Dall Sheep Disagreements: An Alaskan Management Controversy

Wayne E. Heimer, Sarah Watson-Keller, Valerius Geist, Samantha Castle Kirstein, and T. C. Smith III

Dr. David Klein, long-term Alaska Cooperative Wildlife Unit leader at the University of Alaska in Fairbanks, was honored by a special symposium where several of his former students presented papers. The papers were published in the moose-centered journal, ALCES Volume 37. One of these papers was a critique of Dall sheep research and management by Ken Whitten, who has presented several papers at symposia of the Northern Wild Sheep and Goat Council. The ALCES citation for this critical article is given in the abstract reproduced below. We think rebuttal of articles such as this is required, but will not submit our full rebuttal to ALCES because we suspect the primary readership of ALCES will not find the details of our rebuttal particularly germane to their interests. Our submission to ALCES will be summary and tailored to that readership. In contrast, the readership of the Proceedings of the Northern Wild Sheep and Goat Council should have considerable interest in the details of this argument because it is about sheep management, not moose. Hence, we have petitioned the Northern Wild Sheep and Goat Council to include the abstract of Whitten's critique and the text of our rebuttal in this proceedings even though it was not presented in Rapid City. We were, at that point, blissfully unaware if its existence. Readers are encouraged to consider Whitten's entire article in evaluating our rebuttal.

EFFECTS OF HORN-CURL REGULATIONS ON DEMOGRAPHY OF DALL'S SHEEP" A CRITICAL REVIEW

Kenneth R. Whitten
Alaska Department of Fish and Game, 12300 College Road, Fairbanks, AK 99701-1599, USA

*ABSTRACT: Researchers studying Dall's sheep (*Ovis dalli dalli*) associated with a large mineral lick on Dry Creek in the central Alaska Range south of Fairbanks, Alaska, USA, claimed that removal of nearly all mature males by intensive harvest of three-quarter curl or larger males by hunters during the 1980s resulted in accelerated mortality of young males and low productivity in female sheep. Changing to a more conservative harvest of seven-eights and then full-curl males purportedly reversed these trends and resulted in higher overall sustained harvest of males. Review of Dry Creek study reports and of original data records revealed questionable assumptions and errors in data analysis and study design. Conclusions about accelerated mortality of young males were based primarily on resighting data from marked males at the mineral lick, but data from aerial surveys of the larger study area around the lick indicated much higher abundance of males than was apparent at the lick. Reanalysis of data showed that males had low fidelity to the lick, and many years the lick was not observed frequently enough to detect all sheep that may have used it. Harvest only reduced abundance of mature males by about one-half and had no discernable effect on survival of younger males. Low ovarian activity and high rates of parturition in 2-year old females (thought to be associated with alternate year reproduction in later life, and therefore undesirable) were attributed to low abundance of mature males from 1972 to 1979, but most* *data were actually collected either before or after those dates, when male abundance supposedly was high. Harvest of mature males increased through the 1980s, but an apparent correlation with more restrictive horn-curl regulations disappeared in the 1990s. Harvests of mature males under full-curl management in recent years have been far lower than ever occurred under three-quarter curl regulations. I conclude that trends in sheep harvested at Dry Creek were not driven by horn-curl regulations, but by long-term weather patterns that affected sheep productivity, survival, and abundance.*

ALCES VOL. 37 (2): 483-495 (2001)

Key Words: *Alaska, Dall's sheep, harvest, horn-curl, management, mortality, Ovis dalli dalli*

THE SHEEP MANAGEMENT COMMUNITY RESONDS:

Abstract: We understand practice of the natural sciences as systematic effort to find truth outside one's self. At its best, this human enterprise often leads to disparate interpretations because it is difficult to remain objective; and criticism occasionally becomes highly personalized. Still, we appreciate the benefits of critical review, and were most interested and anxious to read what Mr. Whitten (ALCES 37(2):2001) had to say about our collective efforts. Unfortunately, we found the review more hostile than helpful. We rate the review as flawed in four major aspects. First, the evident scholarship is inadequate for the task, and compromises the credibility of the critique. Second, the over-emphasis on aerial survey data, the least reliable data relevant to the issue, focuses distractingly on details and obscures the larger picture. Third, the critique focuses excessively on retrieval of our clearly stated caveats, cautions, and stated assumptions from a relatively minor paper modeling ram survival as ignorant or deceptive; they were neither. Fourth, the review mistakenly represents the certainty with which we presented our earlier work, and ignores large body of qualifying work over the last fifteen years, which frames our conclusions as a working management hypothesis for in-field testing. Alaska's full-curl ram harvest regulation is an example of management and pursuit of biological fact through an articulated working hypothesis based on a synoptic view of Dall's sheep autecology. Unfortunately, the review erroneously reduces this biologically-driven regulation to the level of an arbitrary management convenience which does not culture compliance by hunters. After having considered the critique, we argue that integration of the complete biological data set rationalizes restriction of open harvest of Dall's rams to those at full maturity for purposes of biological conservation and maximum sustained yield.

Keywords: Alaska, Dall sheep, harvest, horn-curl, working management hypothesis, *Ovis dalli dalli*

We, the authors, are a diverse group. We have been collectively studying and managing North American and Dall sheep since the 1960s. Our areas of specialty range from the evolution and behavior of mountain sheep (VG), through typical management-related Dall sheep surveys and research projects (TCS, SW-K, WEH), to economic analysis of Dall sheep hunting (SW-K), rigorous nutritional analyses and the physiology of Dall sheep (WEH), and service on the Alaska Board of Game (SCK). Alaska's present Dall sheep harvest program (its full-curl regulation) resulted from our applied synthesis and implementation of this cumulative experience. Responsibility for Alaska's full-curl regulation is much broader than the critique appreciates, and cannot be assigned to one individual or a couple of researchers.

Collectively we have pursued our share of apparently erroneous directions over this 40-year period, found them to be unproductive, and redirected our thinking to "embrace null hypotheses" when warranted by the cumulative weight of data. It is our hope, and indeed our assertion, that we have done so honestly, and in the best traditions of the natural sciences. Our embrace of the null hypothesis where density-dependent nutritional constraints are concerned has put us at odds with the prevailing dogma of classical wildlife management. We suggest the harsh critique to which we must respond at this time is best defined as defense of this dictum. We must address some of the critique's specific criticisms before offering more significant, management-relevant arguments in our DISCUSSION segment.

Inadequate Scholarship Relating To Criticized Work

We found the review less helpful than we had hoped because of inadequate scholarship. This inadequate scholarship appears, throughout the critique, to highlight our alleged failures of concentration and conscience. Unfortunately, the critique is demonstrably out of touch with the work it criticizes. This is not surprising considering the critique focuses on data and published analyses from "the 1970s and 1980s." Further detailed analysis and synoptic papers, which would have been beneficial for the critique's credibility, have been published over the last 15 years; but were arbitrarily excluded from review. Consequently, the critique is outdated, and simply wrong in many instances. Unfortunately, we are obligated to list at least a few examples to support our conclusion of inadequate scholarship. We'll begin with the summary of our hypothesis in the critique's first paragraph, which says (*emphasis added*):

> Subsequent *early reproduction among females was hypothesized to have stunted female body growth, ultimately leading to alternate year reproduction*, as opposed to annual production of young that would have occurred had females delayed breeding until they were at least 2 years old (Heimer and Watson 1986). (*ALCES 37(2):484 column 1, lines 6-13*)

Even though this interpretation seems intuitively understandable and attractive because it is buttressed by the cumulative experience of domestic animal husbandry, the critique errs in defining it as our position. Work on wild cervid species, specifically caribou (Dauphine, 1976) and red deer (Hamilton and Blaxter, 1980) suggested nutritional limitations (which could lead to stunting) resulted in compromised reproductive performance in these species. Intuitively, one would suspect nutritional limitations might have a similar effect in other wild ungulate taxa, perhaps including Dall sheep. We admit to once being attracted to this idea. However, after WEH had thoroughly investigated the nutritional resource profiles in contrasting populations of Dall sheep in Alaska (Heimer, 1983), we embraced the null hypothesis (that nutrition was not a factor in alternate-year reproductive success) and abandoned the "stunted" line of thinking. The evolution of our thoughts on nutrition may be found in Heimer and Watson (1986 page 30 paragraphs 2 and 3, and page 31). However, that Federal Aid report is sparingly available so we shall quote our explicit summary:

> We conclude differences in ovulation rate are not explained by factors which determine body condition. There was no statistically significant difference in the nutritive values for washed rumen contents, no reasonable expectation of significant differences between the nutritive values for summer range plants, and no difference in breeding body condition between the 2 [radically different] study populations. (Heimer and Watson (1986) page 35 paragraph 3).

Errors as basic as the just-documented misrepresentation demonstrate inadequate scholarship for the critique from its outset.

Still, we can understand how a cervid specialist might project this conclusion to us. After all, it is considered proven that ovulation is a function of female body mass in caribou. By extension, it is intuitively apparent that a sufficiently skinny Dall ewe probably can't ovulate. Still, there is no evidence the caribou body mass/ovulation relationship is relevant to Dall sheep. In contrast to yearling caribou cows (which occasionally ovulate if high quality forage is abundant, as do other members of the deer family), every yearling Dall sheep ewe ever examined, regardless of location or circumstance has shown evidence of ovulation (Heimer 1999). This suggests sheep reproductive physiology is, in fact, distinct from that of the *cervidae*, and takes us to the critique's first apparent assumption.

Assumption #1: Sheep do not have a unique social biology

The assumption, that sheep autecology is no different than generalized ungulate synecology arises in the review's second paragraph, where the critique states:

> Not everyone, however, agreed with the conclusions of the Dry Creek studies. Wildlife managers in Alaska were familiar with numerous situations in which unrestricted hunting of male moose (*Alces alces*) and caribou (*Rangifer tarandus*), which also have complex social structures had resulted in far lower sex ratios and much greater skewing of the age structure toward young males than three-quarter curl only hunting has ever caused in Dall's sheep, yet far greater consequences from harvesting were being claimed for sheep. (page 484 column 1 paragraph 2, lines 1-13)

We argue simply stating that moose and caribou have "complex social structures" reflects inadequate consideration of behavioral adaptations of differing taxa to differing habitats. Contemporary evolutionary thinking argues these differences should have produced disparate survival strategies. We think they have. One of us (VG) defined mountain sheep behavior in the context of adaptation to environment thirty years ago (Geist 1971). A comparable comprehensive work on moose and caribou behavior does not exist. Hence, we cannot compare the social biology of the *bovidae* with *cervidae* in detail. However, this does not mean moose and caribou social structures are the same as those of sheep or that altering social structures should be expect to produce the same results (or lack thereof) in all three species.

As one of us (WEH) has argued in detail moose are cervids adapted to successional habitats; and have a completely different reproductive strategy (including nutrition-driven multiple births) than climax-adapted sheep. Caribou are cervids adapted to climax habitats, while sheep are bovids adapted to climax habitats. Even though both caribou and sheep are climax-adapted species, caribou are largely migratory, and sheep aren't (Heimer 1999). Hence, attempting to discredit our adaptation-based assertion, that sheep social biology is specific to sheep, lacks credence and supporting data at the most basic level (recent texts cited by the critique notwithstanding). The critique's dismissal of our position citing a generalized one-paragraph summary (pp 48-49) in Toweill and Geist (1999) rather than the more rigorous paper (Heimer 1999), with which the critique's author was intimately familiar, also suggests selective exclusion or inadequate consideration of this concept.

The critique's attempt to further credential the assumption that sheep do not manifest unique adaptations to their environment, by citing Murphy et al. 1990, occurs in this same paragraph (lines 13-20), where the critique says:

> Furthermore, researchers studying other populations of sheep were unable to corroborate a relationship between abundance of older males and the survival of young males (Murphy et al. 1990), and increases in production of young, similar to those at Dry Creek after harvest was restricted,…

Invoking Murphy et al. (1990) to support the notion that sheep do not have unique behavioral systems is specious. Murphy et al.'s aerial survey methodology simply did not have the resolving power to address the question he and his coauthors presumed to address. Those data were, as Murphy put it using language stolen shamelessly from (WEH's) review of his manuscript, "snapshots in time." Not only were Murphy et al.'s data 'but snapshots' they were snapshots of differing populations in differing mountain ranges during differing years where unknown pre-existing conditions (with the possible exception of harvest by humans), had certainly affected ram age structures on the days the snapshots were taken.

Citation of Murphy et al. as credible with respect to population parameters highlights a historical bias on the part of the critique. In Murphy and Whitten (1976), use of Adolph Murie's ram skull collection data (Murie 1944) was taken to task for not demonstrating stable population structures. Curiously, that standard was not a concern for Murphy et al. (1990). Nevertheless, this citation of Murphy et al. (1990), and the critique's emphasis on aerial survey data leads to identification of the critique's second assumption.

Assumption #2: Aerial survey data have sufficient resolving power to disqualify other data sets

Much of the critique hangs on the critical author's notice that the 1974 aerial survey by WEH and TCS (Heimer 1975) reported higher percentages of legal rams than those reported in Heimer 1973. We (WEH and TCS) have no quarrel with this 'discovery.' However, we assert the critique formulates two incorrect assumptions based on this 'discovery.' The first is the critique's assumption that the increase from 3.3 percent to 8 percent legal rams was biologically significant. It wasn't. Even after this transient increase, the percentage of three-quarter curl rams remained at half the percentage of full-curl rams in the moderately harvested Tok Management Area. We shall discuss this situation in detail later where the critique retrieves this unstated assumption as fact in criticizing our pooling of ovarian data for analysis. The critique's second failure associated with the 'discovery' of aerial survey data was blurring of chronological events associated with the transient increase in young-but-legal rams reflected in the 1974 survey. The history of the reported increases in legal, three-quarter curl and greater, rams is as follows (if this doesn't interest you, skip to "Criticism of ovarian function analysis):

Heimer (1973) reported the percentage of legal, three-quarter curl rams, calculated from around-the-clock mineral lick observations extending from mid-May through June of 1972, was 3.3 percent. Then, Alaska's 42-day ram harvest season allowed for harvest of any three-quarter curl or larger ram from August 10 through September 20. Following the ram harvest, one of us (TCS) flew a ram composition survey (as prescribed by the survey/sampling regimen of the day (Nichols 1970)), and reported 2% legal rams in December. This sample contained 256 of the 1473-sheep (17%) estimated in the population immediately after lambing in June. Ram abundance should have been lower following hunting season. It was. Also, rams should have been dispersed among ewe populations for rut thus limiting possible errors in adequately sampling ram home ranges.

As for the increase to 8 percent legal rams, the critique correctly reports that a summer 1974 survey (WEH and TCS) indicated 7.8% legal, three-quarter curl or greater rams. Much of the critique turns on the difference between this legal ram percentage and that from the 1972 estimates, and the critique's assumption that it was biologically significant. On page 485, column 2, lines 15-23, the critique states:

> Researchers claimed legal males (three-quarter curl) had declined to about 3% of the population by the *mid-1970s* (Heimer 1973), but aerial surveys of the larger study area showed a very different pattern. There were at least 8% legal males in the *1975* survey, *when males were supposedly at their lowest level.* (*emphasis added*)

We suggest the estimate of 2-3% legal rams in 1972, (the year the data reported in Heimer (1973) were gathered) was credible. After all, it was produced using two differing techniques, which were in substantial, consistent agreement. We think these credible estimates indicated legal, three-quarter curl rams were scarce, and fully mature rams were virtually absent. Similarly, we have no trouble understanding that the 1974 survey (reported in Heimer, 1975) contained 7.8% legal rams. Indeed, a November "ram count" that same year (reported in Heimer (1975) but not mentioned in the critique) indicated almost 10% legal rams in a small (86-sheep) sample. We agree the data indicated the percentage of legal rams had increased. If one assumes these data were accurate, the increase was 2.4-fold. While striking, this percentage increase resulted in population compositions remaining indicative of a severely suppressed ram abundance skewed toward young males. The question is: Was the increase biologically significant? We don't think so (see ovarian function analysis).

Furthermore, this increase was expected based on recruitment data gathered at the mineral lick. Reference to Heimer and Watson (1990), cited by the critique, indicates the yearling recruitments in from 1969-1971 averaged 38 yearlings per 100 ewes, the highest three-year average yearling recruitment in Dry Creek history. These large yearling cohorts were recruited from lamb productions averaging 61 lambs per 100 ewes. No data on ram abundance or age structure are available from these years of spectacular lamb productions, but ram harvests from 1968-1972 averaged 121 rams/year in the area encompassing the study area. This was the highest of any five-year period prior to the full-curl period (critique Table 6.). Obviously, rams were relatively abundant for hunters to kill and report them in the harvests from 1968-1972. The coincidence of this relatively great ram abundance with high lamb productivity is consistent with predictions from our hypothesis that high ram abundance (attended by the presence of more adult rams) facilitates higher lamb productions. This finding illustrates the importance of "internal" population dynamics in interpreting aerial survey data (Heimer 1994).

Excluding the three outstanding years of yearling recruitment from 1968-1972, yearling recruitment between1968 and 1978 averaged only 18 yearlings per 100 ewes. If the three years of high yearling recruitments actually represented what was happening in the population, it is reasonable to think the percentage of legal (but young) rams showed a transient increase between the surveys of 1972 and 1974, and that the percentage of legal, three-quarter curl rams declined in the following years because yearling recruitments which would have driven increased legal ram numbers returned to the low average levels while harvests continued to average about 100 rams per year. Taking aerial survey data as valid unto themselves is risky business. The critique's author seemed to agree when he wrote:

> However, accuracy and precision of past sheep population estimates are unknown, and most long-term data sets show fluctuations in numbers and/or composition which are inconsistent with reasonable mortality and recruitment. These aberrations cast doubt on our ability to detect short-term population changes using existing survey techniques. (Whitten 1997, page 2 paragraph 3).

We could not agree more when aerial survey data reflecting "external" population dynamics are interpreted without the presence of supporting "internal" data estimating yearling recruitment and overall ewe mortality (Heimer 1994). Consequently, we wonder at the critique's emphatic use of aerial survey data to discredit our gathering, handling, and interpretation of independent data sets focusing on body composition, nutritive quality of rumen contents, social behavior, female reproductive success, and harvest statistics.

In attempting to 'debunk' our hypothesis that statistically significant changes in most of the above-mentioned data sets coincided with what we inferred were biologically significant changes in ram abundance, we notice the critique blurs the timelines involved, the second mistake associated with 'discovery' of variable ram percentages in aerial survey data. The critique then attributes these asynchronous timelines relating to aerial surveys to us.

We object. We can't understand why the critique would represent 1972 (or even 1974) as "the mid-1970s" when citing Heimer (1973). After all, the 1973 paper reported data gathered a year earlier, in 1972, which certainly wasn't the "mid-

1970s. Also, we can't find any reference linking the conclusion, imputed to us, "*when males were supposedly at their lowest level*" [in the "mid-1970s"] in the material the critique cites.

The most likely source we can offer to explain this statement is a typographical error in an unedited draft manuscript we (WEH and SW-K) provided to the critique's author as a courtesy circa 1992. That erroneous statement attributed to us (as though it represented our position during the 1970s and 1980s review period chosen by the critique) *was present in that unedited (and unpublished) draft* manuscript. Because of the nature of that draft manuscript, we would rather not receive credit for asserting that rams were at their lowest level in the mid 1970s.

Misinterpreting sequence or chronology would be a less important error if the critique did not similarly blur the chronological relationships between aerially observed ram abundance with respect to ovarian collections. Ovarian activity is more fundamentally related to our hypothesis than ram abundance.

<u>Criticism of the ovarian function analysis:</u> Amplifying these misunderstandings, the critique reaches its rational nadir when it uses aerial survey data to discredit our inference that presence of mature rams in Dall sheep populations facilitates ovarian activity. Here, the critique's approach appears twofold. First, it denies that ram abundance was ever low enough to affect lamb production (and by implication ovarian activity). Second, it alleges that the transient increased percentage of three-quarter curl rams in the Dry Creek aerial survey data invalidated the comparisons of ovarian activity between Dry Creek and the Tok Management Area.

After we had utterly failed to find even the faintest suggestion of nutritional advantage for the strikingly better ovarian performance by ewes in the Tok Management Area compared with Dry Creek in the late 1970s, and after we had noted huge disparities in ram abundance between Dry Creek and the Tok Management Area, we (WEH and SW-K) stated:

> Low ram abundance, which usually includes low Class III [three-quarter] and IV ram [full-curl] abundance, may be the most likely cause of lowered ovarian activity. When ovarian activity was low in Dry Creek (1972-1979), the total ram:100 ewe ratio was 17, and the Class III and IV ram:100 [ewes] ratio was 8. In contrast, when ovarian activity was determined for the Robertson River [Tok Management Area] population, there were 40 total rams:100 ewes and 15 *Class IV* rams:100 ewes. (Heimer and Watson (1986) page 37, paragraph 4, lines 1-8 *emphasis added*)

With overall ram abundance during the ovarian sample period being 2.4 times greater in the Tok Management Area, and the Class IV (i.e. full-curl) ram ratio being almost twice as great in the Tok Management Area as was the three-quarter curl ratio in Dry Creek, we think the critique's argument against valid ovarian sample comparisons vanishes. Our records indicate (almost two decades after the fact) that approximately half of the ovaries sampled from Dry Creek were collected between 1972 and 1975. The rest (slightly more than half of the Dry Creek ovaries) were collected from 1976-1979. If, as the critique argues, pooling these ovarian samples was bad science because there was a transient increase in ram abundance in Dry Creek during the "mid-1970s," the pooled sample should have shown greater statistical variance than it did. Consequently, statistical significance would have been correspondingly more difficult to demonstrate in our relatively small samples (n=19 from Dry Creek and n=13 from the Tok Management area). Nevertheless, the differences were statistically significant ($P<0.05$). Mean ovulation rates in Dry Creek were lower than in the Tok Management Area even though the composition of whole body homogenates and quality of washed rumen contents showed no hint of nutritional difference (Heimer 1983).

Based on the statistical significance of this sample (which the critique, page 492 column 1 paragraph 2, says was compromised), we hypothesized that lowering the overall rams:100 ewes ratio from 40 to 17 was biologically significant. Perhaps even more significant was the decrease from 15% full-curl rams to 8% three-quarter curl rams. There is no rational basis to argue ovulation rates in Dry Creek were not at least coincidentally linked, statistically, to lowered ram abundance.

Nevertheless, the exact percentage of ram population reductions doesn't really matter. Our hypothesis has acknowledged from the beginning that these data were neither necessarily accurate nor precise. However, the changes they reflected were apparently of high biological significance because the adverse affects statistically associated with low ram abundance and the absence of mature rams were reversed when ram abundance increased while ewe population densities remained unchanged (Heimer and Watson 1990). This experiment went significantly beyond inferring cause from a single statistical correlation.

We (WEH and SW-K) have consistently acknowledged (Heimer and Watson 1986 and forward) that we did not have the opportunity to check actual ovarian activity after changes in ram abundance in Dry Creek. We inferred an increase in ovulation among Dry Creek ewes because statistically significant differences in lambs:100 ewes ratios between the two study populations, when rams were scarce in Dry Creek, vanished once ram abundance was reestablished in Dry Creek through changes in ram harvest regulations.

The critique's attempt to discredit the subsequently observed 6.6-fold increase in observed consecutive-year reproductive success following reestablishment of ram abundance and an older age structure in Dry Creek must be discussed in this context. On page 491, column 2, paragraph 1, the critique says:

> The authors…reported the mean young to female ratio for…a good weather period…was higher than the mean for…bad weather. Nevertheless, they argued that factors other than weather also must have affected productivity, because frequency of consecutive-year reproduction increased >6-fold between those periods while young to female ratio only doubled. Heimer and Watson (1986) thought that weather accounted for the change in young to female ratios, but increased abundance of mature males must have cause the larger rise in consecutive-year reproduction.

This analysis represents a misreading of Heimer and Watson (1986). In the 1986 report, we (WEH and SW-K) were dealing with acknowledged, implicit weaknesses in establishing consecutive-year reproductive success. In discussing those weaknesses we identified the sequence of events from ovulation to observation of a pair-bond, which were necessary for us to make a positive consecutive-year finding for any given ewe. The unknowns included weather effects on lamb survival at birth. In this discussion we wrote:

> Hence, the question of the magnitude of weather influence on our ability to accurately detect changes in frequency of consecutive-year reproductive success merits discussion.
>
> We can gain some insight about the magnitude of weather influence on this reproductive parameter by considering the mean lamb:ewe ratios for the 2 differing periods in Dry Creek. During the 1972-1976 period, when consecutively observed reproductive success was 6%, the mean lamb:100 ewe ratio was 29. For the 2nd period, 1981-1984, when consecutively observed success was 40%, the mean lamb:100 ewe ratio was 54. This is an increase of 1.9 times. If our ability to document consecutive-year reproductive production were directly proportional to changes in lamb:100 ewe ratio [accounting for potentially more favorable weather influences], we should have seen a consecutive-year frequency increase of 1.9 times. The documented increase was 6.7 times. This increased frequency was 3.5 times greater than expected from the increased lamb:100 ewe ratio [alone]. Something besides weather appears to be influencing changes in frequency of consecutively observed reproductive success. Pregnancy rates in ewes collected during this period was only 36% of 11 ewes collected in springs of 1972, 1973, 1975, 1976, and 1977. We think this probably confirms the significantly (P<0.05) lower incidence of consecutive-year reproductive success during the mid-1970's was real, and suggests that it resulted from a failure to ovulate and/or breed. (Heimer and Watson 1986, page 29 paragraph 2)

The critique's subsequent mathematical machination is too esoteric for us. The observed increase in documented Dry Creek ewe consecutive-year reproductive success was at least 6.6-fold. That is, it increased from an observed 4-year mean of 6% to an observed 4-year mean of 40% (which subsequently matched the Tok Management Area rate). Over the same period, the lambs:100 ewes ratio doubled (to also coincidentally match the Tok Management Area ratios). The critique's statement, "…the 6-fold increase…could only result in the observed doubling in young to female ratio—no more or less." escapes us, unless further unstated assumptions about the role of weather are invoked.

In the end, we hypothesized the management-desirable results, increased lamb production and subsequent increased legal ram harvests, were caused by a combination of increased lamb production and survival of rams to harvestable age (Heimer and Watson 1990). The critique contests this latter suggestion because it alleges there were problems with a ram survivorship model we dallied with in 1984.

The Ram Survivorship Issue

We (WEH, SW-K, and TCS) engaged in a ram survivorship modeling exercise in 1984. Criticism of this exercise occupies approximately 50% of the 12-page critique. The critique did not review our earlier paper (Heimer et al. 1984), but focused on a summary treatment presented in Heimer and Watson (1986). The caveats the critique retrieves were, for the most part clearly identified in our 1984 paper where we said, in summary:

> We have suggested a major departure from established sheep harvest management. We believe the data are sufficiently compelling that experiments with changes in harvest regime are in order. Still, we realize that much of what we have offered may be equivocal. Most criticism should be directed at our use of presumptive death when we could no longer locate marked rams. Cessation of re-sightings does not necessarily demonstrate a given ram is dead. (p 431 paragraph 2).

In short, what we (WEH, SW-K, and TCS) did was simply to model the survivorship of collared rams, following Deevey's (1947) methods as exactly as possible to produce a comparable survivorship curve. We treated Murie's data (Murie 1944) exactly the same way we treated ours. As a consequence, we violated (in some cases purposefully) the theoretical conventions emphasized in the critique. Some of these conventions were listed earlier by Murphy and Whitten (1976) in their criticism of Deevey. The critique's litany of our "mistakes" stems, not from scholarly research which unearthed our efforts to conceal them; but from our careful documentation of methods used in the modeling exercise.

Setting aside the theoretical conventions was necessary for two reasons. First, if everyone eschews analysis until all theoretical conventions can be satisfied, nobody will ever do anything. Second, we did it to make our work comparable with Deevey's classic treatment of Murie's data. We reproduced Deevey's curve with the techniques we used for both data sets. Using the unedited data, the Dry Creek curve suggested increased mortality among young rams, but the curve did not break sharply as does Deevey's curve. As an experiment in "cleaning up the signal" we edited the data as reported, and produced the curve we published. These methodologically-comparable curves (ours and Deevey's) were identical up to 3.5 years of age. At that point, the curves diverged radically, with the increased mortality phases starting earlier (by almost five years) in the heavily harvested population. Strikingly, the increased mortality portions of the curves had virtually identical slopes, a difference of only one percent in ram deaths per year.

This coincidence in rate between the increased mortality phases of both curves seemed biologically important to us because it was consistent with predictions from behavioral observations and energetic theory. Had these curves not supported these rational connections, we would never have reported them. However, we were comfortable with the hypothesis (drawn in large measure from Geist's (1971) behavioral work) that younger rams assume dominance roles in the absence of older rams for two reasons. First, lambs continued to be born in the virtual absence of mature rams in Dry Creek just as reported by Nichols (1978) from the Kenai Peninsula. However, lamb productions in the Alaska Range were statistically significantly lower when older rams were not present present. Second, work by Hogg (1984) and Jenni et al. (pers commun. 1986), demonstrated rutting behaviors change with altered ram age structures in bighorn sheep.

We found this exciting because the virtually identical slopes in both curves seemed likely, as mentioned above, to represent the mortality cost of ram dominance. After all, 8-year and older rams in un-hunted Dall sheep populations, as well as in other species of sheep (Bradley and Baker 1967) don't die because their teeth are gone or their bones are brittle. They are not "old," yet they die at almost six times the rate after age 8. Why? Probably because the metabolic costs of dominance "age them before their time." The energetic theory and behavioral observations were consistent with what our model produced. We (WEH, SW-K, TCS) covered these arguments in 1984 and 1986 (WEH, SW-K).

Consequently, we (WEH and SW-K) formulated (as quoted above) the hypothesis that absence of dominant Dall rams results in dominant behaviors by young Dall rams (and their paying the associated mortality costs, which are by logical extension, energy-mediated). We proposed further research, aside from our admittedly inferential methods, to test this hypothesis; but these suggestions were not well received. Instead, Alaska Department of Fish and Game leadership sought to set aside the collective work of the wild sheep research community. Apparently, with the critique bearing the ADF&G imprimatur, that quest continues to the present day. Throughout the critique, the author flirts with the agency-generated myth that Alaska's full-curl regulation is not biologically-based. This takes us to the critique's section on the relevance of Alaska's full-curl regulation to modern management.

Relevance Of The Critique To Modern Management In Alaska

On page 484 column 2 paragraph 2 the critique states:

> Although many biologists disagreed with the Dry Creek hypothesis, those ideas held immense appeal for traditional sport hunters because of their implication that trophy hunting was the optimal harvest strategy for sheep. The Alaska Board of Game incrementally enacted more conservative horn curl regulations and by 1993, full-curl hunting for males only was normal for most of Alaska. The Board still receives proposals from the public for more rigorous enforcement of full-curl only management whenever sheep populations are faring poorly. Disagreement and confusion continues among professional biologists….

The critique goes on to say (Page 492, column 2 paragraph 2, lines 1-13) [*Our responses bracketed in italics*]:

> Numerous papers…attempted to explain how abundance of large males moderated Dall's sheep social behavior and ecology and was the key to population vitality. Findings on which those hypotheses were based, however, were unsubstantiated. Harvest never removed all mature males. [Response: *We never alleged it did, only that male age structures were skewed to the point of biological significance.*] Depressed survival of young males in the Dry Creek population never occurred. [Response: *We consistently stressed the inferential nature of our conclusions from population composition data and reported harvests.*] Reduced productivity could not be linked to male abundance, but was correlated with weather. [Response: *While weather could be inferentially tied to production, the statistically significant changes in ovulation rate and observed consecutive-year reproductive success were tightly linked with ram abundance, and not just statistically. After demonstrating these statistically significant linkages, management-level experiments confirmed predictions based on the statistical correlations. Additionally, unpublished multiple regression analysis available to the critique's author gave correlation*

coefficients of –0.295 for winter severity, 0.408 for favorable lambing weather, 0.519 for projected weather effects on breeding condition, and 0.655 for ram abundance over the 16-year period in Dry Creek. Hence, more variation in lamb production was associated with changes in ram abundance, crude as the estimates were, than with physical environmental factors.] Nevertheless, regulations allowing harvest of only full-curl males now apply in nearly all general hunts for Dall's sheep in Alaska. In retrospect, restrictive horn-curl regulations were not necessary for conservation of this mountain ungulate. [*Here the critique presumes to know what would have happened if no changes in harvest management had occurred. This is, of course pure speculation.]*

Significantly, the critique's position inferred from the above-quoted paragraphs reifies ADF&G's mythic position that the Alaska Board of Game established Alaska's full-curl ram regulation as a concession to "traditional sport hunters" rather than out of respect for the specific biological adaptations of Dall sheep. This myth has its roots in the Department's rationalization of its bitter failure to defeat Alaska's publicly-proposed full curl regulation. Here's that story:

Traditionally, the Department biologist most conversant with the data on any proposal before the Alaska Board of Game presents those data to the Board. According to traditional practice, one of us (WEH) would have presented the Department's data on the effects and implications of Dall ram harvesting to the Board. This tradition was set aside when the Board considered Alaska's full-curl regulation. Department leadership was stridently opposed to the proposed regulation and acted specifically to keep WEH from presenting the relevant data. The Wildlife Division Director of the day, Lew Pamplin, ordered WEH's supervisors to make certain "Heimer doesn't get within 200 miles of the Board meeting." (D. Harkness, ADF&G Anchorage Area Biologist pers commun.). Heimer didn't participate, but two of us (SCK and VG) did.

With the Department openly and strongly opposed to the full-curl proposal, and being committed to withholding Department-reviewed and approved data from the Board, the laymen responsible for the full-curl proposal presented the Department's data to the Board themselves. After the laymen's presentation, ADF&G leadership argued the data and analyses were not valid. To counter this assertion, the laymen arranged for VG, the recognized world authority on wild sheep, to testify concerning the validity of WEH and SW-K's work. Based on his lengthy study of the Department's (WEH, SW-K, and TCS's) published work, VG testified that the Department's data were validly gathered and correctly interpreted. Subsequently, SCK, the other of our review group present (who was serving on the Board at the time), supported the official "Board Finding" (a legally-required decision of record), that Dall sheep biology demanded management of ram harvests at the full-curl minimum to produce the maximum sustained yield required by Alaska law. Hence, the record demonstrates the basis of Alaska's full-curl regulation was biological, even though some Department-ordained biologists (including the author of the critique) disagreed. The fact that the Department chose not to participate in presenting its review-approved data does not change the legal finding of the Board. Neither can this critique's shallow reinterpretation of the existing-but-hoary data, its damning misrepresentations of our position, or its invocation of the skepticism of "many biologists" effect that change.

DISCUSSION

In its discussion of the benefits of Alaska's full-curl regulation, the critique states, that although not necessary for conservation, Alaska's full-curl rules have "served a useful purpose." The critique states that this useful purpose has been administrative simplicity and reduction in the need for biological research and monitoring resulting from, "a hands-off, self-regulating, popular, and inexpensive regime of harvest." (page 492 bottom of column 2). The critique closes:

> Management challenges are beginning to change…Full-curl regulations cannot ensure hunter satisfaction…full-curl regulations alone cannot ensure trophy quality…at minimum full-curl size or age. These are problems that hunters now petition the Board of Game to solve through stricter full curl management; [*Here the critique retrieves an earlier statement from page 484 column 2 paragraph 2 that "The Board still receives proposals…for more rigorous enforcement of full-curl…*]…(page 494 column 1 paragraph 1)

We acknowledge the first two of these summary statements are correct, but argue the negative consequences the critique subsequently predicts can only be secondary results of the way the Alaska Department of Fish and Game manages the full-curl regulation. Most of the regulatory enforcement concerns and predicted eventual hunter dissatisfaction are predictable results of ADF&G's continued reluctance to accept the biological basis of the full-curl regulation, even as a working hypothesis. We suggest the critique is evidence this reluctance has its roots in the dogma that "principles of ungulate management" offer a higher probability of management success than the respect for the autecology of a particular species. For example, if the agency's position is that distorting Dall sheep ram age structure is no different than distorting a moose population's age structure, because both have "complex social structures," the full-curl regulation devolves from a biologically based regulation to increase human benefits to an administrative convenience for the agency.

There is little adaptive benefit (beyond avoiding prosecution) for an Alaskan hunter to comply with or philosophically embrace a regulation established for the administrative convenience of the managing agency. Conversely, there is every reason for hunters to embrace, comply with, and build a societal peer pressure to embrace biologically based regulations. It is, after all, in the individual hunter's best interest to identify with biologically based regulations because they are designed and implemented to increase user benefits.

Still, the nature of management in natural ecosystems makes it virtually impossible to assure that any regulation will inevitably produce desirable results because its underlying biology is perfectly known and predictable. Consequently, enforcement of regulations through police powers has been a consistent fixture of North American wildlife conservation. However, coercive conservation has never been the long-term basis of successful wildlife conservation.

The success of North American wildlife conservation has more probably resulted from voluntary compliance with biologically based regulations, which hold the promise of continued or more successful participation by the necessary user/supporter/benefactors. Traditionally, these benefactors have a rational, tradition-based expectation that regulations be biologically based. The support of "traditional sport hunters" for any biologically based harvest regulation (whether it suits them in the short run or not) is predictable, and should not be understood to compromise the biological validity of the full-curl regulation. Similarly, the fact that these "traditional sport hunters" had to take the Department's then-certified data to the Board of Game in the face of Departmental opposition should not implicitly argue against the regulation's biological relevance.

We have never asked the managing agency to endorse the full-curl model as proven truth. Instead, we have championed the notion that it should be included as part of a comprehensive working management hypothesis (Heimer 1999a). We have argued that the hunting and conservation-minded public should be partners in the management enterprise, and that this requires constant testing of our management hypothesis and refinement as appropriate. Unfortunately, many management agencies (including the Alaska Department of Fish and Game in this case) have come to view hunters more as regulated predators than management partners. Arbitrary, administratively convenient regulations reflect this distressing trend. We find it particularly tragic, and indeed risky, when a managing agency elects to justify decisions using self-serving administrative rationale when it could take the higher road in partnering with hunter/conservationists in pursuit of functional biological truths upon which to manage.

Before the Alaska Department of Fish and Game took this road with the full-curl regulation, it had chosen it in moose management with "spike-fork or 50-inch" bull moose regulations. The work of Strigham and Bubenik (1984) on red deer and chamois, plus the work of Child (1983) and Child and Aitken (1989) established an acceptable biological rational for limiting harvest to mature bull moose. Unfortunately, rather than defining the restriction of moose harvests to mature bulls as part of a biologically based working hypothesis for moose management, ADF&G synthesized a finely tuned rationale (Schwartz et al. 1992), which lay in administrative management convenience and efficiency. The critique's presentation of Alaska's full-curl harvest regulation is homologous to ADF&G's "50-inch" moose regulations.

We consider this high-risk, elitist management that respects neither the biological adaptations of the managed prey species nor the human harvesters involved. Our collective approach to Dall sheep management in Alaska has been based on recognition of and respect for both. Additionally, we have tried to be as honest, inclusive, and scientifically rigorous as circumstances (primarily limited by budgets and logistics) allowed. We are saddened that this rebuttal was required, but realize science is a human enterprise where objectivity is difficult. We also realize our interdisciplinary synoptic approach has been unorthodox. Nevertheless, we think we have chosen a practical, biologically based route to providing increased human benefits from Alaska's Dall sheep populations. If we have been mistaken, and if we keep in mind that we are all involved in testing a hypothesis, we should end up better off in the future than in the past. Consequently, we will argue for continuing the experiment in progress and against throwing it out because of narrowly focused critiques such as the one we reviewed here. Thank you for your patience

LITERATURE CITED

BRADLEY, W. G., AND D. P. BAKER. 1967. Life tables for Nelson Bighorn sheep on the Desert Game Range. Trans. Desert Bighorn Counc. 11:142-169.

CHILD, K. N. 1983. Selective harvest of moose in Omineca: some preliminary results. Alces 19:162-177.

_____, AND D. A. AITKEN. 1989. Selective harvests, hunters and moose in central British Columbia. Alces 25:81-97.

DAUPHINE, T. C. 1976. Biology of the Kaminuriak population of caribou. Part 4: Growth, reproduction and energy reserves. Can. Wild. Serv. Rep. Ser. No. 38.

DEEVEY, E. S. JR. 1947. Life tables for natural populations of animals. Quart. Rev. Biol. 22:283-341.

GEIST, V. 1971, Mountain Sheep: a study in behavior and evolution. Univ. Chicago Press. Chicago and London. 371pp.

HAMILTON, W. J., AND K. L. BLAXTER. 1980. Reproduction if farmed red deer: hind and stag fertility. J. Agric. Sci. 95:261-273.

HEIMER, W. E. 1973. Dall sheep movements and mineral lick use. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Rest. Final Rep. Proj. w-172, W-17-3, w-17-4, and W-17-5. Job. 6.1R Juneau. 35pp.

_____. 1975. Sheep research job progress report. Alaska Dep. Fish and Game. Fed. Aid. Wildl. Rest. Proj. W-17-7. Jobs 6.9-6.11R. Juneau, AK. 5pp.

_____. 1983. Dall sheep body condition and nutritional profile. Final Rep. Fed. Aid in Wildl. Rest. Proj. Nos. W-17-8, 9, 11, W-21-1,2. Job 6.12R. Alaska Dep. Fish and Game Juneau. 52pp.

_____. 1994. Aerial survey and Dall sheep population size: Comparative usefulness of external and internal population dynamics for management purposes. Proc. Bienn. Symp. North. Wild Sheep and Goat Counc. 9:43-50.

_____. 1999. A working hypothesis for thinhorn sheep management. pp.25-46. in Alan and Harriet Thomas eds. 2nd N. A. Wild Sheep Conf. No. Wild Sheep and Goat Counc. Thermopolis WY and Desert Bighorn Counc. Las Vegas. NV. 470pp

_____. 1999a. Introduction to the 2nd North American wild sheep conference. pp. 21-24 in Alan and Harriet Thomas eds. 2nd N. A. Wild Sheep Conf. No. Wild Sheep and Goat Counc. Thermopolis WY and Desert Bighorn Counc. Las Vegas. NV. 470pp

_____, AND S. M. WATSON. 1986. Comparative dynamics of dissimilar Dall sheep populations. Fed. Aid in Wildl. Rest. Final Rep. Proj. W-22-1 through W-22-4. Job 6.9R. Alaska Dept. Fish and Game, Juneau, AK. 101 pp.

_____, and _____. 1990. The effects of progressively more restrictive regulations on ram harvests in the eastern Alaska Range. Proc. Bienn. Symp. North. Wild Sheep and Goat Counc. 7: 45-55.

_____, _____, AND T. C. SMITH III. 1984. Excess ram mortality in a heavily hunted Dall sheep population. Proc. Bienn. Symp. North. Wild Sheep and Goat Counc. 4: 425-432.

HOGG, J. T. 1984. Mating in bighorn sheep: Multiple creative male strategies. Science 225:526-529.

JENNI, D., J. T. HOGG, AND C. HASS. 1986. Effects of ram removals on breeding and reproduction in bighorns. Proc.Bienn Symp. North. Wild Sheep and Goat Counc. 5: (verbal presentation only—no published paper).

MURIE, A. 1944. The wolves of Mt. McKinley. U.S. Dept. Int., Nat. Park Serv. Fauna Ser. 5. 282pp.

MURPHY, E. C. AND K. R. WHITTEN. 1976. Dall sheep demography in McKinley Park and a re-evaluation of Murie's data. Journal of Wildlife Management. 54:284-290

_____. F. F. SINGER, AND L. NICHOLS. 1990. Effects of hunting on survival and productivity of Dall sheep. Journal of Wildlife Management 40:597-609.

NICHOLS. 1970. Aerial inventory and classification of Dall sheep in Alaska. Trans. North. Wild Sheep Counc. Williams Lake. B.C. 25-33.

_____. 1978. Dall sheep reproduction. J. Wildl. Manage. 42:570-580.

SCHWARTZ, C. G., K. J. HUNDTERMARK. AND T. H. SPRAKER. 1992. An evaluation of selective bull moose harvest on the Kenai Peninsula, Alaska Alces 28:1-13.

TOWEILL, D. E. AND V. GEIST. 1999. Return of Royalty, wild sheep of North America. Boone and Crockett Club/Foundation for North American Wild Sheep. Missoula MT/Cody WY. 214pp.

WHITTEN, K. R. 1997. Estimating population size and composition of Dall sheep in Alaska: Assessment of previously used methods and experimental implication of new techniques. Fed. Aid Wildl. Rest, Res. Final Rep. Grants W-24-3, W-24-4, W-24-5. Study 6.11

Northern Wild Sheep and Goat Council Symposia

Date	Symposium	Location	Symposium Coordinator/Chair	Proceedings Editor(s)	NWSGC Executive Director
May 26-28, 1970	NWSC 1	Williams Lake, BC	Harold Mitchell		
Apr. 14-15, 1971	NAWSC 1	Ft. Collins, CO	Eugene Decker/ Wayne Sandfort	Eugene Decker	
Apr. 11-13, 1972	NWSC 2	Hinton, AB	E. G. Scheffler		
Apr. 23-25, 1974	NWSC 3	Great Falls, MT	Kerry Constan/ James Mitchell		
Feb. 10-12, 1976	NWSC 4	Jackson, WY	E. Tom Thorne		
Apr. 2-4, 1978	NWSGC 1	Penticton, BC	Daryll Hebert/ M. Nation	Daryll Hebert/ M. Nation	
Apr. 23-25, 1980	NWSGC 2	Salmon, ID	Bill Hickey		
Mar. 17-19, 1982	NWSGC 3	Ft. Collins, CO	Gene Schoonveld	James A. Bailey/Gene Schoonveld	
Apr. 30-May 3, 1984	NWSGC 4	Whitehorse, YK	Manfred Hoefs	Manfred Hoefs	Wayne Heimer
Apr. 14-17, 1986	NWSGC 5	Missoula, MT	Jerry Brown	Gayle Joslin	Wayne Heimer
Apr. 11-15, 1988	NWSGC 6	Banff, AB	Bill Wishart	Bill Samuel	Wayne Heimer
May 14-18, 1990	NWSGC 7	Clarkston, WA	Lloyd Oldenburg	James A. Bailey	Wayne Heimer
Apr. 27-May 1, 1992	NWSGC 8	Cody, WY	Kevin Hurley	John Emmerich/ Bill Hepworth	Wayne Heimer
May 2-6, 1994	NWSGC 9	Cranbrook, BC	Anna Fontana	Margo Pybus/ Bill Wishart	Kevin Hurley
Apr. 30-May 3, 1996	NWSGC 10	Silverthorne, CO	Dale Reed	Kevin Hurley/ Dale Reed/ Nancy Wild (Compilers)	Kevin Hurley
Apr. 16-20, 1998	NWSGC 11	Whitefish, MT	John McCarthy	John McCarthy/ Richard Harris/ Fay Moore (Compilers)	Kevin Hurley
May 31-Jun 4, 2000	NWSGC 12	Whitehorse, YK	Jean Carey	Jean Carey	Kevin Hurley
Apr. 23-27, 2002	NWSGC 13	Rapid City, SD	Ted Benzon	Gary Brundige	Kevin Hurley