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PRELIMINARY OBSERVATIONS ON POPULATION RESPONSES TO AN EXPANDING BIGHORN SHEEP HERD IN ALBERTA.

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Abstract: Population parameters were monitored for 15 years in a Rocky Mountain bighorn sheep (Ovis canadensis) population allowed to expand between 1981 and 1985. Prior to 1981, herd numbers were stabilized at approximately 100 by trophy ram hunting and experimental ewe removals. Pre-expansion years were characterized by high survival rates, high productivity, breeding in yearling ewes and rapid initial horn growth. By 1985, indications of decay in population quality were evident. Mean age became older with females comprising 60% of the population. Overwinter lamb survival decreased from an average of 85% between 1975-84 to 72% in 1984-85. Survival of older animals did not change significantly. The incidence of barren ewes increased to 15% in 1985 compared to a 7% average between 1976 and 1981. Although per capita productivity declined in 1985, the number of lambs increased due mostly to an increase in the ewe population. Lamb production from yearling ewes declined in the last 3 years, and annual horn increments of 1- and 2-year-old rams showed a decrease in length.

Characteristics of wildlife populations are commonly used to assess the health status of individual herds. Poor quality Rocky Mountain bighorn sheep (Ovis canadensis) are recognized by low lamb survival, low lamb production, small horn size, small body size and longer life expectancy while larger horns, larger body size, high fecundity, rapid growth and short life expectancy characterize expanding or high quality populations (Geist 1971). Changes in these attributes presumably are related to changes in range condition and would be expected to vary as the population reaches carrying capacity.

The nature of the Ram Mountain bighorn herd has afforded the opportunity to collect detailed accounts of its population characteristics and to follow these characteristics through an experimental manipulation of animal numbers. Between 1975 and 1981, population numbers were maintained at a stable level through annual ewe collections (Jorgenson and Wishart 1983). Ewe removals stopped in 1980. Trophy ram hunting continued . The purpose of this paper is to describe the characteristics of this herd during its "stable" years and during its increase. These are preliminary observations and further years of work are required to confirm any trends.

METHODS

A detailed description of the Ram Mountain study area was provided by Johnson (1975). The area is located in west central Alberta (52°25'N, 115°45'W) and forms part of the Brazeau mountain range.

Sheep were trapped during May to September in a corral trap baited with salt (Wishart et al. 1982). Rams (≥1 year) were individually identified

with numbered Allflex ear tags while color coded neck collars were placed on ewes (≥1 year old). Colored ear streamers were used to identify individual lambs. Horn measurements (length, base circumference and annual increments) were taken every two weeks if possible for each animal, however, capture frequency was highly variable. Lambs and rams (> 2 years old) were seldom captured more than once each year.

Population size was determined each year from reobservation of marked animals. The only unmarked animals present at the beginning of the summer were lambs but these could readily be counted by pairing with lactating ewes. By September, most lambs were already tagged. Any tagged animal not observed over a field season was assumed to have died the previous winter. The isolated nature of the sheep range reduced emigration and immigration to minimal levels. Animals (N=3) rarely reappeared on the study area after disappearing for a complete field season. Some migration to a small sheep range across the North Saskatchewan River has been documented, however, tagged rams on this area returned to the main study area if they are not harvested by hunters.

RESULTS

Population Size

Between 1975 and 1981, the population averaged 100 animals (range 94-108). With the cessation of ewe removals in 1980, this population had risen to 142 by 1985, an increase of about 31% over pre-expansion years. Density on the summer and winter range combined, had risen from 2.6 in 1975 to 3.6 animals/km² in 1985 (Fig. 1).

Population Structure

Following the last ewe removals in 1980, changes were monitored in the population structure. Comparisons were made in the population structure between years 1975-81 (1981 included, since manipulations made in 1980 influenced 1981's population) and 1982-85. The median age of the population (lambs excluded) in 1981 was 3 years compared with 4 years in 1985. The sex and age structure in 1981 and 1985 are compared in Fig. 2. The greatest age disparity was in the female cohort where the median ages in 1981 and 1985 were 3 and 4 years respectively (Fig. 2). The median age of the male cohort did not change.

Prior to 1982, young females (1-3 years) were the dominant component of the population in most years (Fig. 3). In 1979 they made up about 30% of the total population while older females comprised only 16%. Following the last year of ewe removals, older ewes had been further reduced to only 11% of the population. Four years later this percentage of older females had increased to 25% and they are now the major component. The percentage of younger females in the population has changed very little since 1982.

A considerable decline in the percentage of adult (4+ years) rams has taken place since 1978 (Fig. 3). Between 1975-78, adult rams constituted an annual average of about 24% of the herd, however since 1978 they have been reduced to an annual average of about 15%. The actual number of adult rams present however has not changed.

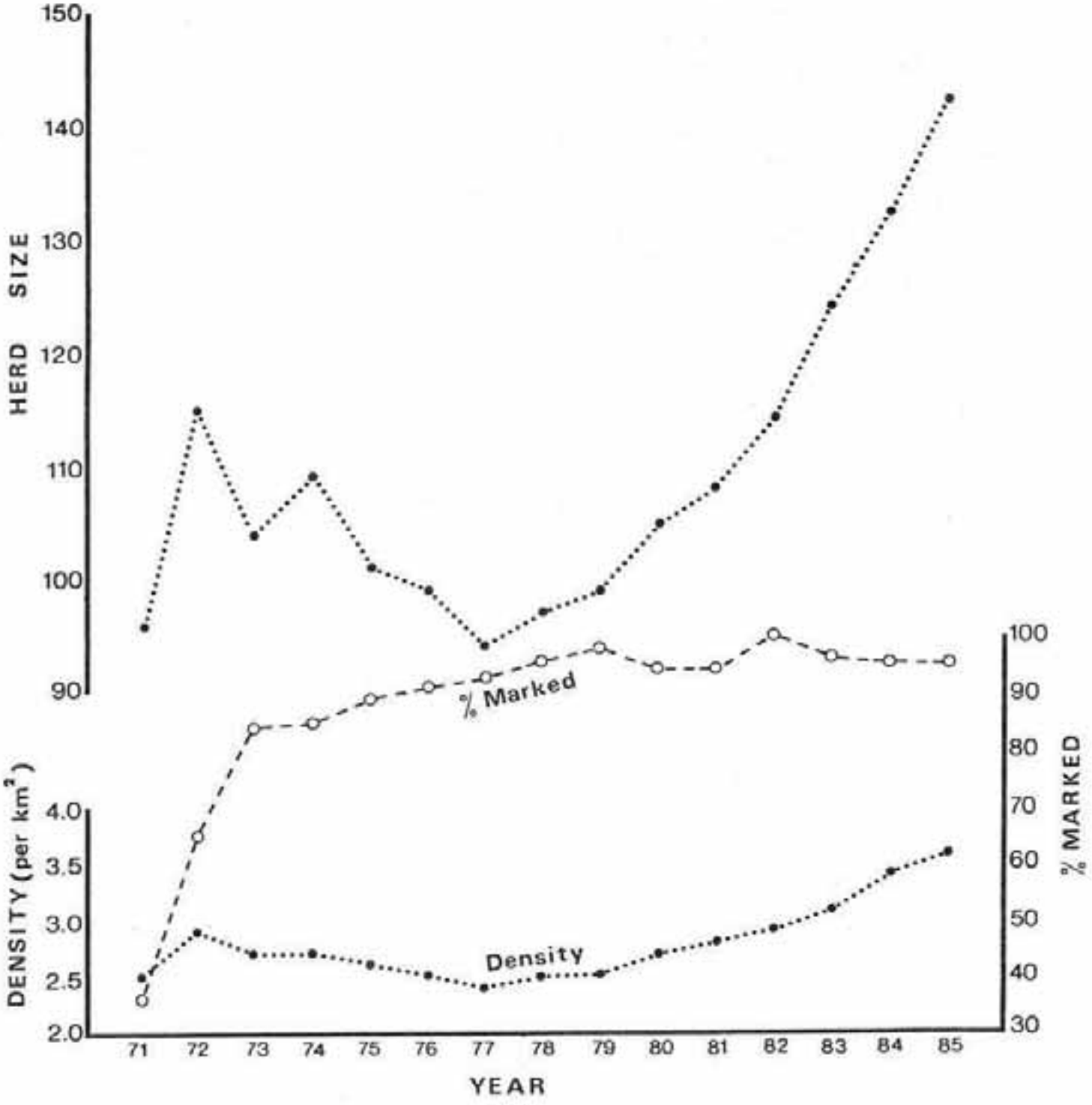

Fig. 1. Population status of the Ram Mountain bighorn herd, 1981-85.

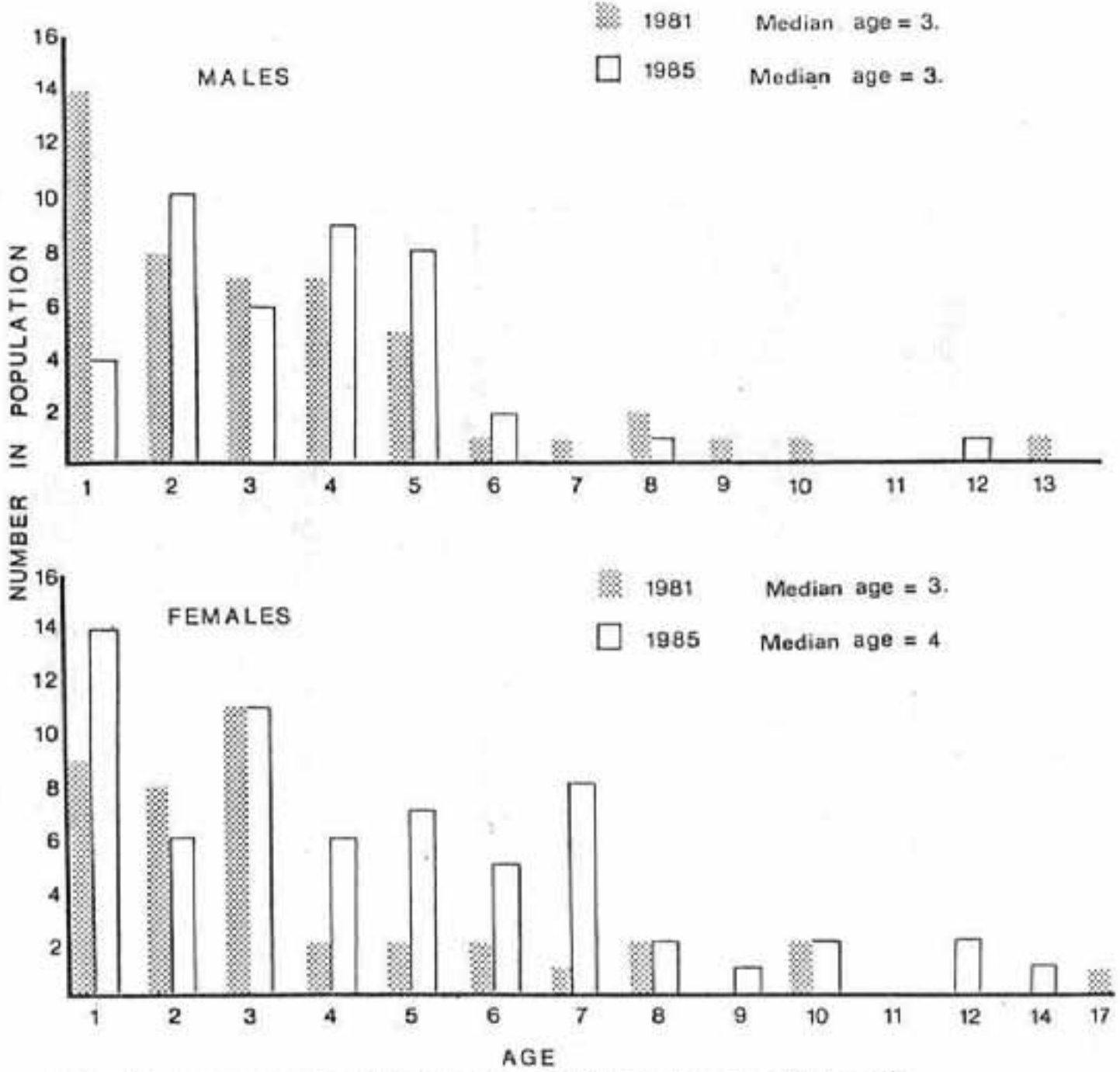

Fig. 2. Age structure of the Ram Mountain bighorn herd in 1981 and 1985.

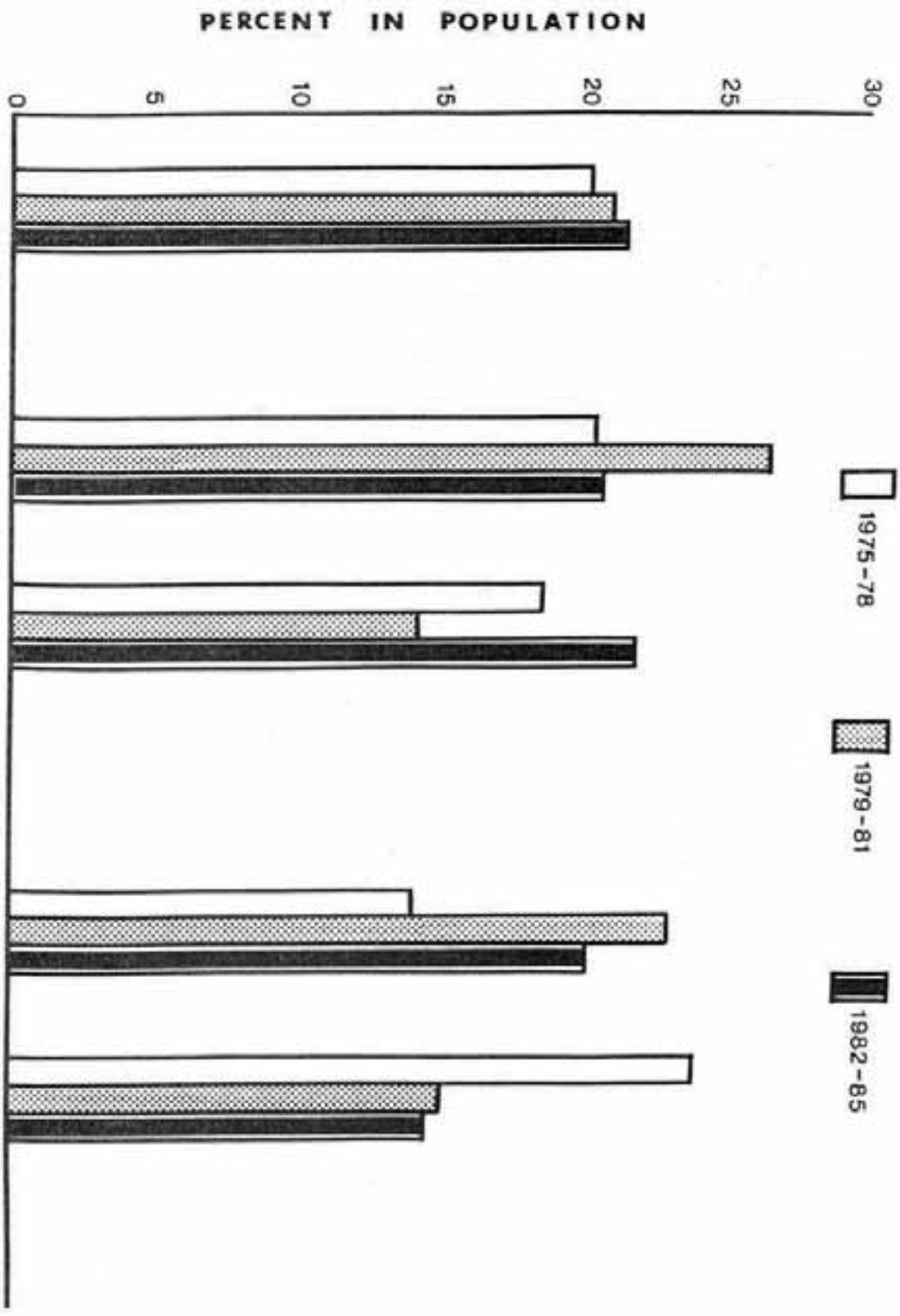

Fig. 3. Age structure of the Ram Mountain sheep population during 3 time periods, 1975-85 (1982-85 is period of population growth).

Survival

Survival rates as discussed here relate to natural mortality only and do not include losses due to hunting, ewe collections and trap-related accidents.

On an annual basis, older rams consistently experienced lower survival rates than young rams or ewes of any age group (except the 1976-77 winter) (Table 1). Although the population expanded from 108 in 1981 to 142 in 1985, combined survival rates for the two periods did not change significantly for any of the three major age groups of either sex (Table 1). Adult ram survival dropped from 83% in pre-expansion years to 68% for the period, 1981-85, however this difference was not statistically different ($X^2 = 4.5$, $P > 0.05$). Prior to 1984-85, annual overwinter lamb survival averaged 80% while in 1984-85 lamb survival was 72% but this was not a significant difference ($P > 0.05$). Male lamb survival was only 50% ($N = 8$) over the 1984-85 winter.

Table 1. Annual natural overwinter survival rates of bighorns from Ram Mountain (1975-85).

	Percent Survival				
		Ewes		Rams	
Year	Lambs (M & F)	1-3 yrs	4+ yrs	1-3 yrs	4+ yrs
1975-76	60(20)[a]	100(15)	100(15)	94(16)	83(24)
1976-77	77(22)	94(18)	87(15)	73(15)	100(20)
1977-78	75(16)	96(23)	92(12)	89(9)	82(23)
1978-79	80(25)	100(23)	100(11)	100(12)	69(16)
1979-80	89(19)	100(22)	92(12)	91(22)	75(12)
1980-81	92(25)	95(22)	100(10)	100(22)	86(14)
Combined 1975-81	79(127)	97(123)	95(75)	92(96)	83(109)
1981-82	89(19)	92(27)	92(12)	72(29)	67(18)
1982-83	81(26)	100(20)	82(22)	96(28)	68(16)
1983-84	81(26)	89(27)	96(24)	80(30)	73(11)
1984-85	72(25)	92(25)	93(30)	89(28)	67(15)
Combined 1981-85	80(96)	93(99)	81(88)	84(115)	68(60)

[a] Sample size.

Lamb Production

Although a record number of lambs were produced in 1985, percent productivity (lambs observed:100 mature ewes) actually declined slightly compared to the 3 previous years (Table 2). During years of population stability,

annual productivity fluctuated considerably and has been lower than that observed in 1985, therefore, the drop observed in 1985 may not necessarily indicate a trend toward lower productivity. Productivity reflects viable lambs only and does not consider those that die soon after parturition. Of the 10 adult ewes not producing lambs in 1985, 7 were barren (15.5% of total adult ewes) while the other 3 lost their lambs shortly after birth.

Table 2. Spring productivity of bighorn ewes on Ram Mountain (1971-85).

Year	Number of Lambs	Number of Reproductively[a] mature ewes	Lambs/ 100 ewes	Lambs/ 100 "ewes"[b]
1971	24	33	73	N/A
1972	24	38	63	N/A
1973	25	32	78	N/A
1974	15	36	42	25
1975	20	28(1)[c]	71	45
1976	22	25(1)	88	52
1977	16	27(5)	59	34
1978	25	28(7)	89	55
1979	19	28(0)	68	35
1980	26	31(9)	84	52
1981	20	27(4)	74	37
1982	26	32(3)	81	50
1983	26	31(0)	84	43
1984	31	37(1)	84	47
1985	36	46(1)	78	55
Mean	23.7	32	74	44

[a] Two-year-old ewes were included only if they were lactating.

[b] Includes all ewes and yearlings.

[c] Number of lactating 2-year-old ewes included.

Annual lactation rates better reflect actual productivity than the number of lambs observed. These values (Table 3) indicate a very high rate of breeding in adult ewes with only a few being barren each. In 1985, there were more barren ewes (7) present than in any previous year.

During aerial surveys, separation of yearlings (male and female) and non-productive 2-year-old ewes is difficult and usually not done. In order to compare productivity on Ram Mountain with other herds in which yearlings and 2-year-olds were not distinguished, production was also calculated as lambs per 100 "ewes". Although percent productivity fell in 1985, lambs per 100 "ewes" indicated an increase in productivity.

Rocky Mountain bighorn ewes normally do not breed until they reach 30 months of age (Geist 1971, Buechner 1960), but at Ram Mountain breeding has been recorded in ewes 18 months old. The annual incidence of yearling breeding based on lamb production at 24 months of age has varied from 0% (N = 6) in 1979 to 82% (N = 11) in 1980. In 1984 and 1985, only one 2-year-old ewe produced a lamb in each year. It appears that the frequency of yearling breeding has declined in the last 3 years when compared with the peak years, 1977-1982 (except 1979 when no yearling breeding was recorded).

Table 3. Annual lactation rates of adult (3+ years) ewes from Ram Mountain (1975-85).

Year	Percent Lactating	Number Barren
1975	81 (27)[a]	5
1976	91 (24)	2
1977	86 (22)	3
1978	95 (21)	1
1979	89 (28)	3
1980	95 (22)	1
1981	91 (23)	2
1982	96 (29)	1
1983	93 (31)	2
1984	94 (36)	2
1985	84 (45)	7

[a] Sample size.

Horn Growth

As a measure of realized horn growth, annual increment lengths of 1 and 2-year-old rams were compared between years. Significant differences were found between some years in both yearling ($F = 9.89$, $N = 8$, $P < 0.001$) and 2-year-old rams ($F = 6.22$, $N = 8$, $P < 0.001$). Average third increment lengths were less than second increments in all years except 1977 (Fig. 4). Generally, the same annual pattern of increment growth was observed for 1 and 2-year-old rams (except 1977 and 1979). The shortest and longest second increments were grown in 1982 and 1979 respectively (Fig. 4). Since 1981 there appears to be a trend developing towards shorter horn increments for yearling and 2-year-old rams.

Fecal Crude Protein Analysis

Significant fecal nitrogen relationships have been established with plant protein, protein intake, dry matter digestibility and body weight change (Hebert 1973). Fecal nitrogen values can conveniently be converted to crude protein and such fecal crude protein indices for plant protein intake have

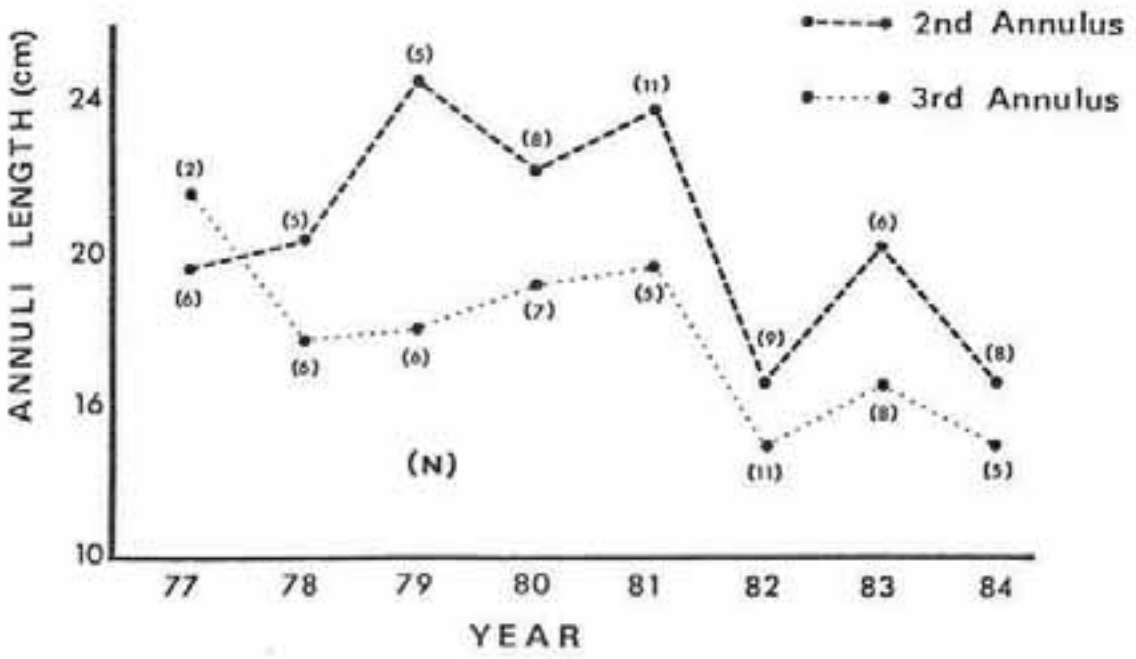

Fig. 4. Annual horn increments from yearling and 2-year-old rams (1977-85).

been established for the Ram Mountain bighorn herd. The annual cycle of fecal crude protein illustrates a typical spring rise in late May-early June followed by a slow steady decline until late November. Levels remain consistently low throughout the winter. In some years, a short fall green-up occurred. The greatest difference between years was in the timing and magnitude of the spring rise. In 1984 and 1985, the rise was later in the year and an overall depression in summer and fall values was noted when compared to previous levels (Fig. 5).

Lungworm Levels

Annual monitoring of fecal lungworm levels has continued since 1977. Larval outputs in 1984 and 1985 (1985 results only up until October) continued the cyclical pattern of high winter and low summer larval shedding observed over past years (Jorgenson and Wishart, 1983). Inter-annual comparison of larval output are best made from winter samples, since this is when output is at the maximum. Summer counts generally tend to be quite low (many negative samples) and often highly variable. Relative annual comparisons indicate a high increase in output in 1985 (Table 4). The 1985 count (median = 1328 larvae per gram of dry feces [LPG] was higher than from any previous year.

Table 4. Late winter larval output from bighorns on Ram Mountain (1977-85).

Year	$\bar{x}$ Larvae/gm[a]	Median	Range	N
1977	101	129	20-189	5
1978	1138	1232	170-2260	13
1979	694	569	293-1169	19
1980	565	543	49-1472	22
1981	670	596	26-1664	15
1982	912	847	366-1500	8
1983	917	731	311-1768	9
1984	802	631	46-2536	19
1985	1676	1328	314-5352	13

[a] The highest count during February, March or April.

DISCUSSION

Data collected in 1984 and 1985 field season indicate a decay in a number of parameters which could be used as measures of population quality of the Ram Mountain bighorn herd. These changes have arisen as the number of animals on the study area has increased. Since most of the evidence, pointing toward a decline was first observed in 1985, conclusions are preliminary and more years of data are required to confirm any trends.

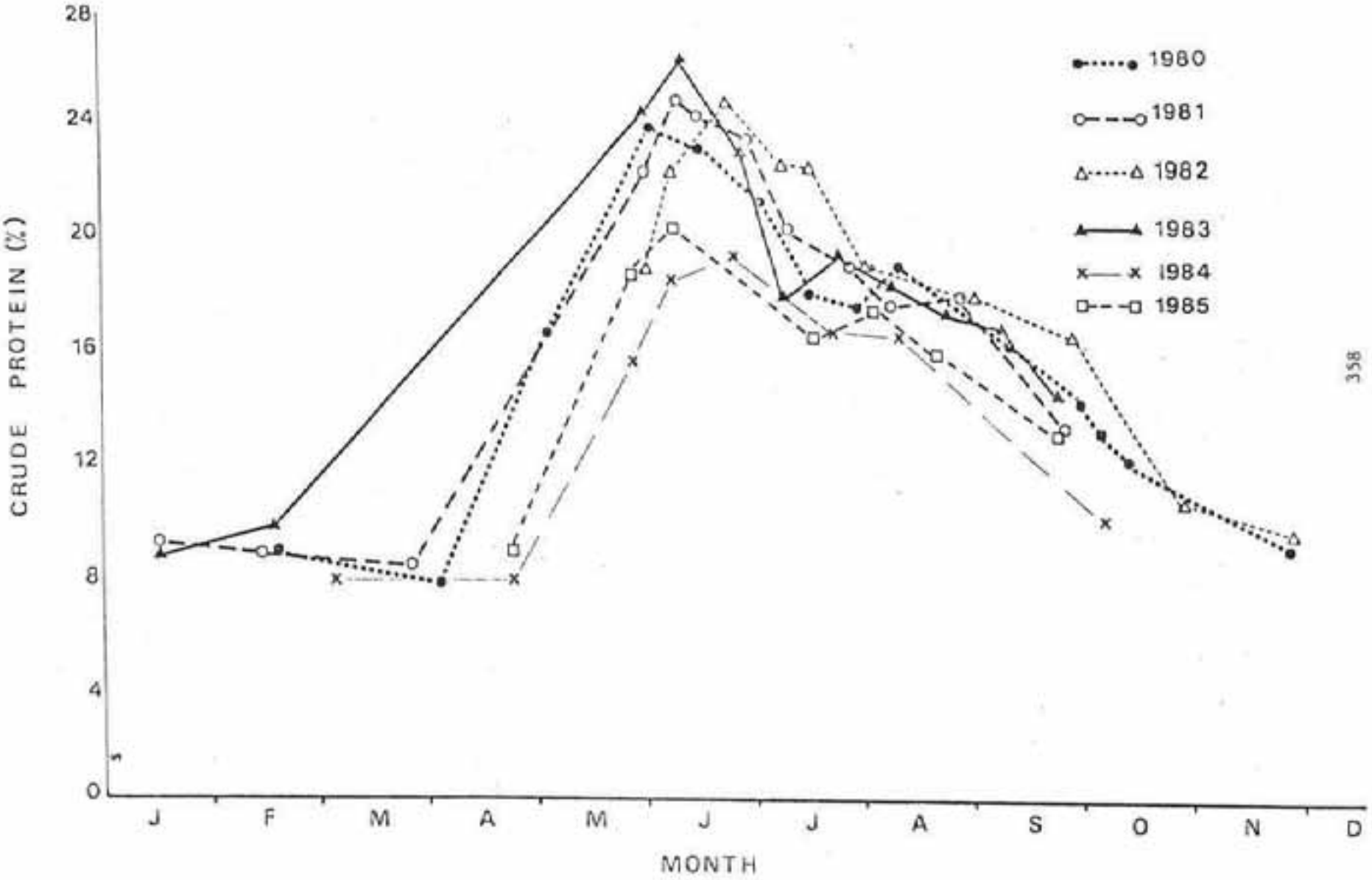

Fig. 5. Annual combined fecal crude protein values from Ram Mountain (1980-85).

Mortality Patterns

Overwinter mortality of lambs, particularly males, may have begun to increase as of 1984-85. Winter severity which directly effects juvenile survival and winter weight loss (Jorgenson and Wishart 1984) was relatively mild in 1984-85 and not considered a factor. High mortality among juvenile males relative to juvenile females has been noted for several mammal species (Trivers and Willard 1973, Clutton-Brock et al. 1982). The theories for such differential mortality range from expression of deleterious recessive alleles on the x chromosome (Myers 1978) to Trivers and Willards (1973) hypothesis that differential mortality occurs postnatally and is a reflection of parental investment.

Another theory suggested by Clutton-Brock, et al. (1984) and Myers (1978) is that higher mortality rates among male juveniles are a consequence of a greater susceptibility of males to food shortage associated with a faster growth rate and requirements for increased nutrition. As the population on Ram Mountain increases and food resources decrease, increased mortality of lambs, and in particular male lambs, would be expected. Mortality of lambs is predominantly winter related on Ram Mountain and while most growth takes place over the summer, lambs naturally gain some weight over winter (Jorgenson and Wishart 1984). Competition for food resources at that time would be of greater consequence than during the summer. Rate of summer weight gain is only slightly greater for (lamb and yearling) rams compared to ewes. It is not until age 2 that differential summer weight gain dramatically increases for rams (Jorgenson and Wishart 1984). Overwinter survival rates of adult ewes has not significantly changed with the increasing population but survival of adult rams has significantly decreased.

Changes in Age Structure

The Ram Mountain population has grown older due primarily to an increase in the number of older females. Previously, these older ewes were removed from the population to simulate a non-trophy hunting season. However, the greatest number of ewes actually harvested are generally from the 2.5-3.5 year age groups (Alberta Fish and Wildlife hunter statistics) with lambs generally making up less than 10% of the total kill. The effect has been to preserve an older age structure in the ewe population.

The ram age structure at Ram Mountain has not changed greatly with the increasing population. Trophy ram harvests and the continued low survival of rams when compared to ewes prevent this segment of the population from getting any older. The differential mortality rate between rams and ewes has also resulted in a sex ratio strongly biased toward females. With ewes no longer being removed from the population, the bias becomes even greater. Clutton-Brock (1982) obtained similar results with red deer.

Productivity

With the increasing population density, a decline in productivity, as measured by lactation rates, was noted in 1985. It was necessary to distinguish lactation from percent productivity because percent productivity takes into

account neonatal mortality which was highly variable between years. An increase in the number of barren females with increasing density has also been observed in red deer (Clutton-Brock 1982, Staines 1978), Himalyan tahr (Caughley 1970), white-tailed deer (Marburger and Thomas 1965), and African buffalo (Sinclair 1977). Since the changes in productivity at Ram Mountain are small and not statistically significant, more years of data are required. Studies in red deer (Mitchell and Brown 1974), domestic sheep (Drymundson 1973), Peary caribou (Thomas 1982), and moose (Saether and Haagenrud 1983) have related fecundity to body condition weight. If fecal crude protein is a good measure of relative forage quality (Hebert 1973, Seip 1983), the results from 1984 and 1985 indicate a decline in the quality of forage on Ram Mountain which could lower the condition of breeding ewes and reduce productivity.

Though actual productivity showed a decline in 1985, the lambs per 100 "ewe" ratio indicated an increase. The reason for this was the relatively low number of yearlings and 2-year-old ewes present in 1985 which, when included in the ewe component brought the lamb:100 "ewe" ratio up when compared to 1984. This gave the false impression of improved productivity in 1985. Generally yearlings and 2-year-olds are non-producers, but distinctions between yearlings (males and females) and 2-year-old ewes are not made during aerial surveys and most of the literature reports productivity in bighorn sheep as lambs per 100 "ewes". Caution must, therefore, be used when interpreting lamb production recorded in this fashion.

Annual Horn Growth Patterns

Studies on red deer and other cervids have demonstrated a negative relationship between antler growth and population density (Clutton-Brock 1982). Food shortages can also have marked negative effect on antler growth (Roseberry and Klimstra 1974, McCullough 1979). Food shortage and high density are interrelated. As the bighorn population has risen on Ram Mountain, second and third annual increments have shown a decrease in length over the last 3 years. Since increment growth would depend both on seasonal horn growth rate and the length of the growing season, changes in annuli length could reflect differences in those variables rather than any variable associated with increasing population density. One would expect declining forage resources to negatively impact horn growth rates more than growing season, however, growing season could be affected if energy supplies were directed away from horn growth at an earlier date. Allocation of food resources towards such a low growth priority item as horn growth could occur later than normal and end earlier than when supplies were more abundant.

Lungworm Levels

The high larval outputs in late winter infers that either reproductive activity of adult lungworms was at a peak or that large numbers of larvae stored in the lungs were suddenly released. Sheep are in their poorest body condition in late winter and the body's defense mechanism would be operating at less than optimal performance. At that time lungworm activity could peak and large numbers of larvae would be shed in the feces. Presumably, the poorer the condition, the higher the winter larval output. A combination

of wet springs promoting an increase in the snail intermediate host population and hard winters should produce very high larval outputs.

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QUESTIONS AND ANSWERS

Wayne Heimer, Alaska: I would just like to make an apology and comment, more so than asking a question, it might lead to a question. Your comments on the shape of the mortality curve for rams, its my impression that there is a fair amount of data from desert bighorns and Stone sheep and other things that seem to fit the interpretation of Mary's data rather well. And going along with that, if the age structure of the rams on Ram Mountain is such that the older rams are about five years old, our conclusion would be that the population had been pretty well smoked, and you could expect this higher mortality of juveniles. That seems in our work to have gone along with the removal of the old age class of rams. I don't know that I'd ask you to respond to that, its a comment I'd like to make. The other thing I need to say and that is if Tom Thorne isn't going to do this, I have to make an apology for ever bringing up this idea of alternate year reproduction. Two years ago Thorne made me take that back and I did. I've written several times that this was a distraction and a mistake, and we probably shouldn't be paying too much attention to it. Out technique was biased. We were emphasizing alternate year reproduction and the way we gathered our consecutive year reproductive frequency stuff suffered. For that reason we've stopped looking at alternate year breeding as a phenomenon and have concentrated on consecutive year reproductive success, which is influenced by a number of things, weather being at least one. I talked about that the other day, but I don't want Tom Thorne to be jumping on my case because people are still saying alternate year breeding when he made me straighten that out a couple years ago. Is that right, Tom?

Tom Thorne, Wyoming: Its just fine. OK I won't comment on the alternate year breeding. As far as the ram portion of it goes, I believe in your Dry Creek herd you're removing all of your older rams or most of them anyway. At Ram Mountain, hunters are not taking all that are available. There's still a good 50% of the older rams that are left up there. Now the lack of older rams is influencing the survival of these younger rams, that kind of situation is only going to happen when you're cropping all your old rams. There's still 4 - 5 mature rams, that are five years old and older that are there every year so that's effecting the survival of the juveniles. Old rams have got to be older than 5 - 6 years of age or else there needs to be more of these older rams than we have got.

Heimer: We don't know what the cropping rate is exactly, but we figure its something over 50% and probably approaching 75%. That doesn't allow for very many actually mature rams in our situation. There's some out there, and if I've mislead you on that I apologize also. We think, a Dall and bighorn sheep differ. If you're considering a five year old Dall ram mature, you're probably making a mistake. I don't know what it would be with bighorn.

Thorne: That does probably apply for Dall sheep. Bighorn rams just don't live very long. By the time ten years of age rolls around, there aren't any rams left. Now in the next few years I'd really like to look at this ram mortality business and try to determine what's happening to these rams. We're definitely losing them. They just disappear. One thing that might be happening is that there could be wounding and crippling losses occurring during the hunting season. It doesn't have to amount to very many rams in order to give me this kind of survivorship curve. I've seen instances of wounding, and I see hunters shoot rams and the ram staggers off into the trees and bush or down onto a piece of cliff. Hunters have no idea where he's gone and that ram is found a couple days later by somebody else. I've also seen hunters flock shooting at groups of rams. The odds on some kind of wounding going on in situations like that is pretty high, and it might just be possible that that kind of loss of rams is higher than we expected or we've ever thought it might be. That's something that needs a lot more looking into and hopefully I can do that in the next few years because I'd really like to try to resolve this issue and find out what's happening to these rams.

Jon Jorgenson: We've come to look more at the socials trends involved with young ram participation as a predisposing factor to predation. There are changes that hopefully will be apparent when you see our paper in print. The predator control had quite on influence on survival of rams and didn't make that much difference for ewes.

Thorne: I can't comment on that. I don't know what sort of predation levels are going on in some of these individuals. John?

John Stelforth, Alberta: My question, Jon, deals with matter of horn growth in relation to population density. An interesting thing from your study indicates when you let the population go from 100 up towards 140-150 that certain unfavorable situation arise as far as decreased horn growth, increased lungworm output and what not. I'm just wondering about that population in relation to what you'd consider suitable or the likely carrying capacity of that range. You know Shakelton's work in Banff and Kootenai after the population declined about 75%, there were tremendous increases in horn growth related to that low population. Your information relating it to spring greenup, certainly has an influence, but I guess my main question and Bill might want to respond to this, is that from a management standpoint, what would happen if you brought this population down to say 60 or 80 animals, if the objective was to produce large trophy rams, you should get better annual growth rates on those rams from a smaller population. Their health should be better. Also, have you been thinking in terms of your long term objectives as far as the population size you want, and how you're going to be cropping those, and how that relates to your carrying capacity for that herd?

Jorgenson: Our plans right now are just to let the population go, at least a bit further, and keep monitoring these things. Last year was the first year we started getting any sort of indications that we might be getting a bit of a decline in the quality. Admittedly, we've only gone from a hundred animals to a hundred forty which isn't very much, only about 40%, but already we're starting to see a bit of a difference. Now as far as the horn growth goes, I showed that growth rates are still going up at Ram, yet the actual horn sizes were going down and that was related to this problem of length of the growing season. You can't regulate that at all. You might be able to do something about forage quality that might increase growth rates, but if you reduce your population, you'd expect that your quality should maintain when you've got a good early green up, and you've got a good chance to jump onto that horn growth then you're going to produce... you're going to lay down an increment during that year. As far as the carrying capacity at Ram Mountain goes, we maintained that population at about 100 animals representing a density of about 2.8 animals per square kilometer. At that 100 population level we feel that we were just below the carrying capacity or just below that maximum sustained yield level. We got our high lamb production, we got our good growth rates, we got our high survival rates, we got our yearlings producing. But there's other factors, like predation isn't that big a problem at Ram, and I haven't mentioned that much about winter as far as winter influences on these parameters go. We've had mild winters, nothing but mild winters in Alberta for the last 10 years. Now, how much of a factor would severe winters have on this? I suspect they'd have the greatest influence probably on survival rates and that big influence would probably influence it much greater at this high density level then it would when we maintained it at 100 animals.