

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

Kenneth R. Whitten

Alaska Department of Fish and Game, 1300 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 1970s resulted in accelerated mortality of young males and low productivity in female sheep. Changing to a more conservative harvest of seven-eighths 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 in 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*

During the 1970s and 1980s the Alaska Department of Fish and Game conducted intensive studies of Dall's sheep (*Ovis dalli dalli*) in the Dry Creek area of the central Alaska Range south of Fairbanks, Alaska, USA. Researchers concluded that removal of nearly all mature males by intensive harvest of three-quarter curl or larger individuals resulted in accelerated mortality of young males (Heimer et al. 1984) and low productivity in female sheep (Heimer and Watson 1986, 1990). Hypotheses explaining the events at Dry Creek were built on the premise that mature males dominate

mating and suppress courtship by immature males in naturally regulated populations of Dall's sheep (Heimer and Watson 1986). When harvest allegedly eliminated mature males, young males were hypothesized to have begun participating actively, but inefficiently, in rut. Rutting at an early age was thought to have caused many young males to deplete their fat reserves and succumb to high overwinter mortality that would normally have affected only older males. Thus, fewer males survived to harvestable age, accounting for a decline in harvest that occurred in the mid-1970s. Young males

also were thought to have harassed adult females, which reduced fitness of females and lowered population productivity. Young males presumably mated with yearling females that older males would have spurned (Heimer and Watson 1986). 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). Changing to more conservative harvest of seven-eighths curl and then full-curl males allegedly reversed these adverse trends, resulting in higher sustained harvest of males throughout the 1980s and into the 1990s (Heimer and Watson 1990).

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 age structure toward young males than three-quarter curl only hunting had ever caused in Dall's sheep, yet far greater consequences from harvesting males were being claimed for sheep. Furthermore, researchers studying other populations of sheep were unable to corroborate a relationship between abundance of older males and survival of young males (Murphy et al. 1990), and increases in production of young, similar to those at Dry Creek after harvest was restricted, also occurred in Denali National Park and other areas where sheep had always been hunted only lightly or not at all (Gasaway et al. 1983, Singer and Nichols 1992, Rachlow and Bowyer 1994). Thus many biologists concluded that adverse weather in the early 1970s, which was recognized to have pre-

cipitated widespread declines of ungulates in Alaska (Gasaway et al. 1983), also could explain the decline in sheep at Dry Creek. Generally favorable weather throughout the state in the late 1970s and 1980s could explain the subsequent increases in sheep numbers and harvest. Indeed, a questionnaire to Alaska Department of Fish and Game sheep managers and researchers in the mid-1980s reported consensus on most aspects of sheep ecology, including effects of weather, but respondents were evenly divided on the proposition that maximum yield could only be achieved under full-curl management (Heimer 1987).

Although many biologists disagreed with the Dry Creek hypotheses, 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 fairing poorly. Disagreement and confusion continues among professional biologists, as exemplified by the opposing conclusions on effects of heavy harvest of mature males reached in recent texts on wild sheep (Heimer 1999, Nichols and Bunnell 1999, Bowyer et al. 2000).

For this paper, I reviewed published reports and original data from the 1970s and 1980s studies conducted at Dry Creek to reassess several key elements of published hypotheses regarding the role of abundance of large males versus other ecological factors in explaining population dynamics of sheep. I examined whether all or most mature males were killed in the early to mid-1970s, whether mortality of young males increased when mature males were scarce

and then recovered after mature males were largely protected by restrictive horn-curl regulations, and whether female productivity varied directly with abundance of mature males.

Main Study Area and Sheep Population

The Dry Creek studies focused on Dall's sheep associated with a large mineral lick in the central Alaska Range south of Fairbanks, Alaska, USA (63°55'N, 145°25'W). Sheep were captured and marked at the lick on Dry Creek from 1968 to 1971. The lick was then observed for varying periods each summer into the 1980s. Researchers occasionally used aircraft and foot surveys to search for marked sheep away from the lick. The area encompassing resighting locations of marked sheep became known as the Dry Creek Study Area. All sheep in the study area were assumed to form a discrete population associated with the lick (Heimer and Watson 1986).

One method for estimating population parameters of sheep at Dry Creek was aerial survey. Contrary to statements in methods sections of published research reports (e.g., Heimer et al. 1984), aerial surveys were infrequent, and only 5 surveys

covering most or all of the study area were conducted between 1970 and 1984 (Table 1). Variable coverage and inconsistent sex and age classifications made it difficult to reliably determine even simple parameters like male to female ratios or percentage of males in the population. Adult females, one-quarter curl males (usually 2-year-olds), and yearlings of both sexes were indistinguishable in observations made from fixed-wing aircraft and were lumped as "female-likes." Inclusion of young males with "female-likes" meant that estimates of percentage of males in aerial surveys always were biased low. Researchers claimed legal males (three-quarter curl) had declined to about 3% of the population by the mid-1970s (Heimer 1973, Heimer and Watson 1986), 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 (Table 1).

Incomplete classification of many groups of sheep also made direct comparison of male to female ratios difficult (Table 2). To calculate male to "female-like" ratios for 1970, I assumed unidentified "female-likes" were composed of young and "female-likes"

Table 1. Numbers and composition (%) of Dall's sheep counted in major aerial surveys of the Dry Creek area, interior Alaska, USA.

Year	Sublegal males	Legal males	Unclassified males	Female-likes ¹	Young	Unidentified female-likes ²	Total
1970	113(8)	101(7) ³	14(1)	624	289	319	1469
1975	189(15)	97(8) ³	17(1)	—	32	902	1237
1980	176(13)	69(5) ⁴	42(3)	773	339	8	1407
1982	205(21)	50(5) ⁴		625	75		955
1984	269(20)	22(2) ⁵		742	280		1313

¹ Includes adult females, yearlings of both sexes, 2-year-old males, and possibly some 3-year-old males.

² Also includes young of the year with female-likes.

³ Three-quarters curl.

⁴ Seven-eighths curl.

⁵ Full-curl.

Table 2. Estimated males per 100 "female-likes"¹ in aerial surveys of Dall's sheep in the Dry Creek area (1970-1984), in comparison to males per 100 "female-likes" calculated from ground composition counts in Denali National Park (1973), interior Alaska, USA.

Year	Males per 100 "female-likes"		
	Dry Creek	Unhunted Denali Park (1973) ²	
1970	Total males	27	45
	Sublegals	13	18
	Legals(3/4)	12	26
1975	Total males	39	45
	Sublegals	21	18
	Legals(3/4)	11	26
1980	Total males	37	45
	Sublegals	23	22
	Legals(7/8)	9	23
1982	Total males	41	45
	Sublegals	32	22
	Legals(7/8)	8	23
1984	Total males	39	45
	Sublegals	36	30
	Legals(full)	3	15

¹ Includes adult females, yearlings of both sexes, 2-year-old males, and possibly some 3-year-old males.

² Data from Whitten 1975.

in the same proportions as in groups that were classified fully. For 1975 I had to assume unidentified "female-likes" were in the same proportion as "female-likes" and young at the lick. Summary reports of the Dry Creek studies claimed only 17 males:100 females in the 1975 survey (Heimer and Watson 1986, 1990), but original survey records do not agree (Table 2). Also, comparison with composition data from unhunted sheep inhabiting Denali National Park strongly suggests survival of young males at Dry Creek was not compromised

by harvest of older males (Table 2). Supposedly chronic heavy harvests in the mid-1970s only reduced abundance of legal males by about one-half and had little or no effect on abundance of younger, sublegal males. Males were not scarce in the Dry Creek area in 1975 compared to 5 years before or 5-9 years after.

Population parameters also were generated from observations at the Dry Creek mineral lick, based on the assumption that all sheep in the study area visited the lick during June each year. There was no objective basis, however, for assuming that all sheep (particularly males) visited the lick. Visitation rates by marked sheep, sex and age composition, and timing of activity at the lick varied markedly between 1972 and 1973 (Heimer 1973), the 2 years in which observations were most complete. Legal males composed 2-4% of the sheep seen at the lick in the early 1970s, values that were very different from the proportions in aerial surveys (Table 1).

Mortality Estimates Derived from Resightings of Marked Males

Early progress reports from the Dry Creek studies recognized that low rates of return by marked males to the lick could mean males exhibited low fidelity to the lick, at least during periods the lick was under observation (Erickson 1970, Nichols and Smith 1971, Heimer 1973). In spite of suspected infidelity of males to the lick and data from aerial surveys indicating males were more abundant in the general population, researchers at Dry Creek concluded by the early 1980s that males were not unfaithful to the lick. These researchers assumed instead that unseen males were dead. A life table based on resightings of marked males was developed to examine mortality rates of sublegal males (Heimer et al. 1984, Heimer and Watson 1986).

Several assumptions were necessary to

construct the life table. First was that living males either returned to the lick every year or were otherwise detected in foot and aerial surveys of the study area. Any male not seen in 2 consecutive years was assumed to have died the first year it was missed. Additional assumptions were that marked males were individually recognizable (i.e., the markers could be read), and that the markers lasted until males died. That these assumptions were routinely violated should have been apparent. As previously mentioned, aerial searches were actually few and far between, and in most years there were no foot searches for marked sheep away from the lick. Two-thirds of the males were marked only with ear tags or small tags hanging from a rope collar, which could not be individually identified from aircraft (Heimer 1973). Even neckband collars with large numerals were seldom readable from the air, and collars were commonly lost, leaving those males with only ear tags. Original records also indicated that some markers broke, frayed, or became otherwise unreadable even from the ground at relatively close range. Observers occasionally noted sheep with markers that appeared intact but were unreadable because of distance, position, or other factors. Finally, some markers were misidentified (e.g., a male was identified by ear tag number at the lick a year after it had been shot and turned in by a hunter).

Another serious breach of assumptions was that after 1975, the lick was observed only in late June-early July, a period during which earlier observers had reported use by males to be low (Erickson 1970, Nichols and Smith 1971, Heimer 1973), and the lick was watched for only 3-8 hr/day (based on original data records). Total numbers of sheep observed entering the lick during 1976-1979, which included multiple visits by many individuals, were usually less than two-thirds of estimated population size.

Clearly, no one should have expected to detect every living marked male when the lick was watched only discontinuously at a time of year when use by males was low, little or no additional survey of the study area occurred, and one-third or more of the population was never observed.

Nevertheless, an analysis of mortality rates of males was prepared based on data from resightings of Dry Creek sheep (Heimer et al. 1984). The life table from which rates were calculated was reportedly based on 116 males captured and marked from 1969 to 1971, but 39 of those males, including all males shot by hunters, were eliminated from analysis and the life table actually contained data from only 77 males (Heimer et al. 1984). Justifications for eliminating males from analysis were unsupportable. For instance, 14 males caught as "sublegals" and shot later as "legals" should have remained in the data set, the purpose of which was to look at survival to huntable age. Also, 16 1- and 2-year-old males tagged in 1970 were eliminated from data analysis on the basis that they were never resighted because unusually severe winter weather caused their early demise (Heimer et al. 1984). Original data files, however, indicate that only 4 were never seen again, while the remainder were resighted numerous times over the next 3-7 years. Heimer et al. (1984) failed to establish that age distribution of males was stable (Murphy and Whitten 1976, Caughley 1977, McCullough 1979) before attempting their analysis of mortality for male sheep. Researchers at Dry Creek also erred in failing to use staggered-entry or product-limit techniques to analyze data from males that were captured at different ages (Kaplan and Meier 1958, Pollock et al. 1989). For example, males captured at 5 years-of-age were erroneously included in mortality calculations for the 1 to 4-year-old age classes.

Problems with improper handling of data

by Heimer et al. (1984) were dwarfed, however, by the frequency with which males known to have been alive (because they were seen or shot by hunters in later years) were not detected at the lick or in any other surveys of the study area (Table 3). Even rates at which male sheep known to be alive failed to return to the lick (Table 3) are biased low because males may have lived past when they were last seen. An unbiased rate of failure of living males to return to the lick, calculated from shot males for which year of death was positively known, was 44% (27 of 62 possible returns to the lick; Table 4).

Calculated rates of mortality for 4- to 7-year-old males in observations at the Dry Creek mineral lick were much higher than reported rates for hunted populations

Table 3. Annual proportions of marked male Dall's sheep known to be alive in the Dry Creek area, interior Alaska, USA, that were not observed during aerial or ground surveys, 1969–1980.

Year	Males not observed/ Marked males available ¹	Percent males not observed
1969	1/3	33
1970	6/22	27
1971	9/40	22
1972	13/71	18
1973	9/55	16
1974	12/37	32
1975	3/22	14
1976	5/9	55
1977	4/6	67
1978	3/5	60
1979	no data	—
1980	1/3	33
1981	1/1	100
1982	1/1	100
1969–1982	67/275	24

¹ Males observed or shot by hunters in later years, but not detected in any surveys of the Dry Creek study area during the year noted.

(Heimer et al. 1984). The assumption that unseen males were dead clearly was not valid, however, and resighting observations of males were not suitable for determining mortality rates. Failure to resight a male resulted from a combination of factors in addition to mortality—marker loss, tag misidentification, and low monitoring effort at the lick and throughout the remainder of the study area. Consequently, conclusions on mortality rates of young males drawn from the life table were unsupportable and incorrect.

Harvest Rates of Male Sheep in the Dry Creek Study Area

Dry Creek researchers frequently claimed that all or most legal males were harvested each year, but their own findings did not support that conclusion. Heimer et al. (1984) reported a cumulative, not annual, harvest of 10/23 males (43%) that were legal when marked. Nonetheless, original records indicate that only 6 males marked when they were already legal were turned in by hunters, whereas 4 others were only presumed to have been shot. Heimer et al. (1984) also reported that hunters took 12 marked males that grew from sublegal to legal size, which was less than the proportion of already legal males that were shot. This outcome was supposedly further evidence that young males disappeared to early mortality before they grew to legal size and became available to hunters. Again, however, numbers in Heimer et al. (1984) are inconsistent with original records. Fourteen males marked as "sublegals" were later shot as legal males, and the true proportion of sublegal males eventually shot by hunters (14/95; 15%) was not significantly different from the proportion among males that were already legal when marked (6/23; 26%; $\chi^2_1 = 1.14, P = 0.29$).

I used original data on resightings of marked males to determine annual harvest

Table 4. Resighting histories of marked male Dall's sheep harvested by hunters in the Dry Creek area, interior Alaska, USA, 1968-1982.

COLLAR	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982
10		C ¹	1	0	0	0	0								
15		C	0	0	0	0	0								
17		C	2												
37		C	1												
59			C	0	0	0	0								
83			C	1	1	1	0								
85			C	0	1	1	0								
87			C	1	1	1									
89			C	1	1										
91			C												
95			C	1											
127				C	1	1	1								
134				C	0										
143				C	2	1	1	1	0						
151				C	1	1	1	0	1	0	0		0		
156				C	1	0	1	2	0	1	0		0		0
170				C											
177				C	1	1									
193				C	1	1									
GS			C	1	1										

¹ C = captured; 0 = not observed; 1 = observed at Dry Creek mineral lick; 2 = observed in study area, but not at the lick.

rates; something the Dry Creek researchers never did. Rates of harvest for rams that were of legal age (i.e., ≥ 5 years old) were 0-21% until sample size dropped to ≤ 3 (Table 5). As with other calculations based on data from marked male sheep, these harvest rates are biased (high, in this instance) because of the high probability that at least some marked males were still alive and available for harvest after they were last observed in aerial or ground surveys, but were never shot. At least 30 males marked as "sublegals" at Dry Creek lived to legal age but were not shot by hunters. Other data also did not indicate high harvest, certainly not approaching removal of all or most legal males every year. Annual harvests of males from a portion of the Alaska Range that included extensive

sheep habitat in addition to the Dry Creek study area were consistently less than numbers of legal males counted on aerial surveys within the study area only. Also, the proportion of marked sublegal males shot later by hunters in the Dry Creek study area (14/95; 15%) was not significantly different from the proportion of marked sublegal males eventually harvested in the supposedly lightly hunted Tok Management Area, approximately 200 km east of the Dry Creek Study Area (6/33; 18%; $\chi^2_1 = 0.16$, $P = 0.69$).

The final argument by Dry Creek researchers for linking conservative horn-curl regulations to higher survival of young males was empirical evidence of steadily increasing harvests, as regulations became more restrictive (Heimer and Watson 1990).

Table 5. Ages in years of marked male Dall's sheep available for harvest in the Dry Creek area, interior Alaska, USA, 1968-1982 (assumes males reached three-quarter curl at age 5 and seven-eighths curl at age 7).

1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982
5	5	5	5	5	5	5	5	6	7	8	9	11	12	13 ¹
	5	6	6	5	5	5	5	7	8	9	10	11		
	6	6 ¹	8	5	5	5	5	7	8	9	10	12 ¹		
	6	7	8	5	5	5	5	7	8	10	11			
	6	7	8	5	5	5	5	7 ¹	9	11				
	6	7	8	5	5	5	5	8	10					
	6	7	8 ¹	5	5	5	6	8						
	6	7	8 ¹	5	5	5	6	9						
	7	7	9	5	5	5	6	9						
	7	7	10	5 ¹	5	5	6							
	8	7		6	5	5	6							
		7		7	5	5	6							
		7		9	5	5	6							
		8 ¹		9	5 ¹	5 ¹	6							
		8 ¹		11 ¹	5 ¹	6	6							
		8			5 ¹	6	7							
		9			6 ¹	6	7							
					6	6	7							
					6	6	7							
					6	6	7							
					6	6	8							
					6	6 ¹	8							
					6	6 ¹	8							
					6	7								
					7	7								
						7								
						7 ¹								
						7 ¹								
						8 ¹								
Harvest rate ² (%):														
0	0	17	20	13	16	21	0	11	0	0	0	33	0	100

¹Denotes harvested males.

²Annual percentage of legal-aged males harvested.

The apparent correlation disappeared, however, after sheep populations in many areas of the state declined during the record deep snows and cold temperatures from 1989 to 1993. Consistently lower harvests were eventually achieved under full-curl management in the central Alaska Range than had ever occurred under purportedly heavy

harvest of three-quarter curl males in the 1970s (Table 6). Most managers and researchers now studying Dall's sheep recognize that harvest figures actually tracked population trends that were regulated by major weather patterns. Changes in horn-curl regulations did not affect trends in sheep populations.

Table 6. Productivity of Dall's sheep and harvest parameters relative to horn-curl regulations, central Alaska Range, interior Alaska, USA, 1968–1997.

Hunting regulation	Year	Hunters	Harvest	Young:100 females	Mean horn length (cm)
3/4-curl	1968	366	138	63	84.1
	1969	262	97	64	83.6
	1970	269	119	55	85.3
	1971	376	133	50	85.6
	1972	359	120	35	82.6
	1973	246	78	38	79.5
	1974	232	101	28	80.8
	1975	217	97	28	82.0
	1976	248	112	36	82.0
	1977	233	116	58	82.0
	1978	248	98	41	80.8
7/8-curl	1979	226	86	65	84.8
	1980	214	88	67	88.6
	1981	252	116	60	88.6
	1982	189	112	31	86.4
	1983	297	121	57	85.6
Full-curl	1984	292	105	51	86.4
	1985	292	102	40	86.4
	1986	357	136	33	86.9
	1987	354	142	53	88.9
	1988	404	154	41	88.2
	1989	410	163	—	87.1
	1990	379	124	—	87.4
	1991	338	109	18	87.6
	1992	230	62	5	86.4
	1993	166	50	12	86.6
	1994	147	49	50	88.6
	1995	164	60	44	90.7
	1996	151	54	51	90.2
1997	178	45	40	89.2	

Effects of Horn-curl Regulations on Productivity of Females

Young to female ratios at Dry Creek were lower in the mid-1970s (about 1972–1976) than in similar time periods before and after (Table 6). Dry Creek researchers realized that variation in young to female ratios correlated with weather patterns (Heimer and Watson 1986). These authors reported that the mean young to female

ratio for 1981–1984 (a good weather period) was higher than the mean for 1972–1976 (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 ratios 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 caused the larger rise in consecutive-year reproduction. Consecutive-year reproduction and young to female ratios were calculated from the same observations, however, and were not independent variables. Mathematically, the 6-fold increase in consecutive-year reproduction could only result in the observed doubling in young to female ratio—no more or less. A single explanation is thus sufficient to explain both parameters.

Ovarian activity in females at Dry Creek (expressed as number of corpora lutea and corpora albicantia divided by years of potential rutting activity) was reported to be lower during 1973–1979, when older males supposedly were reduced, than among females in the lightly hunted Tok Management Area during 1976–1979, when older males presumably were abundant (Heimer and Watson 1986). Most (75%) rutting activity in the Dry Creek sample, however, occurred before 1973, when reduced male abundance allegedly began (Table 7). Furthermore, ovarian activity in females at Dry Creek did not change over time. There was always a mix of higher and lower ovarian activity regardless of how many older males were thought to be present in the Dry Creek population. Females from the Tok Management Area had generally higher ovarian activity than females from Dry Creek, but abundance of males could not explain that difference.

Mating by yearling females, resulting in them giving birth as 2-year-olds, was hypothesized to be detrimental to long-term productivity and was thought to have resulted from a lack of mature males (Heimer and Watson 1986). Early mating in the Tok Management Area from 1978 to 1984 was less common than recorded at Dry Creek, but original records show that data suggesting early breeding at Dry Creek were recorded during 2 periods (1969–1971 and

1981–1984) when older males were thought to be abundant; no data were collected from the period when older males supposedly were reduced (Table 8).

Benefits and Limitations of Full-curl Management for Dall's Sheep

Numerous papers have expounded on various aspects of the Dry Creek hypotheses and 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. Depressed survival of young males in the Dry Creek population never occurred. Reduced productivity could not be linked to male abundance, but was correlated with weather. 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. However, full-curl rules have served a useful purpose. In the 1990s, attention and funding for wildlife management in Alaska gravitated more toward subsistence issues and to moose, caribou, and their predators. Money for sheep research and monitoring dwindled. Hunters generally were satisfied with restrictive horn-curl management (Whitten 1994) and full-curl regulations definitely increased mean horn lengths of harvested males (Table 6). Demand for hunting nontrophy sheep in Alaska has remained low, and hunting of female sheep, which could potentially affect populations, occurs only at low levels in remote subsistence hunting areas or in a few closely regulated permit hunts. Thus, the unanticipated benefit of full-curl management has been as a hands-off, self-regulating, popular, and inexpensive regime of harvest.

Table 7. Ovulation rates¹ and years of potential rutting activity (x)² for female Dall's sheep collected in the Dry Creek area interior Alaska, USA.

ID no.	Rate ¹	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979
3696	0.20			x	x	x	x	x	x	x	x	x	x								
3897	0.25										x	x	x	x							
5009	0.38													x	x	x	x	x	x	x	x
3896	0.43							x	x	x	x	x	x	x							
3892	0.56					x	x	x	x	x	x	x	x	x							
3889	0.67					x	x	x	x	x	x	x	x	x							
3891	0.67					x	x	x	x	x	x	x	x	x							
3895	0.67								x	x	x	x	x	x							
4385	0.67								x	x	x	x	x	x	x	x					
5012	0.70												x	x	x	x	x	x	x	x	x
5036	0.71													x	x	x	x	x	x	x	
3624	0.75	x	x	x	x	x	x	x	x	x	x	x	x								
3888	0.78					x	x	x	x	x	x	x	x	x							
3580	0.80								x	x	x	x	x								
3890	0.89					x	x	x	x	x	x	x	x	x							
4745	0.90								x	x	x	x	x	x	x	x	x	x			
3894	1.00													x							
4743	1.00													x	x	x	x	x			
3559	1.50											x	x								
3697	3.00										x	x	x								

¹Total corpora lutea plus corpora albicantia divided by years of potential rutting activity.

²x denotes a year of potential rutting activity, assuming females first ovulate at age 18 months and then annually thereafter (Heimer and Watson 1986).

Table 8. Early breeding, as evidenced by pregnant yearling or parturient 2-year-old females, in the Dry Creek and the Tok Management Areas, interior Alaska, USA.

Location/Years	Parturient	Nonparturient
Dry Creek 1969-1971	7 ¹	23
Dry Creek 1981-1984	4	13
Tok Management Area	2	25

¹Number of female sheep.

Management challenges are beginning to change, however. Full-curl regulations cannot ensure hunter satisfaction when success declines because of crowding, competition among hunters, or naturally low populations of sheep. Full-curl regulations alone cannot ensure trophy quality when heavy harvest crops males 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; but horn-curl regulations alone are not the solution. Hunter dissatisfaction will dissipate in some areas as Dall's sheep recover from recent weather-induced declines in population size and more mature males again become available for harvest. In other instances, relief will come only through stricter control of hunter numbers, or hunters will have to learn to be satisfied with less aesthetic hunting conditions and minimum-sized, full-curl horns as trophies.

REFERENCES

- BOWYER, R. T., D. M. LESLIE, JR., and J. L. RACHLOW. 2000. Dall's and Stone's sheep. Pages 491-516 in S. Demarais and P. R. Krausman, editors. *Ecology and management of large mammals in North America*. Prentice-Hall, Upper Saddle River, New Jersey, USA.
- CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, New York, New York, USA.
- ERICKSON, J. A. 1970. Sheep report. Dall sheep movements and lick use. Big game investigations. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Annual Research Progress Report, Volume XI. Grants W-17-1 and W-17-2. Jobs 7 and 6.1R. Juneau, Alaska, USA.
- GASAWAY, W. C., S. D. DUBOIS, D. J. REED, and S. J. HARBO. 1983. Estimating moose population parameters from aerial surveys. *Biological Papers of the University of Alaska*, Number 22. Fairbanks, Alaska, USA.
- HEIMER, W. E. 1973. Dall sheep movements and mineral lick use. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Final Report. Grants W-17-2 through W-17-5. Job 6.9R. Juneau, Alaska, USA.
- _____. 1987. Publication of Dall sheep findings and development of future research direction. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Final Report. Grant W-22-5. Job 6.10R. Juneau, Alaska, USA.
- _____. 1999. Thinhorn sheep—Alaska. Pages 46-49 in D. E. Towell and V. Geist, editors. *Return of royalty, wild sheep of North America*. Boone and Crockett Club and Foundation for North American Wild Sheep, Missoula, Montana, USA.
- _____, and S. M. WATSON. 1986. Comparative dynamics of dissimilar Dall sheep populations. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Final Report. Grants W-22-1 through W-22-4. Job 6.9R. Juneau, Alaska, USA.
- _____, and _____. 1990. The effects of progressively more restrictive regulations on male harvests in the eastern Alaska Range. *Biennial Symposium of*

- the Northern Wild Sheep and Goat Council 7:45-55.
- _____, _____, and T. C. SMITH. 1984. Excess male mortality in a heavily hunted Dall sheep population. Biennial Symposium of the Northern Wild Sheep and Goat Council 4:425-433.
- KAPLAN, E. L., and P. MEIER. 1958. Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* 53:457-481.
- MCCULLOUGH, D. R. 1979. The George Reserve deer herd: population ecology of a *K*-selected species. University of Michigan Press, Ann Arbor, Michigan, USA.
- MURPHY, E. C., F. J. SINGER, and L. NICHOLS. 1990. Effects of hunting on survival and productivity of Dall sheep. *Journal of Wildlife Management* 40:597-609.
- _____, 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.
- NICHOLS, L., and F. L. BUNNELL. 1999. Natural history of thinhorn sheep. Pages 23-77 in R. Valdez and P. R. Krausman, editors. *Mountain sheep of North America*. University of Arizona Press, Tucson, Arizona, USA.
- _____, and A. C. SMITH. 1971. Sheep report. Dall sheep movements and mineral lick use. Big game investigations. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Annual Research Progress Report, Volume XII. Grants W-17-2 and W-17-3. Job 6.1R. Juneau, Alaska, USA.
- POLLOCK, K. H., S. R. WINTERSTEIN, C. M. BUNCK, and P. D. CURTIS. 1989. Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* 53:7-15.
- RACHLOW, J. L., and R. T. BOWYER. 1994. Variability in maternal behavior by Dall's sheep: environmental tracking or adaptive strategy. *Journal of Mammalogy* 75:328-337.
- SINGER, F. J., and L. NICHOLS. 1992. Trophy hunting of Dall sheep in Alaska: an evaluation of the biological implications. Biennial Symposium of the Northern Wild Sheep and Goat Council 8:28-48.
- WHITTEN, K. R. 1975. Habitat relationships and population dynamics of Dall sheep (*Ovis dalli dalli*) in Mt. McKinley National Park, Alaska. M.S. Thesis, University of Alaska, Fairbanks, Alaska, USA.
- _____. 1994. Effects of horn size and hunter success of satisfaction with Brooks Range sheep hunts. Biennial Symposium of the Northern Wild Sheep and Goat Council 9:81-91.