predicts reducing the population will result in increased population growth rate (by producing "surplus individuals" resulting from increased reproduction). By extension, this construct predicts any reduction of static populations (assumed to be at density-limited carrying capacity) will result in a compensatory increase in productivity (and recruitment) as the population strives to, again, reach carrying capacity. This is the dominant theory in ungulate biology, and it is taught as the guiding principle of wildlife management.

In contrast, the other school argues the adaptations of thinhorn sheep to high-latitude, climax ecosystems where predation by wolves, coyotes, and other predators is unchecked, limit the biological surplus from thinhorn populations to mature rams. This argument hangs heavily on the "winter nutritional bottleneck" argument presented above.

Summary: Biology aside, the political realities of modern times force recognition of and provision for subsistence harvest of thinhorn sheep. This area of thinhorn management will obviously require more management effort in the future. In jurisdictions where subsistence harvests can be regulated, regulations protecting ewes may be required for the long term benefit of sheep populations and the users who depend on them. Where the opportunity to harvest any sheep from an intact ecosystem is not negotiable, education of subsistence hunters so they harvest mature surplus rams must take priority (Heimer 1998).

Predation management: Management of non-human predators to benefit wild sheep has been sparingly practiced, if not completely absent, in modern times. This was not always the case. Prior

to the 1960s, predator reduction was considered good management policy by federal governments, and resulted in extirpation of many predators from bighorn sheep habitats in the Western United States. These extirpations resulted primarily from economic pressure by domestic livestock producers; wild sheep were never a significant consideration. Modern predator reductions have been primarily driven by moose and caribou scarcity.

On thinhorn ranges, the wolf has long been considered the chief predator, and several long-term fairly large-scale wolf control programs to benefit thinhorns have been undertaken by private citizens, guides, and outfitters. These efforts were funded by individuals with interests in sheep abundance. Although records were kept of when and how many wolves were removed, and the subsequent high sheep population densities were, in specific cases, studied and maintained for decades, most modern biologists discount these results as "anecdotal." These biologists maintain that no sheep-related benefits resulted from these predator mediated reductions in environmental resistance.

To be persuaded that predator reductions actually benefit prey populations, today's practicing biologists generally demand quantitative assessments of predator and prey population sizes prior to predator reduction. Additionally, standards of rigor and demands for data (e.g., specific locations of predator removal, effects on measured predation rate, and the numeric and functional responses of prey populations) are rising. Unfortunately, data of this quality are prohibitively expensive and virtually impossible to collect where potentially dominant variables (like weather and alternate prey cycles) cannot be controlled. Perhaps more unfortunately, retrospective inference drawn from historical accounts is discouraged as unscientific.

Given these increasingly rigorous standards it isn't surprising that conclusively compelling reports demonstrating benefits associated with reduced thinhorn predation are lacking. Even intensive studies of moose and caribou which are lavishly funded often fall short of the level of assurance demanded by many modern managers in order to

predict a general response (Nat. Res. Counc. 1997). Consequently, the issue whether or not predator reductions can be expected to have a predictable positive result on prey population growth remains controversial; and seems dominated more by philosophical positions and standards of academic rigor than whether greater human benefits have been associated with longer-term reductions in environmental resistance resulting from predation. The issue has become one of management appropriateness as much as functional response.

Compounding the problem for thinhorn sheep is the fact that data on thinhorn population responses to predation have most often been gathered as "add ons" to studies where stated research objectives focused on higher profile prey. Hence, the actual yield of thinhorn-specific predator/prey research has been small and its interpretation remains greatly influenced by personal point of view.

This means formulating a working management hypothesis for thinhorn sheep with respect to predator management becomes a matter of judgment and balance. The choice turns on whether one limits the data base to the few inferential conclusions from quantitative studies relating wolves to thinhorn sheep or takes a more inclusive view of the subject.

Several published studies of which I am aware indicate no measurable benefit accrued to Dall sheep from wolf control. These include Gasaway et al. (1983). These authors concluded wolf control (implemented to benefit caribou and moose) did not benefit sheep in the area because yearlings:100 ewes ratios for sheep which should have benefited from wolf control were no different than in a nearby national park where no wolf control was practiced. However, recent neonate lamb mortality studies in the formerly wolf-controlled area (which now has wolf populations estimated equivalent to or higher than before the 1976 wolf control program began) showed wolves seldom preyed on Dall lambs throughout their first year (Scotten 1997). Hence, the early conclusion by Gasaway et

al. (based on the assumption that wolf predation would focus on newborn lambs just as it does on caribou and moose calves) appears to have been in error. Wolf predation on sheep focus on adults (Murie 1944), and by my inference.

Additionally, Barichello and Carey (1988) presented an abstract which reported no changes in Dall sheep populations attributable to an 80 percent reduction in wolf numbers within an 11,200 sq km area containing a Dall sheep population. This population was monitored 1980-1986, and compared with another Dall sheep population where a controlled wolf reduction had not occurred. Both populations showed variability in lamb production, recruitment, and age structure; but no changes the authors could ascribe to decreased wolf predation on the sheep population within the wolf control area. In a creative attempt to control variables in this study, the wolf control and the "experimental control" area (where wolves were not reduced) were given the opposite treatments after the controlled population of wolves had recovered (Hayes et al. in press). In a recent telephone interview, R. Hayes (Yukon Territory wolf specialist, pers. commun.) told me that caribou and moose populations in both areas of wolf reduction responded with significant increases in calf survival and strikingly significant increases in population size. In contrast, there was no notable increase in Dall sheep production, recruitment, or overall population size. Only a slight (but statistically insignificant) increase in full curl ram numbers was noted over five years of study. Hayes suggested that variability in lamb production and survival (which did not appear to correlate with wolf population density) "swamped" (my term) any population changes which might have occurred in the Dall sheep populations as results of wolf population reduction.

(Author's late note: During the June 2000 meeting of the Northern Wild Sheep and Goat Council in Whitehorse, Yukon, I had the opportunity to interview R. Hayes (Yukon Territory wolf specialist) about final impacts of the wolf control program on Dall sheep. In discussion of the overall impact, Hayes reiterated no statistically signifi-

cant changes in lamb: 100 ewes or yearling:100 ewes ratios had been seen. However, he stated the investigators had always suspected their wolf-project sheep count area used to measure the effects of wolf control on sheep was too small. When they finally secured funding to census the entire area affected by wolf control (after the project had ended), they found the number of adult Dall sheep had increased by 35 percent when compared with the pre-wolf control total count. This finding supports the conclusion that wolf predation focuses on adults, and that assessment of lamb or yearling ratios is an inadequate methodology for assessing wolf control impacts on Dall sheep populations. The finding was too late to include in the monograph reporting on the Yukon project. It had already been accepted for publication.)

On the other side of this argument, Heimer and Stephenson (1982) presented wolf density, wolf population reduction percentage, and sheep population size data which indicated the 1976 Alaska wolf reduction program (Gasaway et al. 1983) was associated with an immediate reversal of a declining trend in presumably affected Dall sheep populations in the Alaska Range. Similarly, Bergerude and Elliott (1998) inferred positive results for thinhorn sheep from wolf population reductions in northern British Columbia. Unlike Barichello and Carey (1988), Bergerude and Elliott took the more inclusive view of their results.

In contrast with the conflicting and fragmentary nature of specific inferences from wolf control programs peripheral to thinhorn sheep, a massive amount of "anecdotal" evidence (with which some modern biologists "lump" Murie 1944) suggests wolf predation is a significant limiter of Dall sheep population size and growth. Rearden (1999) cites Frank Glaser's papers reporting on early market hunting as saying:

> That winter [1916-17] I never saw a wolf track or heard a wolf howl in the Alaska Range. I wondered about that, for I had heard wolves were plentiful in

Alaska. Eventually I learned why the animals were scarce.

Market hunters operated in practically every drainage on the north slope of the Alaska Range within dog team freighting distance of Fairbanks. In 1917, a warden estimated that during the previous four years, 2,800 sheep had been killed for the market within 200 miles of Fairbanks. Sheep were far more abundant than they have ever been since.

. . . I met many market hunters. .

. . . To keep foxes, wolves, wolverine, and other animals from eating the meat, they [Lucke and Steele], like other market hunters of the time scattered little pill-like balls of sheep gut-fat laced with strychnine around their meat caches. This at least partly explains the absence of wolves when I arrived. (Rearden 1999, pp 33-34)

Having evaluated much of this anecdotal information, I now think the comparatively high sheep populations of the Eastern Alaska Range, where I've been involved with sheep for almost 30 years, were results of predator control. This country is classic "prime" Dall sheep habitat and readily accessible to sheep hunters. Consequently, it has supported intense hunting by humans for many decades. There are accounts of market hunting, and poisoning in the area (Rearden (1999), and physical evidence of market hunting still exists there (Heimer et al. unpublished data). Additionally, there is considerable evidence for a long-term, effective predator control effort by the Territorial government in the area (mimeo records of Warwick and Palmer, Alaska Dept. Fish and Game files).

When federal territorial predator control programs ended at Alaska statehood, wolves began to increase. In the 1960s a local guide, Bill Waugaman, commissioned Bill Hutchinson, generally regarded as the greatest aerial wolf hunter in Alaskan history (B. Hinman, Alaska Dept. Fish and Game regional supervisor during the "Hutchinson era", pers. commun.) to implement a wolf control program in the area. By many accounts (B. Waugaman, master guide, M. Rinio and S. Scott, Hutchinson acquaintances, Al Wright, air taxi operator, pers. commun.), this wolf control program was successful, if for no other reason than it kept wolf numbers at levels much lower than today's wolf densities. At the close of the "Hutchinson era," (when aerial shooting, Mr. Hutchinson's forte) was outlawed, moose, caribou, and sheep were at recorded high levels. Whether they were as high as Glaser (Rearden 1999) reported is unknown, but wolves were certainly more abundant than in Glaser's day. Seeing wolf tracks, hearing wolves howl, and sighting wolves was not unusual in the early 1970s when I spent several months each year afield in the area. This prey abundance has been typically assigned to federal predator control during territorial days (Gasaway et al. 1983), but was probably significantly augmented by private wolf control efforts such as Waugaman/Hutchinson. With cessation of private wolf control wolf populations began to increase.

These increasing wolf populations coupled with human overharvests of moose and caribou (Gasaway et al. 1983) soon resulted in declining moose and caribou populations. The Dall sheep population of the area held up longer than the moose and caribou populations, but had begun a slow downward trend by the early 1970s. When the 1976 wolf control program in the area was carried out, moose recovered, caribou populations began to increase, and the sheep population decline apparently stopped (Heimer and Stephenson 1982). Sheep regained their former numbers, and remained stable at high densities until the late 1980s when a series of bad winters resulted in a significant population decline (Whitten and Eagan 1995, Scotten 1997). In the interim, coyotes colonized the area in significant numbers (Heimer, unpublished data), and became a significant docu-

mented mortality source on Dall sheep lambs (Scotten 1997). Additionally, wolves re-established population levels equivalent to or greater than those observed prior to the 1976 wolf control program.

Even though these Dall sheep populations (estimated at 5,000 sheep from a total count of 4,142 sheep reported by Heimer and Smith 1975) remained at high densities through the mid-1980s (in spite of intermittent severe winter events) they showed no credible signs of density-dependent nutritional stress. However, population estimates following a series of consecutive extreme winters from 1989-90 through 1993, suggested a decline of 60 percent (Scotten 1997).

Since 1993, winters have been "normal to mild," and Alaska Department of Fish and Game biologists feel recovery has been underway since 1994 (S. Arthur, Alaska Dept. Fish and Game sheep biologist, pers. commun.). It has now been six years since the last harsh winter was followed by a lamb production failure of the scale which precipitated the population decline. If the "compound interest effect" most recently identified by Wishart et al. (1998, and this conference) had been operating with low environmental resistance, a spectacular population increase should have been noted. There are no indications of such an increase, even though lambs:100 ewes ratios have regained what would have been maintenance levels prior to the advent of coyotes in the area.

Viewed synoptically, these data (defined as "anecdotal" according to the rigor standards of contemporary research biologists) suggest predators, including both wolves and coyotes, are a significant check on Dall sheep population recovery in the Alaska Range. Still predator control to benefit Dall sheep in Alaska is considered not only unthinkable, but against Alaska Department of Fish and Game and Alaska Board of Game policy (K. Whitten, Alaska Dept. Fish and Game Regional Research Coordinator, pers. commun.). I have found no formal record of this Department policy, and have been unable to validate Mr. Whitten's interpretation of Board of Game policy.

Predator control has generally been avoided by modern management agencies because social and political forces acting on agency decisions have made it a *de facto* agency responsibility. As a result, public participation in significant predator reductions has become stigmatized as unacceptable (Heimer, Predation Session this conference). When done by management agencies, predator management is logistically difficult, expensive, and easily curtailed by the increasingly powerful groups which oppose management for human consumptive benefit. A deep schism exists between some sheep-interested publics (primarily hunters, who fund conservation) and the agencies which manage their sheep for them.

My position in this working management hypothesis is that sheep managers should advocate and implement predator control when it appears likely predators are depressing populations below an empirically determined base effective population size (Heimer 1992) or slowing recovery to stated population size or harvest management goals. After all, I argue, what's the worst thing which can happen if we mistakenly control predators to benefit selected thinhorn populations? If it has no effect over the long term, we can stop; and wolf and coyote populations will quickly recover. The major risk is not biological. Additionally, my bias is toward conducting research through management actions. Managers will certainly be more likely to test the validity of a working management hypothesis if it suggests action than if it doesn't.

If a positive effect on thinhorn sheep populations from wolf population reduction exists, data indicate it must result from reduced predation on adults (not lambs). This differing effect of wolf predation on survival of neonates between sheep and other ungulates represents a specific instance where sheep management thinking should differ from generalized ungulate management. Wolf predation continues to be a consistently demonstrable negative influence on moose and caribou calf survival, yet a consistent "non-factor" on lamb survival. Hence, longer-term studies designed to produce data with greater resolving power than those required for moose and caribou will be

necessary if predator biologists are to document whether wolves are, in fact, a controlling factor with respect to thinhorn sheep.

Summary: Long-term anecdotal information suggests certain benefit to thinhorn sheep from reducing and maintaining a lowered level of environmental resistance due to predation. Shorter term quantitative studies, favored by most contemporary managers, have failed to demonstrate consistent beneficial results to sheep or sheep hunters. Conclusions regarding the management efficacy of predator control appear to be influenced by individual point of view. Those with a broad point of view and willingness to accept credible "anecdotal" evidence postulate a benefit. Those unwilling to accept anecdotal evidence and holding a narrower focus deny any benefit. The more quantitatively aware modern biologists are, and the more accountable their agencies are to public pressure against wolf control, the less likely they seem to consider a benefit might result from lowering this component of environmental resistance. If I have this right, there may be the attendant risk of inferring "absence of proof is proof of absence." These differences in perspective will be reflected in recommendations to managers at the end of this volume.

Disease prevention: Another management-altering component of environmental resistance to wild sheep population growth is the presence of exotic diseases. Unlike bighorn sheep management, which is dominated by introduced diseases from domestic livestock, disease does not seem to be a factor in thinhorn management. Thinhorn sheep presently exist in basically pristine ecosystems, and have never shown any inclination toward periodic disease-related die-offs (Heimer et al. 1982). Large numbers of Dall sheep from Interior and Arctic Alaska have been tested for antibody titers to diseases of domestic livestock, and the tests have been overwhelmingly negative (Heimer et al. 1982, Zarnke 1992). Additionally the pharyngeal microflora of Alaskan Dall sheep from the remote Brooks Range, where exposure to diseases of domestic livestock is least likely, have been characterized (Heimer et al. 1992). While benign

strains of *Pasteurella* bacteria are common in Dall sheep, and presumably in Stone's sheep as well. Those forms of *Pasteurella* which precipitate bighorn die-offs have not been isolated from Dall sheep in the wild. Penned Dall sheep have been experimentally infected with pathologic strains of *Pasteurella* from domestic sheep, and have developed pneumonia. These sheep were euthanized (B. Foreyt, Professor of Veterinary Medicine Wash. St. Univ., pers. commun.). There has never been a disease-related thinhorn die-off in the wild, probably because domestic sheep, generally acknowledged to be the carrier of those *Pasteurella's* which kill wild sheep, have never come in contact with wild thinhorn sheep. Should this ever happen results would most likely be disastrous. Tests on Dall sheep leukocytes indicated a six-fold greater susceptibility to *Pasteurella* cytotoxins than for bighorns (Foreyt et al. 1996).

The absence of domestic livestock pathogens from thinhorn populations does not mean disease is not a factor in the biology of these sheep. The common diseases identified from thinhorn populations are contagious ecthyma and lumpy jaw (Heimer et al. 1982). Contagious ecthyma is caused by a pox virus, and is not considered a management-alterable factor in thinhorn sheep.

Lumpy jaw may influence longevity in sheep because it deforms the mandible and leads to loss of teeth and poor tooth alignment which may interfere with feeding. Data relating the effects of lumpy jaw to overall survival are lacking. Murie (1944) speculated the high lumpy jaw frequency in the skulls he collected predisposed infected sheep to predation. From this speculation came the romantic notion that wolves prey only on the "unfit," and actually benefit their prey populations (Heimer 1995b). After capturing and examining almost 400 Dall sheep in the Alaska Range, just 50 miles east of where Murie worked, I calculated the frequency of lumpy jaw in living sheep was virtually equal to that among Murie's death assemblage. Hence, I conclude lumpy jaw does not necessarily predispose Dall sheep to predation, and that the frequency which struck Murie as so high was actually just the frequency of infected sheep in

the population. In Dall sheep lumpy jaw is now thought to be caused by a common bacterium, *Corynebacterium pyogenes*, introduced below the gum line as a result of eating coarse forage (Heimer et al. 1982).

Summary: While virtually all other management mistakes can be corrected, introduction of exotic diseases cannot. Thinhorn sheep management will be forever changed if domestic sheep ever come in contact with wild thinhorns. For this reason, the highest management priority for thinhorn sheep managers must be continued exclusion of domestic sheep from thinhorn ranges. This exclusion of domestic sheep will be most effectively pursued through legislation.

Often diseases and parasites are considered together. Because thinhorns exist in pristine habitats, their parasites are generally considered to have "come with them" from Asia or be normal faunistic components of their habitats. Parasites of Dall sheep have been reasonably well cataloged (Neilson and Neiland 1974, Veitch et al. 1998).

Disturbance: If thinhorn sheep colonized habitats created by retreating glaciers, it should follow that their suite of adaptations includes the ability to adapt to disturbance. After all, glacial habitats are noisy and unstable places. Ice groans, creaks, cracks, and falls from the terminus while unstable moraines produce continual rock falls and land slides. Additionally, glacial winds produce plenty of noise as they sculpt and scour the freshly exposed soils. These disturbances have presumably been, and remain, basic features of thinhorn sheep habitats. Certainly these glacial disturbances are of a somewhat differing character than overflights by military aircraft, helicopter tourism, mining, road-building, heli-mountain biking, and goat packing. However, barring actual habitat degradation, a manager's perception of difference may be more based in aesthetics than biology. For all the disgust which these human activities evoke from thinhorn sheep managers and wilderness advocates, there are scant data which suggest measurable negative effects on population production and growth rate. In fact, a fairly rich literature and large volume of

anecdotal evidence suggests these conventional human disturbances have no measurable effect on thinhorn sheep. Heimer (1981, 1988) reported Dall sheep in Alaska have apparently tolerated road and bridge building, pipeline construction work, coal mining, automobile traffic, intense human contact (both hunting and viewing), and intrusive scientific investigation. Others in this conference will report on the adaptability of bighorn sheep to apparent human disturbance.

Depending on a manager's point of view, this ability to persist and thrive in disturbed habitats can be seen either as a tolerance for disturbance or tenacious, adaptive refusal to leave established functional ranges. While the existing data suggest thinhorn sheep are highly adaptive to human disturbance as long as habitat is not actually degraded, managers focus considerable effort on mitigating or preventing human disturbance, and disturbance studies continue to proliferate (e.g., see Krausman et al. 1998). Usually these studies focus on short-term avoidance reactions or temporary changes in location.

I've found only two references to permanent range abandonment resulting from disturbance. Legendary Alaskan bush pilot, Jack Wilson cites an example of permanent range abandonment in his recent memoir (Wilson 1997). Wilson said sheep were so disturbed by the first helicopters ever flown into Alaska's Wrangell Mountains that lamb/ewe bands left Nikolai Ridge and never returned. Wilson's book is charming, but lacks biological credibility in other details of sheep abundance and distribution. The other account of range abandonment resulting from disturbance comes from the Kenai Peninsula where Dall sheep were alleged to have abandoned traditional range as a result of the disturbance accompanying an either sex hunt to reduce the population. After the hunt, Nichols (1976) was unable to reconcile the reported ewe harvest with the number of ewes counted from aircraft before the harvest effort. Expanding his search area, he subsequently located what he concluded were the missing ewes in a separate but adjoining area. Because no range abandonment had been reported prior to these

observations, and has never been documented since (even using radiocollars); and because a Kenai Refuge biologist and a number of local residents reported the "found sheep" had always occupied the area where they were located (A. Thayer, USFWS Kenai Refuge and Arctic Refuge staff, pers. commun.), I elect to discard these accounts.

I consider it unfortunate that the more advanced modern studies focus on overt short term behaviors or physiological stress indicators because the underlying premise used to extrapolate to harm from disturbance remains unsubstantiated. The conclusion that these indicators demonstrate harm rests on the presumption that there is no "fat in the sheep energy budget" and that every expenditure of energy must be directed toward obtaining enough calories to survive. My observations indicate that there is, in fact, some "disposable income" in a Dall sheep's energy budget, a surplus of calories which can be expended in "play" or reactions to short-term stress without compromising reproductive fitness. I can't explain every sheep behavior I've observed in terms of energy acquisition or conservation. Furthermore, assuming thinhorn sheep can tolerate no exogenous stress without compromised reproductive fitness fails to consider the adaptive ability to "learn" which disturbances constitute threats and which don't (Geist 1975, Toweill and Geist 1999). An exogenous stressor, whether it be an industrial development like a mine, road, pipeline, or a capture net (Heimer et al. 1980), which produces no "memorable" negative consequence will eventually be tolerated by sheep.

If there is an exception to this general rule, it may involve aircraft effects. With respect to flying objects, it is rational to postulate an adaptive conflict. Presumably sheep evolved with aerial predators, and Dall sheep respond to fixed-wing aircraft in the same way they respond to eagles. Ewes "bunch up" and lambs "hide" underneath their ewes. I've seen both rams and ewes make threat-jump behaviors at SuperCub aircraft, just as they do at eagles. However, the universal response to helicopters is flight (to which I've observed no

adaptation during my 20 years of using helicopters (including early piston-driven ships) to study Dall sheep). Recent publications by exponents of small, piston-powered helicopters (Scotten 1997, Scotten and Pletscher 1998) assign sheep helicopter avoidance to flight noise associated with the engines and rotor systems of turbine-powered helicopters. Data which might test this hypothesis have not been gathered. Exponents of these small helicopters also claim sheep respond no differently to them, in spite of their rotary wing design, than to small fixed-wing aircraft. Here too, no data have been presented despite a large body of contrary, experience-based opinion.

I suggest that if sheep evolved non-flight adaptive responses to "fixed-wing" predators (ewes "bunching up" and lambs "hiding" under their ewes) the common flight behavior associated with helicopters may be associated with the absence of "fixed" wings. Clearly, definitive work is required if a consistent position on helicopter disturbance of thinhorn sheep is to emerge.

Summary: In spite of the data suggesting disturbance should not compromise thinhorn reproductive fitness, thinhorn managers expend considerable effort, and generate considerable endogenous stress for themselves, attempting to preclude or mitigate disturbance-caused stresses to the sheep they manage. While the existing data suggest this *might not* be necessary for long-term conservation, I still consider it an appropriate approach to management. Most of the great damage done to wild sheep populations has occurred because developments which were, in fact, critical to sheep welfare, were not considered, precluded, or mitigated.

DISCUSSION: When I first introduced the working management hypothesis concept to peers at the Alaska Department of Fish and Game, it was not warmly received. In fact, it was actively resisted and harshly criticized. Over the intervening dozen years I've wondered why, and have come to some explanatory hypotheses.

One might be inclusion of adaptation theory, local, anecdotal, and "gray" literature as the rationale for

management practices rather than strict adherence to the structured principles which drive selection for papers in the "white" literature. While there is a certain risk associated with consideration of a broader information base, there is a concomitant risk in relying solely on refereed publications. The "white" literature's filtering process for data and ideas functions well in keeping erroneous conclusions from circulation, but is not infallible. Additionally, the filtering process is so rigorous and the time demands (and delays) so burdensome, that many management-relevant data simply don't show up in the approved published literature. Most state management agencies do not pay biologists to force their management-relevant data through this "filter," but only for production of final, in-house, research reports. Additionally, the peer-reviewing or refereeing process tends to select data consistent with existing dogma and reject truly new findings or original ideas because they carry the risk of being "wrong." "Wrongness" becomes an important consideration because so much professional status (tenure and career advancement) is attached to publication of "white" literature. "Gray" literature carries a greater risk of "wrongness" because it is less rigorously reviewed, but compensates by being more dynamic and of much broader scope.

With these considerations in mind, I decided greatly expanding the data base used to formulate a working hypothesis for management was a risk worth taking. For me, being "wrong" was a lesser consideration than improving management. After all, the reason for making a hypothesis is to test (not protect) it. Science truly progresses when the overall mental construct (usually called the hypothesis) is "wrong," (i.e. when data compel acceptance of the hypothesis). If we don't define a working management hypothesis which "risks" being "wrong," progress in biologically-based management will proceed at a glacial pace.

Hence, I was less interested in producing a definitive or perfect statement of natural history than identifying the hypothetical nature of our decision making process for the publics whose resources we manage. Under this scenario, the public and the managers share the risk of making "wrong" management decisions for the promise of an improved future. When the public and its managers jointly make a "wrong" decision, both should realize the opportunity for management progress (as opposed to management stasis) has just presented itself. Rather than assigning blame or feeling guilty, both the publics and their managers should factor the experience into the working hypothesis and pursue progress.

Second, I've hypothesized managers didn't embrace the working management hypothesis concept because, in spite of its open-ended approach, it limits options by managers. If there is no defined management framework, such as a publicly-articulated hypothesis, managers have considerably greater latitude to pursue programs driven by unstated principles (usually of wildlife management, with which the public is increasingly unfamiliar). This limitation of management expression is perceived as threatening by many managers.

A part of this "discomfort phenomenon" may result from perceived force toward a consistent rationale for defining positions. Management opinions regarding predation and disturbance effects on thinhorn sheep are contemporary examples. State and provincial thinhorn managers of Dall sheep attending this conference are in general agreement that wolf control will provide no benefit to Dall sheep or humans. As stated earlier, this position derives from a choice to discount voluminous anecdotal data and local knowledge while accepting small, area-specific, short-term studies which have been unable to document measurable responses on the part of the sheep to generalized wolf population reductions. Conversely, when it comes to disturbance from human activities, the same state and provincial managers are in general agreement that human disturbance must be precluded or maximally mitigated. In this case, the choice criteria are the opposite of those driving the predation decision. With respect to disturbance, area-specific, short term studies where disturbance has not affected sheep reproductive fitness are rejected in favor of a generalized assumption that human-caused disturbance must be harmful.

Finally, articulation of a data-based working management hypothesis for sheep indicates several areas where successful sheep management should depart from the generalized ungulate model. Many mangers are sufficiently committed to the overarching principles of ungulate management (received from their university professors) they're unwilling to allow the specific consideration of thinhorn sheep adaptations to their environments on equal footing with classic nutritional models.

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QUESTIONS, ANSWERS AND COMMENTS - WAYNE HEIMER PRESENTATION

MIKE DUNBAR, OREGON: Wayne, I have a question on your statements about nutritional range resource limitations. When we were working together in the Brooks Range during the early 1990s, we took blood samples which indicated severe nutritional deficiencies in early winter. Nutritional stress indicators in those samples were equivalent to what we would have seen in western bighorns in January or February, and I predicted some bad things were going to happen there. They subsequently did, yet your hypothesis minimizes concern about nutritional constraints. How do you explain our experiences in the Brooks Range?

WAYNE HEIMER: Your prediction was, indeed, correct. Those sheep populations subsequently declined. The decline appears to have been due to reproductive failure which could clearly be nutritionally mediated. I infer this nutritional stress must have resulted from unusual weather. Poor reproductive years aren't unusual for Alaskan Dall sheep. They happen occasionally. I think your predictions were notable because they were associated with a string of bad weather years that led to overall declines of Dall sheep, not only in the Brooks Range, but across Alaska. In discussing sheep adaptations, which I think argue against consistent expectation of density-dependent nutritional constraints, I certainly didn't mean to say that events such as you predicted do not occur. My explanation is events like the Alaska Dall sheep decline are rare and unpredictable. To the extent that sheep are not adapted to handle them, sheep populations will suffer under these unusual stochastic weather influences. However, because such events are rare, particularly in consecutive years, I see no management yield in emphasizing them as conceptual components of the working management hypothesis for thinhorn sheep. I don't think they really bear on density-dependent nutritional constraints. There doesn't seem to be a benefit from trying to reduce population size to prevent them, and we can't go up there and feed the critters. We're stuck managing sheep in a pristine ecosystem.

KEN WHITTEN, ALASKA: Between 1989 and 1993, we had the first, third, and I think, the sixth worst winters on record [in the Alaska Range] accompanied by summer droughts, and there's no doubt that there were nutritional problems. We had very low pregnancy rates in caribou in the spring of 1993. In the same area [where Heimer worked], lamb:ewe ratios were below ten lambs per hundred. We doubted that most ewes could get pregnant in these conditions, and we've since then had mild winters and seen a lot of recovery.

But we saw very similar conditions in the early 1970s, and there's basically an alternative hypothesis to explain the temporarily increased harvests than successful full curl management. Currently, we have our lowest harvests ever coming out of this area under full curl. The alternative explanation is that the harvest increases had nothing to do with changes in harvest management, but that the increases resulted from weather and nutritional conditions which changed productivity and survival.

HEIMER: It's true that the harvest of full curl rams from my old study area in the Alaska Range is currently the lowest ever recorded. However, I'm sure Ken didn't mean for you all to understand that the populations there are producing low harvests simply because of full curl management. Last year's harvest was just short of half of the average (135-ram) harvest under full curl regulations. Coincidentally, the population reduction after the bad winters was estimated at 60 percent. Additionally, the tiny cohort produced when there were only nine lambs per hundred ewes should have reached full curl a year ago, and you can't harvest rams which were never produced. We've anticipated this decrease in harvest for eight years. Hence, I don't blame the low harvest on full curl management, but on the weather mediated production failures of the early 1990s.

Additionally, coyotes are now a major predator on lambs. We could never even document coyote presence there till the mid-1980s. Conditions have certainly changed with increases in environmental resistance, but I have to question the assumption that ewes couldn't have gotten pregnant because of summer droughts of the 1990s or very similar weather in the 1970s. Here's why:

A minimum of 25 percent of marked yearling ewes in my old study area got pregnant in the early 1970s. That is, over eight years of observation, an average of 25 percent of marked two-year-old ewes had lambs with them two weeks after delivery. This means weather couldn't have been "that bad" in the early 1970s. Also, if 25 percent of the yearlings could get pregnant, adult ewes should have had an even higher pregnancy rate. During this time, only 125 miles down the Alaska Range in my high-quality study area (where there was a low-density population with high lamb production, high growth rates, and an abundance of full curl rams), yearling ewes didn't get pregnant. Once we adjusted the ram abundance and age-structure in the crowded study area (through full curl management), early pregnancy became a rare event in both populations even though all yearling ewes ever studied ovulate at 18 months (confirmed by ovarian histology and lamb production on second birthdays). Hence, I'm leery of speculating about what might have happened to Dall ewe reproduction in the past based on what caribou are doing now. I think Dall sheep and caribou differ more than Ken thinks they do.

As I said in this presentation, the management course we took, adjusting human harvest to favor lamb production and young ram survival (establishing the full curl regulation), was the easiest management approach available at the time. There's nothing we can do about the weather but worry about it. Other management actions to restore the depressed sheep populations in Alaska will involve predator reductions, and be more difficult.