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## TROPHY HUNTING OF DALL SHEEP IN ALASKA; AN EVALUATION OF THE BIOLOGICAL IMPLICATIONS

FRANCIS J. SINGER, National Park Service, Natural Resources Ecology Laboratory, Colorado State University, Fort Collins, CO 80523

LYMAN NICHOLS, Box 783, Cooper Landing, AK 99572

**Abstract:** Several hypotheses were investigated concerning the possible negative effects of trophy hunting removal of large-horned Dall sheep (*Ovis dalli dalli*), including the social disruption, magnet, depressed survivorship, and immature ram incompetence hypotheses. Observations on production, breeding behavior, and survival of hunted and unhunted populations were made from 1970-84 in the Kenai Peninsula, and from 1981-85 in central and north-central Alaska. No evidence was obtained that legal harvests of all or most  $\geq 3/4$ -curl (1968-1979) or  $\geq 7/8$ -curl (1979 to end of study) reduced production or recruitment rates in Dall sheep. The depressed ram survivorship hypothesis was not supported by the data, young ram ( $< 3/4$ -curl:100 ewes) versus old ram ( $> 3/4$ -curl:100 ewes) were not correlated. Limited evidence was gathered that breeding occurred later and young rams courted ewes more aggressively in hunted populations (juvenile ram incompetence). Ewes accepted mounts at a higher rate in the unhunted versus hunted central Alaska herd. Observations concerning the magnet hypothesis were equivocal; mid-sized rams departed rut groups an equivalent amount in both populations in central Alaska, but more young rams associated with ewe-young groups outside of the rut in the hunted herd. No short-term effects of trophy hunting under the  $7/8$ -curl regulation were observed on productivity, or ram survival of Dall sheep in Alaska, but the implications of more aggressive courtship, fewer accepted mounts per ewe-hour of observation and greater association of rams with ewes in winter in hunted herds needs to be investigated. Further, research involving greater replication of treatments study sites and greater use of control and manipulated populations is suggested.

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Trophy hunting, the harvest of only older males, in mountain sheep has been hypothesized to result in a number of undesirable population and behavioral consequences (Morgan 1973, 1974, Geist 1971, 1974, Heimer and Watson 1982, Heimer and Watson 1990, Festa-Bianchet 1989). These hypotheses may be characterized (Hogg 1983, Murphy et al. 1990) as:

1. The social disruption hypothesis: Young rams are observed to be more socially disruptive than are dominant, large-horned rams. Younger rams, in the absence of large-horned rams, wastefully court anestrus ewes (Geist,

1971, 1974, Nichols 1972), more wildly chase estrus ewes (Morgan 1973, 1974, Geist 1971), guard estrus ewes less (Geist 1974, Nichols 1972), and court anestrus ewes year-round (Geist 1974). Young rams are more overtly aggressive and more likely to attempt to mount any ewe (Geist 1971:171). Older rams control the activity of younger rams and prevent the excessive harassment of ewes (Geist 1974). Although age-specific differences in rut behavior were documented by Geist (1968), quantitative behavior differences are needed between populations under differing hunting regimes (Festa-Bianchet 1989, Murphy et al. 1990, Shackleton 1991).

2. The magnet hypothesis: In the absence of large-horned rams, young rams are more likely to remain with ewe-young groups throughout the year (Dunbar and Dunbar 1981, Hogg 1983). The largest-horned rams are followed away from ewe groups by younger rams; older rams tend to draw younger rams away with them (Geist 1974, Dunbar and Dunbar 1981). Adult male mountain sheep (*Ovis canadensis*) segregate spatially and by habitat from ewe-young groups (Geist and Petocz 1977, Shank 1982). Spatial segregation of rams outside of the rut may enhance individual fitness of rams by reducing sexual-agonistic behavior at a time when reproduction is not possible (Morgantini and Hudson 1981).
3. The immature ram incompetence hypothesis: Depressed production and recruitment have been hypothesized in Dall sheep populations in Alaska subjected to intense cropping of trophy rams (Heimer and Watson 1982, 1990). Predictions were that conception rates in yearling ewes would be higher in hunted than unhunted populations, resulting in smaller body size and reserves, and subsequently in alternate year or intermittent reproduction in ewes (Heimer and Watson 1982).

Breeding may be later and pregnancy rates lower in populations where all the breeding is done by young males. Bubenik (1971, cited in Stringham and Bubenik 1974) suggested that when young males assume breeding in hunted populations, the rut is later and young may subsequently be born later than the optimum birth date. Dall sheep lambs born late in the lambing period are smaller by the onset of winter and they survive at lower rates (Bunnell 1982). Young rams may be less competent in breeding ewes. In domestic sheep, young rams were less able to detect estrus ewes and estrus ewes were more likely to recognize and display their receptivity to older, sexually active rams (Orgeur 1991). Hogg (1983) speculated that ewes were less receptive to young rams since young rams might be less competent at intromission, and since older rams possess, on the average, superior genotypes and produce superior young (Trivers 1972).

Scarcity of rams in intensely cropped populations might result in lower pregnancy rates, since estrus in ewes is less pronounced when

insufficient number of rams are present (Nichols 1972). Weakly estrus ewes, such as those coming into estrus for the first time are less likely to be bred when insufficient rams are present (Fraser 1968, Grubb and Jewell 1966).

4. Depressed ram survivorship hypothesis. Young rams in the absence of older rams, participate more heavily in the rut, and as a result they may acquire the higher natural mortality rate typical of mature (> 8 years old) rams (Geist 1971, Heimer and Watson 1984). Young rams are reported to court estrus ewes more aggressively and to court anestrus ewes more than do mature rams (Geist 1971, 1974; Nichols 1978). Young rams that are allowed to rut after larger rams are harvested may acquire even higher mortality rates than 8+ year-old rams, since juvenile rams have smaller body size and are *a priori* metabolically disadvantaged to survive the winter (Heimer et al. 1984).

These concerns over the possible effects of trophy hunting of rams in Alaska resulted in progressively more restrictive harvests; in 1968  $\geq 3/4$ -curl restriction was instituted, in 1979 the limit was raised to  $\geq 7/8$ -curl, and in 1989 the limit was raised to full-curl. The purpose of this paper is to review the effects of trophy hunting removals of Dall sheep on productivity, survival, and breeding behavior. The results reported were obtained from the authors' intense classification and behavioral data from hunted and unhunted populations in the Kenai Peninsula, from 1974-84, and in central and north-central Alaska, from 1981-85.

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## STUDY AREAS AND METHODS

Population demography and breeding behavior were studied on the Kenai Peninsula 1970-84 (Nichols 1971, 1972, 1978). The Dall sheep at Cooper Landing were unharvested, while the Surprise Mountain herd was subjected to  $\geq 3/4$ -curl harvest. Nichols (1971, 1972, 1978) describes the Kenai study areas, where he classified sheep annually from fixed-wing aircraft each of the 15 years. The Kenai Peninsula study populations were located only 8 km (5 miles) from each other, although the Sterling Highway separated them and apparently minimized interchange, based upon observations of marked animals (Nichols 1978). Breeding behavior studies were conducted 11 or 16 November - 17 or 20 December 1971 and 1972. All checking, breeding, and guarding interactions

between Dall sheep were recorded following Geist (1968, 1971). An interaction was defined as when 2 sheep come together and perform behavioral displays toward each other (Geist 1971:156). Guarding, breeding, and checking interactions (Geist 1971) were recorded each day. During 1970-78 all or nearly all  $\geq 3/4$ -curl rams were harvested from the Surprise Mountain study area, from 1980-89, all or nearly all  $>7/8$ -curl rams were harvested, and in 1989 the regulation was raised to full-curl in the hunted area. Lamb:ewe ratios were gathered during fixed-wing (Super Cub) surveys by the junior author, 1970-92, as described in Nichols (1978).

The Savage River (unhunted) and Usibelli Mine (hunted) study areas in the central Alaska Range where repeated ground and helicopter classifications were made in 1983 and 1984 are described in Singer et al. (1991). Apparently all legal ( $\geq 7/8$ -curl) rams were harvested from the area each hunting season, although during the late-rut each year (21 Nov 1983, 9 Dec 1984), 1 or 2  $7/8$ -curl rams were observed in the breeding groups. These animals either were not harvested or they moved onto the study area. Breeding observations were made between 15 November-16 December of 1983 and 1984. Two teams of 2 people each hiked over and observed sheep on each study area each day. All ram-ewe and ram-ram interactions observed were recorded. All behavioral displays (Geist 1968, 1971) were recorded during each interaction.

Mounts were expressed as no./ewe-hour, where ewe-hour = no. ewes x no. hours of observation, to correct for observation effort. More limited observations, primarily on activity, were made on a second unhunted population in Denali National Park at Igloo Creek in 1984 (see Singer et al. 1991); only classification data from Igloo Creek in 1984 are presented. Group classifications were obtained from the Savage River (unhunted) and Usibelli Mine (hunted) study populations during March-April of each winter. Helicopter classifications were conducted in June of 1984 and 1985.

Comparisons of population composition from aerial surveys were made between the hunted and unhunted Kenai and central Alaska study areas in order to test for lowered survivorship of young rams in the hunted herds. Comparisons were also made in portions of Gates of the Arctic National Park and Lake Clark National Park just after closure to sport hunting and several years later. The hypothesis that harvests of  $\geq 3/4$ -curl rams resulted in depressed survivorship of younger rams ( $< 3/4$ -curl) was additionally tested from 25 general surveys throughout Alaska, 1974-84. This hypothesis was tested with linear regression under the assumption that the ratios of young ( $< 3/4$ -curl:100 ewes) rams would be directly correlated with ratios of older ( $> 3/4$ -curl:100 ewes) rams if the depressed survivorship hypothesis held. Differences in ratios were tested with the Kolomogorov-Smirnov test using each complete aerial survey as a sample.

Rut behavior was observed in the Kenai Peninsula study areas for 21 days in 1970, and for 22 days in the unhunted area and 25 days in the hunted area in

1971. Observation conditions were good in 1970 on both areas, although low clouds limited visibility on the hunted area during the late rut in 1970.

Rutting behavior of Dall sheep groups was observed for 74 hours in the hunted central Alaska area and 55 hours in the unhunted area in 1983 ( $n = 28$  days) and 1984 ( $n = 29$  days). Plowed road access was available right to the study areas in 1983 and 1984 and visibility was unrestricted in the treeless terrains: typically 2-5 rutting groups might be visible at any time. We hiked to different points in the study areas each day and we attempted to observe different groups each day.

## RESULTS

### Comparability of Study Populations

The Kenai Peninsula study populations of Dall sheep were very similar in terms of density and productivity. Dall sheep density in the hunted area was 3 sheep/km<sup>2</sup> and density in the unhunted area was 2.2 sheep/km<sup>2</sup>. Lamb ratios did not differ between the hunted and unhunted areas, 1970-92 (t-tests,  $P = 0.07$ , Fig. 1). Lamb ratios in the hunted herd were higher in 1980-92 ( $\bar{x} = 53 \pm 14.1$  lambs/100 ewes) than during 1970-79 ( $\bar{x} = 27 \pm 14.5$ ,  $t = -4.0$ ,  $P = 0.001$ ). Lamb ratios were also higher in 1980-92 in the unhunted area, ( $\bar{x} = 39$ ) than during 1970-79 ( $\bar{x} = 30$ ), but the difference was not significant ( $P = 0.18$ ). A 4th degree polynomial fit suggested upward trend in productivity for both areas through about 1986, followed by a downward trend. Lamb/ewe ratios fluctuated a great deal annually, apparently in relation to weather, but the fluctuations were highly synchronous between the hunted and unhunted areas. Synchrony, when both populations increased or decreased together, was observed in 15 year intervals, while asynchrony was observed in 4 intervals (sign test,  $P = 0.01$ ,  $n = 19$  intervals with data). Considerably fewer rams per 100 ewes were present in the hunted area ( $23.2 \pm 7.2$ ) than in the unhunted population ( $54.0 \pm 12.7$ ), 1970-84, due to the removal of nearly every legal sized ram each hunting season.

In the central Alaska study, population characteristics were similar for Dall sheep in both study areas. Densities ( $\bar{x} = 2.5 \pm 0.4$  sheep/km<sup>2</sup>,  $\bar{x} \pm$  standard deviation) and group sizes (summer  $\bar{x} = 7 \pm 6$ , winter  $\bar{x} = 12.9 \pm 9.9$  sheep/group) did not differ between the 2 study areas (t-tests,  $P > 0.05$ ). Slightly fewer rams per group were observed in the hunted (rams/group, median = 3.5) than in the unhunted area (rams/group, median = 2.9), but the difference only approached significance (median test,  $\chi^2 = 2.16$ , d.f. = 5,  $P = 0.14$ ). Lambs per 100 ewes ( $\bar{x} = 36$  lambs/100 ewes) and yearlings ( $\bar{x} = 15/100$  ewes) did not differ between the 2 study areas either in 1984 or 1985 (Mann-Whitney U tests,  $P > 0.05$ ).

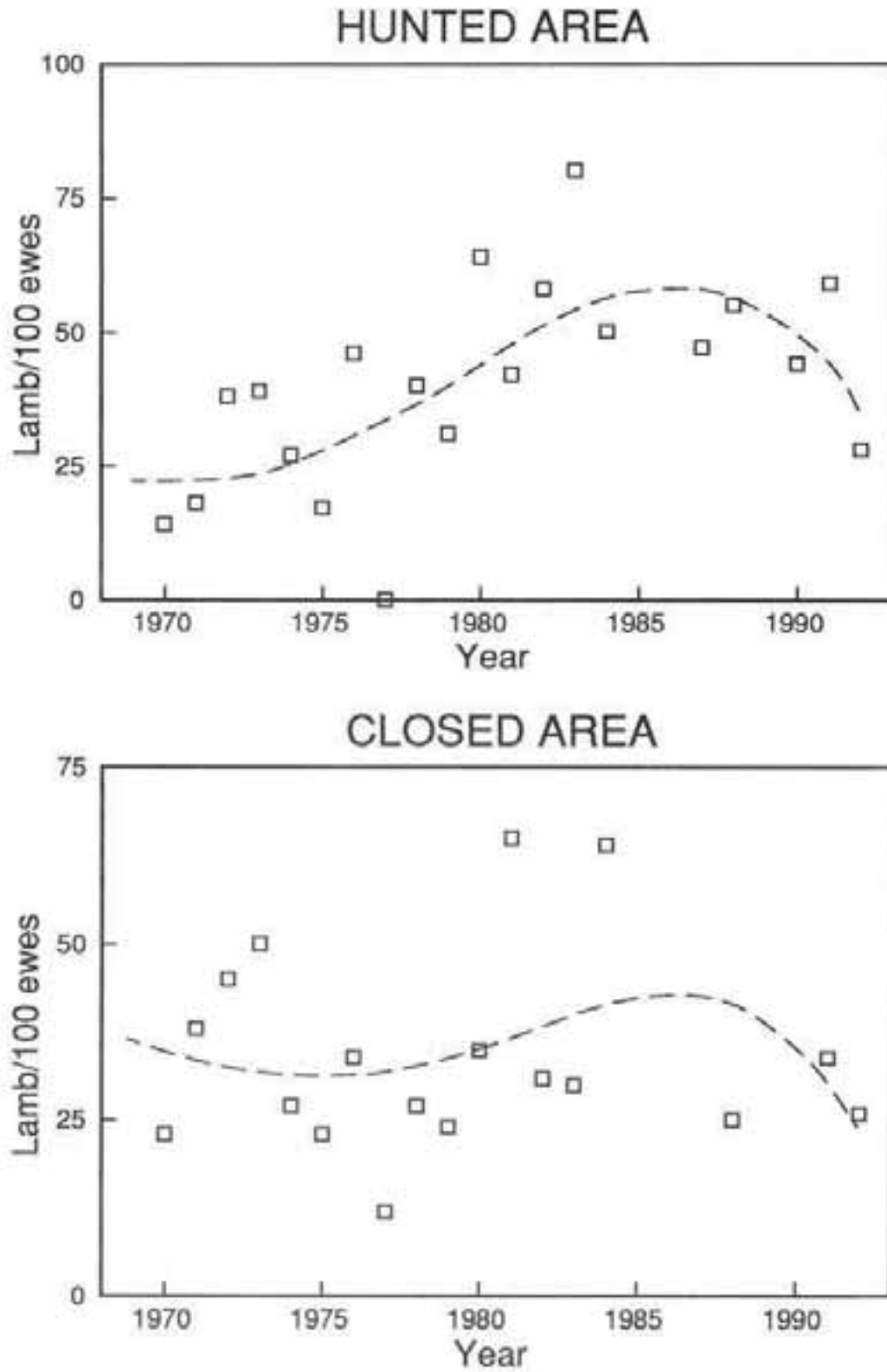


Fig. 1. Lambs per 100 ewes observed on the hunted and unhunted study areas on the Kenai Peninsula, 1970-1992.

Both pairs of hunted and unhunted study areas were highly similar with regard to Dall sheep population characteristics. Direct comparisons of rutting behavior between these pairs of hunted and unhunted areas appeared justified.

### Social Disruption

Young rams approached ewes differently in the hunted and unhunted areas in central Alaska herd (Table 1); younger rams in the hunted herd performed one-half as many twists, twice as many butts, and seven times as many sniffs urine ( $P < 0.05$ ). Other behavior displays were performed in equivalent proportions ( $P > 0.05$ ). Interactions observed per day were lower in the hunted Kenai population both in 1970 and 1971 (Nichols 1971, 1972), the opposite predicted by the social disruption hypothesis. Ewes accepted an equivalent proportion of mount attempts by rams in the hunted and unhunted central Alaska populations during the early rut, but during late rut (when more ewes were in estrous) ewes in the unhunted population accepted a higher rate of mount attempts, about 2 times as many, as in the hunted area (Fig. 2).

Guarding or tending of ewes, the cooperative close association of a ram and an estrus ewe during the ewe's cycle, was observed less in the hunted central Alaska population, although the rate of guarding was low in both hunted and unhunted Dall sheep populations. Guarding by younger rams in the hunted Kenai population was weaker and more confused; ewes were guarded for 1-2 hours at the most during the 1-2 day estrus period in Dall sheep (Nichols 1972). We observed only 1 tending pair in the hunted central Alaska herd, and 5 tending pairs in the unhunted herd during 2 rut seasons. Only 0.3% of all interactions in the hunted herd and 1% in the unhunted herd involved guarding behavior displays. Tending pairs involved mostly the largest-horned rams (the only 7/8-curl observed in the hunted herd during 1 rut; 4 full-curl plus rams and 1 3/4-curl ram in the unhunted population).

### Magnet Effect of Older Rams

Evidence for the magnet effect of older rams varied. Ratios of mid-sized rams declined significantly during the late rut from both the hunted (Usibelli) and 2 unhunted (Savage River, Igloo Creek) herds in the central Alaska Range, suggesting the leadership of older rams was not required for young rams to depart from ewe-young groups (Fig. 3). We observed several ram-only groups of mid-sized horn classes 1-3 km (0.6-2 miles) from the rutting groups, suggesting the drop in ratios was due to the departure of mid-sized rams from the rut groups and not to movements of the other age classes. Mid-sized rams lost considerable opportunities for breeding by departing the rut groups, since most of the breeding of ewes occurred during the second half of the rut (Fig. 3).

All rams (mostly younger rams), however, associated more with ewe-young groups during late winter in the hunted population ( $P < 0.05$ , Fig. 4) in comparison

Table 1. Ram displays by all rams in each herd towards ewes during ram-ewe interactions in an un hunted and hunted herd of Dall sheep, central Alaska Range, 1983 and 1984.

Behavior displays/ 100 displays by all rams	Unhunted (Savage River)	Hunted (Usibelli Mine)
Low stretch	13	13
Twist	43	25
Rush	5	5
Horn threat	1	0.3
Sniff rear	15	16
Sniff urine	3	21
Lip curl	4	4
Butt	6	11
Front kick	5	3
Mount	2	2
Guard	1	0.3
Sample size (No. displays observed)	1,940	2,388

to the un hunted population, providing evidence for the magnet hypothesis during late winter period. More rams were also seen in ewe-young groups during summer in the hunted population, but the difference was not significant ( $P > 0.05$ ). The higher ram:ewe ratios in the hunted herd were even more significant in that rams per 100 ewes were less in the hunted herd during summer aerial classifications (45 rams versus 71 rams per 100 ewes,  $P < 0.05$ ).

#### Immature Ram Incompetence

Later breeding dates were observed in the hunted central Alaska area populations, and less breeding activity was observed in the hunted Kenai area in comparison to the un hunted areas. On the Kenai Peninsula, fewer total interactions were observed per day of observation per sheep group in the hunted population than in the un hunted population both in 1970 (7.5 versus 17) and in 1971 (18.7 versus 31) (Nichols 1971, 1972). Breeding was initiated nearly 2 weeks later in the hunted Kenai population in 1971 (Nichols 1972). Rutting



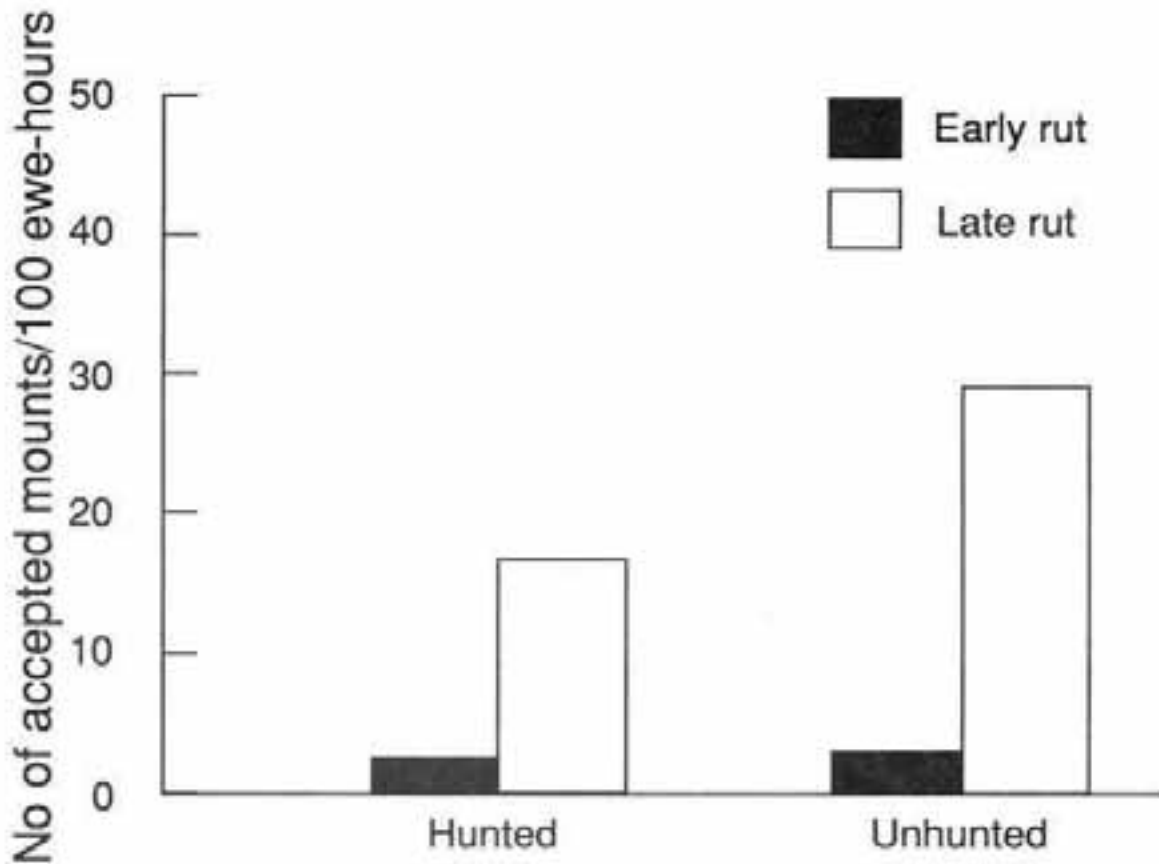


Fig. 2. Number of mount attempts by Dall sheep rams accepted by ewes per 100 ewe-hours of observation during early (15-30 Nov) and late (1-15 Dec) rut in the hunted and unhunted central Alaska study populations. ( $\bar{n}$  = 51 mount attempts in the unhunted herd,  $\bar{n}$  = 59 hunted herd). Observation times during early rut were  $\bar{n}$  = 153 ewe-hours in the unhunted herd and 161 ewe-hours in the hunted, while late rut observation times were 58 ewe-hours in the unhunted herd and 121 hours in the hunted herd.

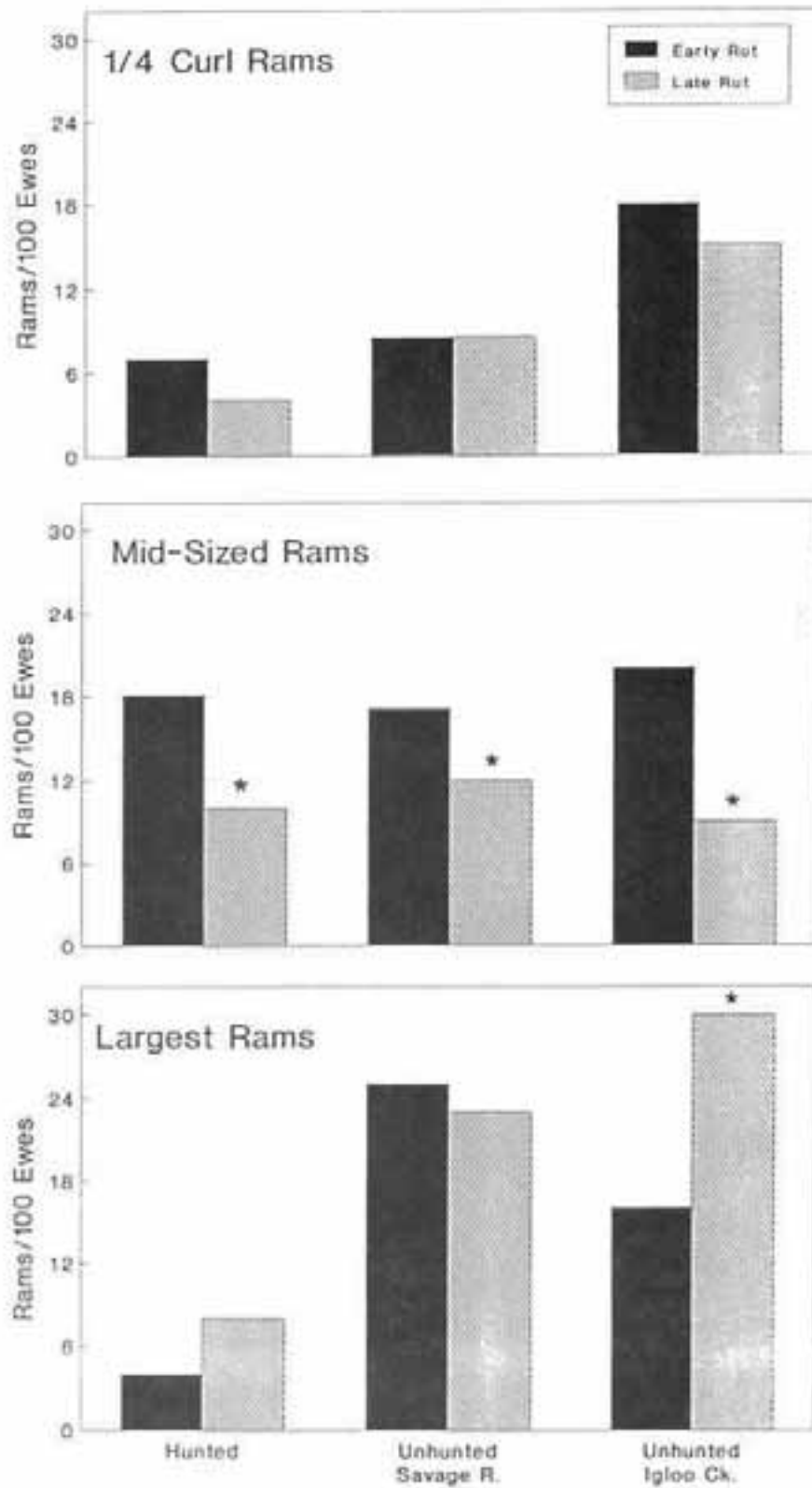


Fig. 3. Change in ram:ewe ratios during the late rut in 1 hunted and 2 unhunted populations of Dall sheep in Alaska in 1983 and 1984. Asterisk denotes a significant difference between early and late rut periods,  $P < 0.05$ .

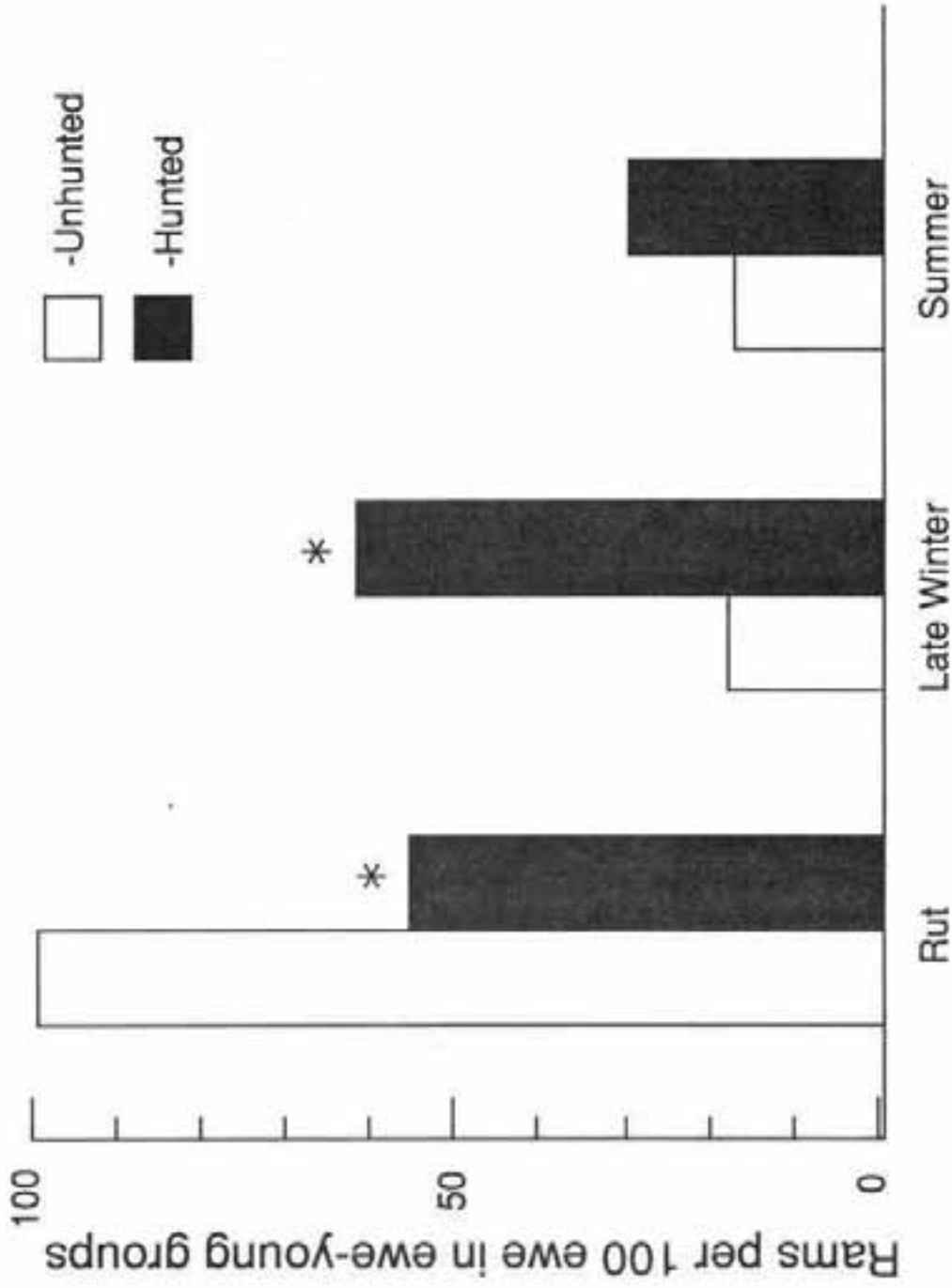


Fig. 4. Rams per 100 ewes in ewe-young groups in the rut, late winter (Mar-Apr), and summer (Jun) in the hunted (Usibelli) and 1 unhunted (Savage River) Dall sheep populations in central Alaska. Asterisk denotes significant difference,  $P < 0.05$ .

observations and similar lambing chronology suggested breeding dates were more similar between the areas in 1970. A wider range of lambing dates, however, occurred in the hunted population in 1972. Later breeding dates were also observed in the central Alaska Range hunted population in 1983 and 1984 (Fig. 5).

Less guarding behavior and less gathering of rams about estrus ewes were observed in the hunted compared to the unhunted Kenai population. As a result, estrus condition was more difficult for the observers to detect in the hunted population. Mounts were attempted in the hunted population with less preliminary indication of the ewes receptivity (Nichols 1972). More twists were performed in the hunted central Alaska Range population by rams toward ewes (Table 1). Possibly as a consequence of these courting differences, a higher proportion of mount attempts were accepted by ewes in the unhunted area (no. mounts per ewe-hour of observation) than in the hunted area during late rut ( $P > 0.05$ , Fig. 2), when most ewes were in estrous.

No evidence of depressed production or recruitment based on classification ratios was observed in either the Kenai (Nichols 1978, Murphy et al. 1990) or central Alaska study populations. Pregnancy rates were not available for the study populations and we do not know if they differed.

#### Depressed Survivorship of Young Rams

No evidence of depressed survivorship of young rams in the absence of large-horned rams was observed in either the Kenai, Lake Clark National Park, Gates of the Arctic National Park or other Alaska herd comparisons ( $r^2 = 0.133$ ,  $P > 0.05$ ,  $n = 25$  surveys, Murphy et al. 1990). No depressed survivorship of young rams was demonstrable by classification techniques in the central Alaska hunted areas 4 years after adoption of the more conservative 7/8-curl regulation; ratios of young rams ( $< 5/8$ -curl) in the hunted central Alaska herd (35 young rams per 100 ewes) did not differ from the unhunted central Alaska herd (38 young rams per 100 ewes,  $P > 0.05$ ) during helicopter classifications.

## DISCUSSION

### Social Disruption

Compared to mature males, young male ungulates court females in a less ritualized, more hurried, and more aggressive fashion (Geist 1971, Ozaga and Verme 1985, Valdez et al. 1991). Apparently as a result, adult ewes accepted a higher proportion of attempted mounts in the unhunted area. Although we observed differences in courtship behavior and accepted mounts between young rams in hunted compared to unhunted sheep herds in central Alaska, we observed no differences in production or recruitment of young in the Kenai or central Alaska. Despite differences in courtship behavior (as we observed for young rams), when

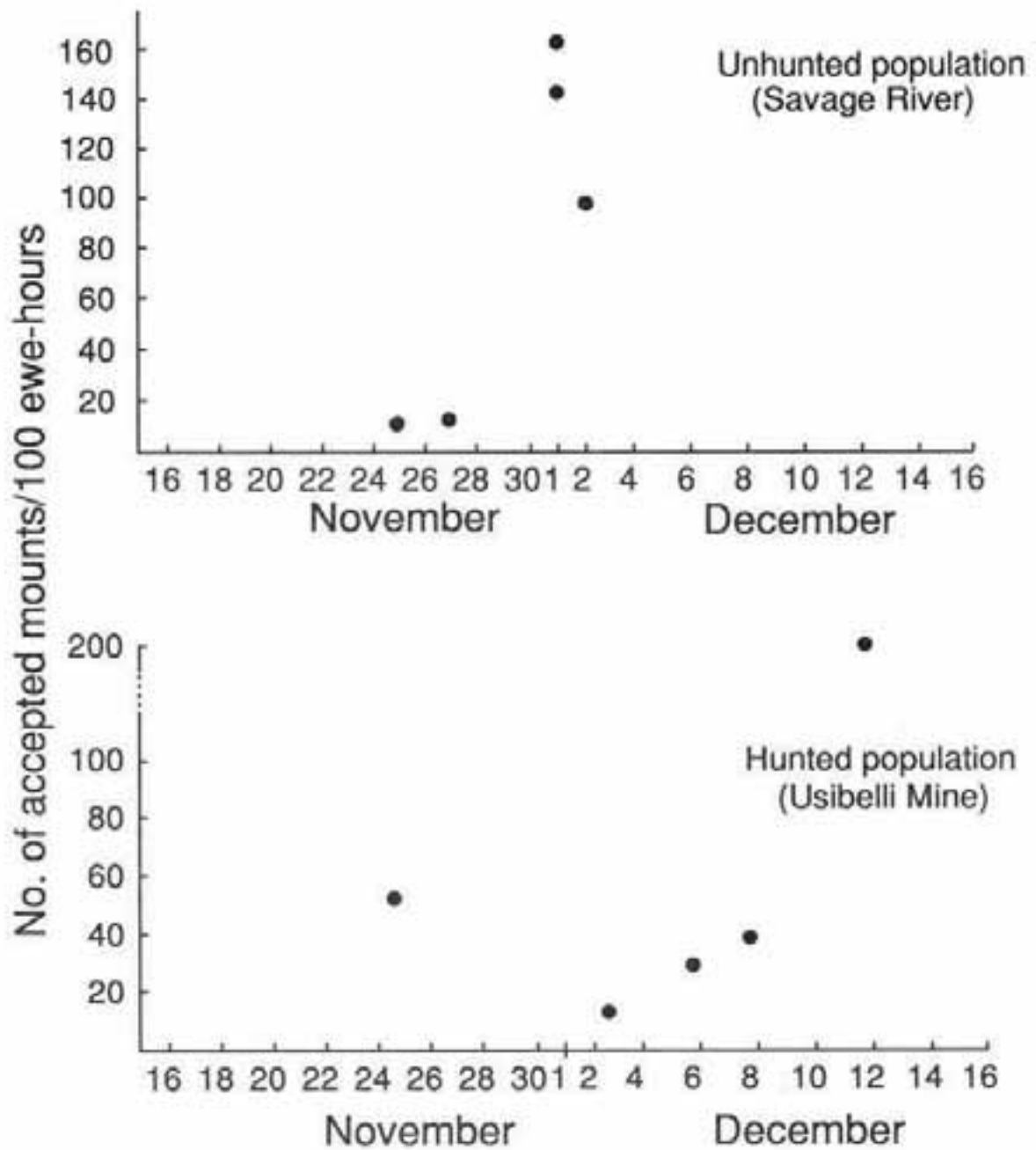


Fig. 5. Dates of copulations in hunted and unhunted Dall sheep populations in central Alaska in the breeding seasons of 1983 and 1984. ( $\bar{n}$  = 59 mount attempts in the hunted herd,  $\bar{n}$  = 51 in the unhunted herd). Copulations are expressed as no./100 ewe-hours of observation where ewe-hour = no. ewes x no. hours.

yearling white-tailed deer (*Odocoileus virginianus*) bucks assumed all breeding activity, there was no difference in breeding dates, pregnancy rate of does or any other evidence of lower sire quality (Ozaga and Verme 1985). The high level of synchrony of lamb ratios between the Kenai study areas suggested some other factors such as weather, and not hunting, was responsible for the variations between years in lamb success.

Ewes were potentially subjected to more stress in the hunted central Alaska area. Young rams in the hunted area were more aggressive in their courtship, and ewes were more likely to run away than to walk away from courting rams (Singer et al. 1991). The observation of more rams in ewe/young groups in late winter in the hunted versus unhunted area, raises the possibility of greater energetic costs to both adult ewes and young rams during a critical period.

#### Magnet Effect of Older Rams

Our data relative to the magnet hypothesis was equivocal; the magnet hypothesis was not supported by our observations during the late rut, but the hypothesis was supported by our observations during late winter.

Equivalent early departure of mid-sized rams from rut groups in the hunted central Alaska population did not support the magnet hypothesis. Breeding activity was more intense during late rut and we suspect the unsuccessful competition with large-horned rams for estrus ewes caused the mid-sized rams to leave. The remaining smallest rams (mostly 1/4-curl) do compete less with the largest rams; interactions are more frequent and intense between rams of most-nearly equal sizes (Geist 1971). Early departures of mid-sized rams in all 3 herds resulted in a loss of immediate breeding opportunity for them, but possibly their residual reproductive value and fitness may be enhanced. Geist (1986) reported some subadult male cervids opt out of rutting [the "dove" strategy of Barash (1982)], although these males were successful when the opportunity arose, and some became dominant breeders later in life. We speculate that the energy savings to mid-age classes of rams leaving rut groups during late rut contributes to their long-term survival and fitness. Since early departures of mid-sized rams was observed in both areas, no apparent effect of harvest removals on the energy saving strategy was observed.

Young rams, however, associated about 3 times more with ewe-young groups in the hunted central Alaska herd in late winter, thereby supporting the magnet hypothesis. Adult male and female mountain sheep typically segregate during all of the year except during the rut (Geist 1968, 1971, Shank 1982, Aschcroft 1986). The selective force for the segregation remains equivocal. Female ungulates occupy better ranges in many instances (Watson and Staines 1978, Shank 1985, Beier 1987), but Wehausen (1980) and Shank (1982) observed the opposite. Male bighorn sheep were found on better ranges than female-young groups. Male ungulates typically initiate the separation from female-young groups

(Charles et al. 1977, Geist and Petocz 1977, McCullough 1979, Shank 1982). Sexual segregation of ungulates outside of the rut period reduces energetically expensive sexual and agonistic behavior between males and females (Rand 1952, McCullough 1979). Avoidance of sexually agonistic stimuli outside of the rut by rams should maximize their individual fitness (Morgantini and Hudson 1981).

The magnet hypothesis predicts that older rams are required to lead young rams to segregated ranges. An alternate explanation for winter associations of young rams in ewe-young groups is that, in wolf-occupied habitat, young rams seek out the oldest and most experienced sheep to aid them in detecting and avoiding predators--in this case older ewes. Festa-Bianchet (1989) reported young rams (< 3 years old) were more vulnerable to predators and diseases than older rams. This hypothesis is consistent with our observations that rams in the hunted population associated most with ewe-young groups during the late winter, a period of more intense wolf predation (Murie 1944, Haber 1977), than during the summer. Successful departure of some young rams from ewe-young groups without old ram leadership during late rut, suggests the leadership is not required.

#### Immature Ram Incompetence

We observed no discernible, short-term deleterious effects of trophy hunting on reproduction or recruitment rates in Dall sheep. Our data were limited to aerial or ground classifications, and we did not compare pregnancy rates or early neonatal losses between the populations. We obtained preliminary evidence suggesting breeding occurred later and ewes accepted fewer mount attempts in the hunted populations. We suggest further more detailed work on the question of later breeding since visibility conditions were limited during late rut in the hunted Kenai population in 1971. Observation conditions were excellent in the central Alaska population in 1983 and 1984. although we did not try to monitor nighttime breeding activity, we observed 1,291 rutting interactions between rams and ewes during 127 hours of daytime group observations. In his classic study of mountain sheep, Geist (1971) observed 596 interactions between Stone's sheep rams and ewes, and 205 for bighorns, or 62% of our total. A more definitive study than ours, with a great deal more replication, will require considerable time and personnel.

We conclude that guarding or tending occurs at a much lower rate in Dall sheep in Alaska than in other mountain sheep. Only 16% of estrus ewes in our central Alaska Dall sheep populations were observed in tending pairs under conditions of uninterrupted views of the tundra rutting ranges, versus 50% of estrus pairs of mountain sheep in Montana (Hogg 1984). A tradeoff in reproductive fitness may exist between remaining with and defending an estrus ewe and maximizing the probability of siring her offspring (Hogg 1988), versus attempting to breed other estrus ewes present in the area. The larger density of breeding sheep (and estrus ewes) present in Dall sheep study populations may explain the lower rate of guarding (Nichols 1972).

### Depressed Survivorship of Young Rams

Our data, based primarily on aerial surveys, do not indicate that hunter-reduced numbers of older rams adversely affects the survival of young rams in Alaska. However, aerial surveys are essentially snapshots in time of population composition; variation due to cohort differences in size and survivorship (Murphy and Whitten 1976) could obscure harvest-related effects on survival of sublegal rams. Our most robust test of the hypothesis is the Surprise Mountain-Cooper Landing comparison, where no evidence of depressed survivorship was detected from aerial classification data even though virtually all 3/4-curl and larger rams were cropped over a 15-year period of study (Murphy et al. 1990). Stewart (1980) and Hoefs and Barichello (1984) also failed to find evidence of the depressed survivorship hypothesis.

Several other studies involving tagged males provide conflicting evidence. Festa-Bianchet (1989) reported higher than expected mortality rates in young mountain sheep rams from a herd subjected to hunting in Alberta, but he had no control study area. His control was skull remains from the un hunted Denali Park Dall sheep population (Murie 1944). Biases in skull collections may preclude their direct comparison of mortality studies involving the tagging of live animals (Murphy and Whitten 1976, Festa-Bianchet 1989). Festa-Bianchet (1989) reported high mortality of yearling rams, which he could not attribute to hunting effects. Yearling rams are not observed to participate in breeding even in trophy-hunted populations (this study, Singer et al. 1991, Shackleton 1991). Either 4-5 year-old rams or 5-6 year-old rams, not yearling rams, (depending on the size class of the hunting restriction) do most of the breeding, and therefore assume higher mortality rates (Geist 1971, Murphy et al. 1990).

Heimer et al. (1984) reported a high disappearance rate of young rams from a hunted population during a period of less restrictive (3/4-curl) harvest. The high disappearance, however, could have also been due to dispersal. No comparable data on disappearance rates were available for young rams from un hunted populations.

Evidence that more restrictive harvests increase survivorship of rams is reported from the eastern Alaska Range (Heimer and Watson 1990). Thirty-three percent more rams were harvested from this area following raising the size class restriction from 7/8-curl to full-curl (Heimer and Watson 1990). Ewe numbers were apparently stable during the period. Hunter participation increased 58% during the full-curl harvest, but Heimer and Watson (1990) rejected this as an explanation for the increased harvest of rams. There were no control populations for the study (i.e., a comparison population where the ram harvest remained at 7/8-curl), ewe fecundity and survival increased at Dry Creek during the study and weather and wolf numbers also varied (Heimer and Watson 1990). Festa-Bianchet (1989) stressed that behavior observations of rutting males, causes of death, and



experimental manipulation of hunting regimes are necessary to determine if the depressed survivorship hypothesis applies.

## RESEARCH RECOMMENDATIONS

We recommend further research into the possible effects of trophy hunting of male mountain and Dall sheep. Greater replication of study conditions, and use of control study areas, or use of the same areas for control and manipulations (crossover experiments) establish cause and effect relationships. Longer term studies are suggested (1-2 decades or more) especially if crossover experiments are conducted. In particular, we recommend further research into the possibility of later breeding dates, the behavioral and ecological implications of more rams associated with ewe/young groups during late winter, and the implications of decreased competition among males in hunted areas.

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