Moose Population Research and Management Studies in the Yukon

Limiting Factors on Moose Population Growth in the Southwest Yukon

by
Douglas G. Larsen
David A. Gauthier
Rhonda L. Markel
Robert D. Hayes

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D.G. Larsen[1]

D.A. Gauthier[2]

R.L. Markel[1]

R.D. Hayes[1]

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[1]Yukon Department of Renewable Resources, Box 2703, Whitehorse, YT

[2]Department of Geography, University of Regina, Regina, SK

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D.G. Larsen

D.A. Gauthier

R.L. Markel

R.D. Hayes

Approved

Director, Fish and Wildlife Branch

Brian O. Pelchat

Senior Big Game Biologist

Big Game Section

Yukon Fish and Wildlife Branch

Department of Renewable Resources

Government of Yukon

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ABSTRACT

The demand for moose (Alces alces) in the southwest Yukon has exceeded the supply, as moose populations either declined or remained stable at low densites throughout the early to mid-1980's. In order to identify factors limiting moose population growth, the effects of grizzly bear (Ursus arctos) predation and wolf (Canis lupus) predation, were assessed inductively, through documentation of the causes and rates of moose mortality from a radio-collared sample of female and calf moose. In addition, we attempted to assess the effects of wolf predation deductively, through the reduction of wolf numbers. We also evaluated the effects of hunting, weather, moose productivity, forage, and emigration on moose numbers.

Wolf populations were reduced, on average, by 62% (44%-88%) of their pre-reduction levels, between the winters of 1982/83 and 1986/87. Wolf densities declined from 12 wolves/1000 km^2 (pre-reduction) to 5 wolves/1000 km^2 (post-reduction). Wolf reduction levels were not consistent over the experimental areas or period. Reduction levels $\geq$ 40% were considered sufficient to test limitation. Grizzly bear population reductions averaged 4% (0%-11%) between 1984 and 1987. Grizzly bear reductions were considered insufficient for an adequate test. "Liberalized" hunting regulations did not significantly increase the number of grizzly bears killed by hunters. The total moose harvest, excluding poaching, was estimated between 7%-9% of the pre-hunt population annually. The harvest by hunters other than Indians declined by 83% between 1979 and 1987.

Moose pregnancy rates, birth rates, and twinning rates were 89%, 112 calves/100 females and 27%, respectively. Seventy-one percent of all calves were born over a 10-day period (20 May-29 May) for a median calving date of 25 May.

Neonatal sex ratio was skewed ($P<0.05$) in favor of females (34 females:22 males). One hundred thirty-four adult females and 135 calf moose were radio-collared and monitored between 1983 and 1988. Cow age averaged 8 years with 84% between 5 and 13 years old. The proximate cause of female mortality was determined for 16 females; 8 were killed by wolves, 4 by grizzly bears, 2 by grizzly bears or wolves, and 2 from unknown predators. The average annual survival rate of adult females was 89%. Mean calf survivorship to 6 months was between 22% and 27%. Grizzly bears accounted for 58% (N=54) of moose calf mortalities, wolves for 27% (N=25) and black bears for 4% (N=4). The majority of calf deaths (93%), from all causes, occurred between birth and 1 November. The majority of deaths from grizzly bears (95%), occurred within the first 8 weeks of parturition.

The response of the moose population to wolf reduction was largely inconclusive. Mean female survival rates (92%) were not different ($P=0.30$) in areas where wolf numbers were reduced, compared to areas with no wolf reduction (88%). No significant ($P>0.10$) increase in moose numbers was documented after a mean wolf reduction of 66% over 4 years, although the trend was towards increasing moose numbers. We were only able to assess the effects of wolf reduction on moose population size in 1 of the 3 experimental areas. The causes of calf mortality were not significantly different ($P=0.23$) between experimental and control areas, or between pre and post-wolf reduction in the same area ($P=0.34$). Mean survival to 6 months in wolf reduction areas (31%) was significantly higher ($P=0.06$), compared to non-wolf reduction areas (21%) over the same years, as well as higher ($P=0.03$) in the wolf reduction area prior to the reduction program (17%). Calf survival to 6 months were correlated with percent wolf reduction ($r^2 = 0.44$, $P = 0.02$) but not with wolf numbers ($r^2 = 0.02$, $p = 0.52$). Multiple regression analyses between calf survival to 6 months and wolf numbers, grizzly bear numbers and maximum snow depths during the winter preceding calving, explained 66% of the variation in calf survival.

Snowdepths in the winter preceding birth may have affected calf survival. Mean calf survival to 6 months was higher ($P=0.05$) in years with snow depths <80 cm the winter preceding birth (22%) compared to years with snow $\geq$80 cm (11%).

We conclude that grizzly bears were the primary limiting factor on this moose population followed by wolves. Population models predicted that grizzly bear accounted for 48% of all deaths in this moose population over 1 year, wolves 29% and reported hunting 9%. The implications of this study are that the secondary (wolves) and tertiary (hunting) limiting factors must be substantially reduced for an extended period before moose numbers will increase in the southwest Yukon. Increases would occur over a shorter term period if the primary limiting factor (grizzly bears) was reduced. The value of maintaining sound study designs as well as, the outcome of selected management scenarios are discussed.

BACKGROUND AND OBJECTIVES

Moose in the Yukon are utilized by licensed hunters, Indian hunters and others for a variety of purposes including meat consumption, recreation, traditional uses and viewing. Low or declining moose populations in the southwest Yukon have resulted in a lower harvest by licensed hunters between 1979-1987. The primary causes of moose mortality in the Southern Yukon was documented to be grizzly bear predation followed by wolf predation and hunting (Larsen et al. 1989). The primary focus of this paper is to assess the effects of predation as well as a variety of other potential limiting factors to moose population growth over a wider geographical area then above study. The results of the earlier study are incorporated in this paper.

Specifically, the objectives of our study were to: **1)** determine if wolves and grizzly bears were limiting moose population growth by measuring the rates and causes of female and calf mortality; **2)** determine if wolf reductions resulted in a measurable change in female and calf survival rates and changes in moose population size. **3)** assess the effects of moose productivity, emigration, winter and spring weather severity, reported harvest of moose, and forage on moose numbers; **4)** assess the levels of wolf and grizzly bear reduction achieved; and **5)** assess future management strategies.

Moose in the southwest Yukon exist in a complex, dynamic, and interactive system involving 3 potential natural predators - wolves, grizzly bears, and black bears (*Ursus americanus*), 3 potential alternate prey species - Dall's sheep (*Ovis dalli*), woodland caribou (*Rangifer tarandus*), and mountain goat (*Oreamnos americanus*) and human harvest of all predator and prey species. The interactions among predator and prey species may be confounded by annual variation in weather patterns, long-term habitat changes, changes in productivity, movement of animals out of the study area and hunting patterns. Although moose harvest by hunters other than Indians has been documented since 1979, harvest data from Indian hunters was not available until 1988.

TESTING LIMITATION HYPOTHESES

Two different study approaches have commonly been used to investigate the interrelationships between moose, predators, and their environment. The "inductive" approach is to document the causes and rates of moose mortality by studying a sample of radio-collared animals in the population (Franzmann et al. 1980, Ballard et al. 1981, Gasaway et al. 1983, 1986a). The "deductive" approach is to manipulate the most likely limiting factor(s), while at the same time monitoring changes in other factors which may potentially act concurrently to limit population growth, and document the response of the moose population to the manipulation. The deductive approach allow managers to simultaneously study moose-predator interactions while enhancing moose populations, (Ballard and Miller 1989, Gasaway et al. 1983, Stewart et al. 1985, Boertje et al. 1987, and Crete and Jolicoeur 1987). The inductive approach allows managers to identify the most likely limiting factors before manipulation. We used both inductive and deductive approaches to test limitation hypotheses in this study.

Modifications due to changing policy and direction were made to the original deductive design (Larsen and Gauthier 1985) over the course of the program. These changes resulted in a fundamental condition of the deductive approach being violated, i.e. that the potential limiting factors must be reduced substantially in order to force the system beyond its "normal" state and thus provide an adequate test of limitation. We will show how these modifications resulted in an inadequate reduction of both grizzly bear and wolf numbers which made it, in some cases, impossible and in others difficult to test limitation hypotheses. As a result, the role of predators in limiting moose population growth was confused rather than clarified.

We would accept that wolf predation was a primary limiting factor to moose population growth if 1) wolves were responsible for the largest proportion of the estimated annual deaths in the moose population, or 2) wolves were identified as the primary source of mortality of radio-collared calves and adults, or 3) calf and female moose survivorship, or numbers of moose, increased significantly following the removal of wolves, compared to the period prior to removal in the same areas, and to the control areas during the same period, or 4) there were significant correlations between moose survivorship and wolf numbers throughout the wolf removal area.

We would accept that grizzly bear predation was a primary limiting factor to moose population growth if: 1) grizzly bears were responsible for the largest proportion of the estimated annual deaths in the moose population; or, 2) grizzly bears were identified as the primary source of mortality of radio-collared calves and females. We were not able to test the effects of grizzly reduction on moose demography as insufficient numbers of bears were removed.

We would accept that the reported harvest was a primary limiting factor if hunting was responsible for the largest proportion of the estimated annual deaths in the moose population, or if adult male to female moose sex ratios were skewed sufficiently to cause reduced production (i.e. pregnancy rates below 80%). We were not able to test the effects of reduced hunting on moose demography as population estimates were not made after harvest reductions occurred.

We would accept that climate was a primary limiting factor to moose population growth if: 1) calf survivorship decreased substantially in winters when shown depths exceed 80 cm (Coady 1974) or, the year following a winter when snow depths exceeded 80 cm; or 2) there was a significant correlation between calf survival and snow depths the preceding year, or, the cumulative effects of snow depths during the preceding 3 winters (Mech et al. 1987) or; 3) calf survival decreased substantially in years when the mean spring (01 May - 01 July) temperature was below the 30 year average; or 4) there was a significant correlation between calf survival and calving/post-calving temperatures; or 5) there were significant correlations between snow depth and female or calf survivorship.

We did not collect data to directly assess if forage was limiting population growth. However, we suggest that the following conditions would strongly support forage/climate as a primary limiting factor: 1) if adult pregnancy rates were below 80% (Blood 1974) and twinning rates were <20%, or 2) marrow fat content of wolf-killed adult moose in winter was consistently $\leq$ 20% (Franzmann and Arneson 1976, Peterson et al. 1984) indicating extensive malnutrition, or 3) late winter physical condition was considered poor through a subjecture evaluation by a veterinarian, and packed cell volume (P.V.C.) levels were below standards set by Franzmann and LeResche (1978) and Franzmann et al. (1987).

Finally, we would accept emigration affected moose numbers if a substantial proportion of radio-collared females (collared within a prescription area) emigrated from the area and did not return during the study period.

STUDY AREA

The study area consisted of 3 experimental areas where wolf numbers were manipulated: Haines Junction - 4890 km^2, Rose Lake - 6310 km^2 and Lorne Mountain - 1020 km^2. Wolves were not manipulated within 2 control areas: Teslin - 2580 km^2 and the Auriol Range - 1190 km^2 (Figure 1).

The physiography within both the control and experimental areas is diverse. The control areas vary from precipitous mountains rising to 2259 m in the Auriol Range, to rounded undulating mountains in Teslin. The physiography in the experimental areas is characterized by rugged mountains throughout. In all areas, narrow and deep valleys separate precipitous mountain ranges, with wider U-shaped valleys found in the less precipitous areas. Small icefields, cirque basins and talus slopes were common at higher elevations with permafrost being discontinuous (Oswald and Senyk 1977). Two major drainages bisect the study area with the western portion (Auriol Range and part of Haines Junction) drained by the Alsek River, and the eastern portion drained by the Yukon River. Numerous large lakes occur throughout the study area.

Both experimental and control areas lie within the Boreal Forest Region, interspersed with tundra (Rowe 1972). Treeline varies from 1050 - 1350 m. The subalpine zone, from treeline to approximately 1500 m, is largely composed of shrub birch (Betula sp.) and willow (Salix sp.). White spruce (Picea glauca) dominates the forest cover on lower slopes, terraces and plateaus. Black spruce (Picea mariana) is less common and occurs on moist sites. Stands of lodgepole pine (Pinus contorta) occur along with aspen (Populus tremuloides) throughout the study area. Subalpine fir (Abies lasiocarpa) is found near treeline in the southern portion of the study area. Both experimental and control areas have a history of fires, resulting in a mosaic of several habitats. The most extensive burn, and thus potentially the best moose habitat, occurred in the Teslin area in 1958.

Weather throughout the study area is characterized by cool, short summers and long, cold winters. Pacific coastal weather systems have a moderating effect on temperatures throughout the year. The study area lies in the rainshadow of the Coastal Mountains, resulting in a semi-arid climate. Average (30 year) annual temperatures varied between -1.2°C to -3.2°C and total annual precipitation from 261 to 326 mm. Weather data was obtained from the Department of Environment stations in Haines Junction, Whitehorse (airport), and Teslin.

Snow depths in both the experimental and Teslin control areas are generally below 80 cm. Above average snow accumulations rarely occurred over the past 2 decades. Snow depths in excess of 80 cm are detrimental to calf moose survival (Coady, 1974). Stations in Whitehorse and Teslin recorded snow depth $\geq$ 80 cm in 1971/72, in Haines Junction and Teslin in 1975/76, and in Haines Junction in 1982/83. Snow depths were not available from the Auriol Range, however, it is likely depths commonly exceed 80 cm in late winter (Kluane Parks personnel pers. comm.). Spring temperatures during calving (May/June) varied little over the study period. The physiography, climate and vegetation have been described in more detail by Oswald and Senyk (1977) and Davies _et al_. (1983).

Large carnivores occur throughout both the experimental and control areas (Appendix 1). Grizzly bear densities have been estimated at 40 bears/1000 km^2 in the Auriol Range (Pearson 1975) and at 16 bears/1000 km^2 in the Rose Lake area (Larsen and Markel 1989). We speculate that grizzly bear densities in the remaining areas were similar to densities in Rose Lake. Black bear densities were unknown but likely close to grizzly bear densities, with the possible exception of the Auriol Range, where grizzly bears may be more numerous. Pre-reduction wolf densities were similar (12 wolves/1000 km^2) throughout the experimental areas (Hayes _et al_. 1985, Hayes and Baer 1986). Density in the Teslin control area was documented at 18 wolves/1000 km^2 in 1983/84 (Hayes and Baer 1986). Wolves were not censused in the Auriol control area, but likely occurred at densities similar to the experimental areas (R.D. Hayes, Yukon Fish and Wildlife Branch, Whitehorse, pers. comm.).

Sheep were the most abundant prey species, followed by moose and caribou, however, prey numbers varied substantially throughout the experimental and control areas (Appendix 1). Moose and caribou densities were highest in the east (Teslin and Lorne Mountain) and lowest in the west. Sheep densities followed a reverse pattern, with the highest densities in the west and no sheep in the east. Snowshoe hare (_Lepus americanus_) numbers were low throughout the Yukon in 1983 (Slough 1984), reaching densities of 20 hares/1000 km^2 in southwest Yukon (Boutin _et al_. 1986, Ward and Krebs 1985). Beaver (_Castor canadensis_) are uncommon based on availability of marginal habitat (B.D. Slough, Yukon Fish and Wildlife Branch, Whitehorse, pers. comm.).

METHODS

Predator Population Status and Reductions

Wolves

Wolf numbers and distribution in the study area were estimated from aerial surveys and radio-collared packs (Hayes et al. 1985 and Hayes and Baer 1986). Fall population estimates were based upon mid- to late-winter counts, plus wolves which were killed or known to have died in winter. This method does not estimate the total over winter natural mortality and therefore underestimates the fall wolf population.

Wolf populations in the experimental blocks were reduced through aerial hunting between the winters of 1982-1983 and 1984-1985. Removal was done primarily by government personnel from helicopters (October to April), although some were also killed by resident hunters and trappers. Attempts were made to remove all pack members except for radio-collared animals. Wolves continued to be removed in lower numbers after 1985 by trappers and hunters. Harvest by residents was determined through a hunter questionnaire (Kale 1982) and non-resident harvest through compulsory registration.

We considered reduction levels of $\geq$40% of the original wolf population to be sufficient to reduce the numbers of wolves, and thus potentially allow the moose population to grow. This minimum reduction level was based on other studies which suggested lower levels would not cause a decline in wolf numbers (Gasaway et al. 1983, Keith 1983, Peterson et al. 1984 and Ballard et al. 1987). Reduction levels were expressed as: a) annual reductions - the difference between the number of wolves alive in the fall and late winter of each year, and b) cumulative reductions - the proportion of the 1982-83 wolf population alive by late winter each year.

Grizzly Bears

Grizzly bear densities throughout the study area (except the Auriol Range) were assumed to be similar to those documented in Rose Lake in 1985 (Larsen and Markel 1989). This assumption was made because the Rose Lake estimate was obtained in the centre of the study area and the habitat and hunting pressure in this area were comparable to the remaining areas. The bear population size prior to 1985 was calculated by adding the number of bears removed from the area in the preceding year to the 1985 estimate. Population estimates after 1985 were calculated by subtracting the number of bears removed from the area each year from the 1985 estimate. Our extrapolations assume that the populations were stable, exclusive of removals by man (e.g. hunting, removal of problem bears and capture mortalities). If there was a sustainable yield, the effects of these extrapolations would be to overestimate the population in 1984, therefore underestimating the removal rate; and underestimate the population in 1986, 1987, and 1988, therefore overestimating the removal rate.

A grizzly bear reduction program was in effect between 1984-1987 in the Rose Lake and Lorne Mountain areas and between 1985-1987 in the Teslin area. The reduction program continued after 1987, however this analysis was restricted to the pre 1987 period. Removal was carried out exclusively by resident and non-resident hunters. Hunting regulations were liberalized in areas identified for bear reduction (appendix 2) as follows: a) 1 bear/lifetime for non-residents changed to 1 bear/year; b) 1 bear/4 years for residents changed to 1 bear/year c) spring seasons from 0-60 days changed to 65-80 days; d) fall seasons from 0-90 days changed to 105 days; and e) areas previously closed to non-residents were open to guided hunts. Selective harvesting of males has been encouraged through the use of disproportional trophy fees for both residents and non-residents, and more recently a disproportional point system for outfitters (Smith and Pelchat 1989). Harvest by both resident and non-resident hunters was determined from compulsory registration. In addition to hunting, bears were killed due to threats to human life and property, and from drug related complications during bear studies.

Moose Population Status

Estimating Moose Population Size and Composition

Moose density was estimated from aerial surveys using either a stratified random sampling technique (Gasaway *et al*. 1986b, Larsen 1982) or a total area count. All surveys were flown in early winter (November - December). A total area count involved surveying the entire area, but concentrating search effort in areas of known or expected high moose densities. This type of survey was carried out in the Auriol Range (1979-86) and in the Teslin area (1974-78) using helicopters (Kluane Park unpubl. data; Hoefs 1974, 1976, and 1979). All other areas were stratified with a fixed-wing aircraft and censused with a helicopter (Larsen 1982; Larsen and Nette 1988, Markel and Larsen 1983, 1984, 1985; Johnston and McLeod 1983; Johnston *et al*. 1984; Jingfors and Markel 1987). On average, 23% (range 13-43%) of the habitable moose range was sampled and intensively searched (averaged 1.9 min/km^2). Habitable moose range was defined as habitat below 1500 m elevation, excluding precipitous slopes and large water bodies.

A sightability correction factor was not developed as we were confident most moose were observed during the intensive helicopter surveys (Larsen 1982). If moose were missed, the bias would be to underestimate moose density, but would not affect conclusions based on changes in density as the bias would have been consistent throughout this study. Sightability of moose was felt to be excellent as a result of the open subalpine habitat which moose utilized in these areas, the presence of snow, and the clumped distribution of moose during the following the rutting period (Larsen 1982). Population and composition estimates with 90% confidence intervals were calculated by summing the strata estimates. (Gasaway et al. 1986b).

Classification of adult moose differed between areas where total area counts were obtained (Auriol Range 1979-87, Teslin 1974-80), and areas where stratified sampling estimates were made. During the former counts, no distinction was made between yearling and adult females. In these areas the actual adult female ($\geq$30 month) population would be overestimated, resulting in an underestimation of calf survival rates. This bias was minimal as there were few yearlings in the stratified counts throughout the study area (see Results). Moose on stratified counts were classified as adult females and bulls, yearlings ($\geq$18 month.) or calves (Larsen 1982).

Estimating Adult Cow Productivity, Age, Natural Mortality, and Movement

Between March 1983 and April 1985 female moose were captured in the 3 experimental and Teslin control areas. Moose were immobilized with various combinations of carfentanil, xylazine hydrochloride, fentanyl citrate, and hyaluronidase (Larsen and Gauthier 1989).

Pregnancy was determined through rectal palpation (Arthur 1964, Haige et al. 1982). Timing of birth and the number of calves born was determined through daily visual monitoring of radio-collared females during calving periods in 1983 (Rose Lake and Teslin), and 1985 (Rose Lake), and weekly monitoring in the 1984 calving period (Rose Lake, Teslin, Haines Junction, and Lorne Mountain). Visual monitoring was discontinued once a calf was observed. In 1985, calf sex was determined at the time of collaring in Rose Lake and verified by the presence of antlers in the summer and fall of 1986. Cow age was determined by tooth-cementum annuli from incisors (Sergeant and Pimlott 1959, Gasaway et al. 1978).

Annual natural mortality rates of females were based on mortality rates of radio-collared females for the years 1983 - 1987 inclusive. Collars with 6-hour mortality switches were used (Telonics, Mesa Arizona) and all immobilized moose were visually monitored within 48 hours of handling to detect capture-related deaths. The frequency of electronic monitoring after capture varied with the season, area, and year (Appendix 3).

Natural survival rates of adult females were estimated annually (1 March - 28 February) as follows: Number of females collared at time t and still alive at time $t + 1$ divided by the number of collared females at time t. Only those animals monitored throughout an entire period were included; animals which we lost contact with due to radio-collar failures, and animals collared part way through a period were excluded in order to minimize sampling biases.

Mortality signals detected from an aircraft were used to determine female death. Mortalities were either investigated on the ground and the cause of mortality determined by evidence at the site (Larsen et al. 1989), or investigated from the air and the cause of mortality unknown. Mortalities were assigned to the calendar year in which the mortality signal was first detected, although in a few cases (3 out of 46) the female may have died in the preceding year. Range fidelity of collared females and their calves to the 3 experimental and Teslin control areas was determined from aerial relocations between May 1983 and March 1987.

Estimating Causes and Rates of Calf Natural Mortality

Three types of marked calf/female groups were used in this study between 1983 and 1986 (Appendix 4); collared calf with collared female (group 1), collared calf with uncollared female (group 2), and uncollared calf with collared female (group 3). Newborn calves were collared in the Rose Lake experimental area in 1983 and 1985, and in the Teslin control area in 1983 following procedure described by Larsen and Gauthier (1989). Collared calves were combined with uncollared calves to determine survival rates as there was no difference in survival between groups (Larsen and Gauthier 1989). Calves from groups 1 and 3, whose mothers were immobilized, were excluded from the calf survival estimates for the year in which the female was immobilized, as postnatal calf survivorship may have been affected by immobilizing pregnant females (Larsen and Gauthier, 1989).

All calves were aged at the time of capture following criteria described by Larsen _et_ _al_. (1989), and visually monitored within 24 hours to determine abandonment. In 1983, calves were monitored 1-4 times daily from collaring to the end of June, weekly through July, twice per month to December, and once per month to May. In 1985, calves were monitored 1-4 times daily between collaring to the end of June, daily to July 15 and once in September, October, November, and March. Group 3 calves were monitored at the same frequency as the collared female. All monitoring was done from either a helicopter or fixed-wing aircraft at altitudes > 600 metres above ground level.

The proximate causes of calf mortality were determined from groups 1 and 2. All mortalities were investigated _in situ_, immediately upon receiving a mortality signal and the cause of death was verified by the presence of sign at the mortality site (Larsen _et al_. 1989).

The rate of calf survival was estimated from groups 1, 2, and 3 over 3 time intervals: summer (17 May - 1 November); winter (2 November - 1 March); annual (17 May - 1 March). The winter and annual intervals used do not encompass the entire winter (November - May) and annual (May - May) periods, as contact with calves was not consistently maintained after 1 March. The summer period represented the most complete data from both the experimental and control areas.

Two methods were used to estimate calf survival to 6 months of age. The first compared the number of calves in the November aerial survey to the number of calves born in the spring of the same year. The number of calves born was estimated by multiplying the number of adult females in spring by the mean (1983-85) birth rate. The number of adult females present at calving was assumed to be similar to the number of adult females (≥30 months) estimated in November aerial surveys. We recognize that adult females died between May and November, therefore, the number of adult females and their calves in spring were underestimated, resulting in an overestimation of calf survival rates. Also the estimated calf survival rates in the Auriol Range (1979-87) and Teslin (1974-80) areas may have been biased. Calf survivorship to 6 months in these areas was calculated as above, but based on females ≥18 months of age, rather than ≥30 months. This bias was not significant as yearlings comprised a small proportion of the overall population and, thus, of the female populations (see Results).

The second method compared the number of calves with collared females in November, to the predicted number of calves born that spring. This technique was used in the 3 experimental and Teslin control areas where collared females were present. The number of calves predicted to be born was calculated by multiplying the number of collared females present in the spring by the mean birth rate. This method was not used in the year the female was immobilized, due to the negative effect of immobilization on post-natal calf survivorship (Larsen and Gauthier 1989).

Winter and annual survival rates were estimated for the 3 experimental and the Teslin control areas. Winter calf survivorship was estimated by comparing the number of calves in groups 1 and 3 as of 2 November, with the number of calves alive in March. Annual survival was estimated by comparing the number of calves present with collared females in March, to the number predicted born in the preceding spring. In all calf survival analyses, only those calves with which radio contact was maintained throughout an entire period were used. Calf survival rates were estimated using the same formula described for females.

Estimating Moose Harvest

Moose throughout the 3 experimental and Teslin control areas were harvested by licensed resident and non-resident hunters and non-licensed Indian hunters. The licensed resident harvest was determined by hunter questionnaire (Kale 1982) and the non-resident harvest through compulsory reporting between 1979-1987. Personal interviews were conducted in 1988 with Indians in communities in and around the study area (R. Quock, Yukon Fish and Wildlife, unpulb. data). The Indian harvest results should be treated as preliminary until additional surveys are conducted to verify these initial findings. Until verification is made we use a range of values for Indian harvest, based on 2 independent estimates, i.e. consumption and harvest rates (Quock and Jingfors, 1988). Harvest by Indians prior to 1988 was largely unknown.

Harvest trends in this paper are based exclusively on resident non-Indian hunting statistics as this group represents the most complete data on both harvest and effort. The success rate of resident hunters was calculated as the number of hunting days required to kill a moose. Harvest intensity was calculated as the number of moose harvested/1000 km^2 of moose habitat, while harvest levels were calculated as the number of moose harvested divided by the estimated pre-hunt population in the same year. The pre-hunt population was calculated by adding the post-hunt population (estimated from the annual fall censuses) to the harvest. This analysis could only be done in the years and area population estimates were made.

Hunting regulations were categorized as; least restrictive (areas and years with 90 day bull season and no female season), moderately restrictive (90 day bull season and no female season) and most restrictive (15-45 day bull season and no female season). Harvest reduction areas were designated as those areas where the non-Indian annual harvest was less than the 1979-87 mean (minus one standard deviation) for that area.

Estimating Physical Condition of Moose

We determined if moose killed by wolves during the winter period (November - April between 1982-88) were starving, by assessing the marrow fat content collected from long bones (Neiland 1970). Wolf kills were located through intensive monitoring of radio-collared packs or incidental to wolf surveys. The condition of radio-collared female moose were assessed at the time of capture through gross external physical examination and packed cell volume levels (Glover and Larsen 1988).

Weather Parameters

Winter severity was classified according to both a snow index (Gasaway et al. 1983) and maximum accumulated snow depth. Snow depths on the 1st and 15th day of each month (when available) were plotted, and the area under the curve measured to determine a winter snow index (WSI). Winters were standardized by dividing each year by the area with the least snowfall. Winters were considered severe for moose calves if snow depth exceeded 80 cm (Coady 1974), or if the WSI exceeded the long-term average (1968-85) plus 1 standard deviation. Both single year and multiple year effects of maximum snow depth were tested. The cumulative effects were determined by summing the maximum snow depth for the preceding 3 years (Mech et al. 1987). Spring/summer severity (1 May - 31 July) was based on mean daily temperature. Years with a mean temperature below the long term average (1968-86), minus 1 standard deviation, were considered harsh.

Weather data was obtained from Environment Canada permanent stations in Whitehorse, Haines Junction and Teslin. We assumed that the weather recorded at Haines Junction represented conditions in the Haines Junction and Auriol Range areas, Whitehorse represented Rose Lake and Lorne Mountain areas, and Teslin represented the Teslin area.

Population Models

We present two simple models. The first was used to demonstrate the relative and absolute significance of the different causes of mortality in this population over one annual cycle. The population size and composition in the model were based on the sum of the moose populations (Haines Junction, Rose Lake, Lorne Mountain and Teslin) in the first year they were censused. Population extrapolations were based on average productivity and mortality rates documented in this paper. We have assumed that all moose $\geq$1 year old died at the same rate and from the same natural causes as adult females, and that the population was closed (i.e. ingress=egress).

The model was then used to predict the effects of different management prescriptions on moose demography. We considered only the most likely management scenarios where grizzly bears, wolves and hunting were manipulated. For these extrapolations, we have assumed: a 1:1 relationship between the number of wolves, grizzly bears and their predation rates on moose; and that no compensation among the remaining wolves and grizzlies, or any other limiting factor, would occur after the removal of predators. We suspect compensation may be important, but have no information from this study or from other studies reported in the literature which would allow us to quantify its effects. The assumptions in this model are unsubstantiated, therefore the following predictions should be viewed as best-case scenarios and thus used cautiously.

A second model was used to compare observed to predicted moose population estimates, as a means of evaluating the accuracy of the survival and productivity values used in this report. This comparison was only possible in the Rose Lake area. Observed population estimates were based on fall aerial surveys in 1983 and 1986. The model used survival rates specific to the Rose Lake area, rather than the average rates used in the preceding model.

Analysis

Unless otherwise stated, statistical differences between means were determined by student's t-test analysis and differences in proportions by log-likelihood-ratio analysis. Unbalanced analysis-of-variance (ANOVA) tests were used to assess differences among means. Multiple and single linear regressions were used to develop predictive equations describing the relationships between survival rates of calves (6 month, 10 month) and adult females with predator numbers and weather parameters. Multiple regressions were conducted and the maximum coefficient of multiple determination (R-square) and the minimum Mallow's C(p) statistic were used as criteria for selection (Daniel and Wood 1980, Montgomery and Peek 1982). The backward elimination and maximum R-square improvement techniques were used to define the "best" 1-variable, 2-variable equation, etc. In all tests, an alpha level of 0.10 was used to determine significance, unless otherwise specified.

RESULTS

Wolf Reduction

Wolf population estimates and the effects of wolf reduction on wolf densities have been discussed by Hayes et al. (1985) and Hayes and Baer (1986, in prep.). A summary of that data are presented in Table 1. Wolf reduction was not consistent from 1983-85, or throughout the experimental area. Removal rates were low (<40%) in the first year of the reduction program in Haines Junction and the first 2 years in Lorne Mountain. Following the reduction program, wolves continued to be removed by trappers and hunters in all 3 experimental areas. Wolf reductions were considered sufficient ($\geq$40% of pre-reduction levels) to test limitation on moose survivorship and population growth in Haines Junction 1984 through 1986, Rose Lake 1983 through 1987, and Lorne Mountain 1985 through 1987 (Table 1). The annual and cumulative reduction levels in those areas averaged 43% and 62%, respectively. Wolf densities prior to reduction (1982 fall estimates) averaged 12 wolves/1000 km^2 and during reduction 5 wolves/1000 km^2. In the remaining areas and years (<40% of pre-reduction levels) annual and cumulative reduction levels averaged 19% and 25%, respectively. Wolf reductions of $\geq$70% occurred in Rose Lake during the winter of 1984/85 and 1985/86 and Lorne Mountain during 1985/86.

Grizzly Bear Reduction

The overall magnitude and duration of grizzly bear reduction was insufficient to test the short-term effects of removal on moose survivorship and changes in population size. The mean annual bear removal rate (% of the bear population removed from all known human causes), was 4% (range 0-11%) in Rose Lake, Lorne

Mountain and Teslin over the 4 year reduction program (1984-87) (Table 2). Removal was not consistent over the 3 prescription areas, therefore, regional differences occurred. In the Haines Junction area, originally identified as a non-reduction area, 8% (range 3-13%) were annually removed between 1984-1987. No bears were removed in the Lorne Mountain area.

Estimates of population size and thus reduction levels are approximations, nevertheless, we feel their accuracy is adequate for our purposes. Although the level of removal was too low to substantially change the bear population over the short term, and thus to provide an adequate test for a short term study on limitation, the long term effects may be more profound. Forty seven percent of the bears removed between 1984-1987 were females and 54% of those were $\geq$6 years of age.

The level of bear removal increased in all areas as a result of an increase in non-hunting mortalities. The mean ($\pm$SE) number of bears removed between 1984-87, regardless of area (4.0 ± 1.0) was significantly (P=0.03) greater than for the preceding 10 years (1.6 ± 0.3). Thirty-two percent (20/63) of the bears removed between 1984-87 were the result of non-hunting causes compared to 8% (3/35) between 1979-83. Control kills, drug related deaths, and experimental relocations were the source of most removals (Spreadbury 1984, Larsen and Markel 1989, B. Smith unpubl. files).

Liberalized hunting regulations did not substantially increase the number of bears killed in the reduction areas. The mean ($\pm$SE) number of bears killed annually by hunters (2.4 ± 0.7) from the reduction areas during the reduction period was less; although not statistically significant (P=0.25), than in the non-reduction areas (4.0 ± 1.4) during the same time period (Table 3). As well, the mean number of bears killed in the reduction areas in the reduction period was not significantly different (P=0.44) than the mean (1.8 $\pm$ 0.30) in the remaining areas between 1974-1987.

Moose Harvest

The reported harvest by non-Indian hunters in the 3 prescription and Teslin control areas has declined by 83% (range 72%-100%) between 1979 and 1987 (Table 4, Figure 2). This decline was consistent between the control (72%) and the 3 experimental areas (88%). Hunting effort has also declined consistently in all areas, but the success rate (days effort/kill) has remained relatively constant in all areas except Lorne Mountains (Figure 2). The number of days hunting required to kill each moose increased substantially in that area after the decline in the moose population in 1982. The decline in the Lorne Mountain population was likely more severe then in the other areas (Table 5).

Harvest levels from all hunting groups combined were highest in the Rose Lake area, followed by the Haines Junction and Lorne Mountain areas. The kills by non-Indian hunters represented 6.3% of the pre-hunt population annually in Haines Junction, 5.7% in Rose Lake, 5.4% in Lorne Mountain, and 3.3% in Teslin. Indians killed between 40 and 89 moose throughout the study area in 1988 (R. Quock, unpubl. data) with approximately half of those taken in the Rose Lake area. The combined average harvest by non-Indians and Indians represented between 6.6% and 8.5% of the prehunt moose population throughout the study area.

Based on the range of harvest by Indians, resident non-Indian hunters accounted for the majority (52%-66%) of the total harvest, followed by Indians (25%-41%)

and non-residents (7%-9%). These results are considered preliminary for several reasons. First, the Indian harvest data was based on a single study conducted in 1988. These results need to be verified with subsequent estimates. Second, the 1988 harvest by Indian may not represent the level of harvest which occurred by this group during the earlier part of the study.

Non-Indian harvest reduction occurred in Haines Junction 1985-1987, Rose Lake 1985 and 1987, and Lorne Mountain 1987. Moose population estimates were not made in the majority of these areas after harvest reductions occurred.

Moose Population Status

Abundance and Composition

The mean moose population estimates in the Haines Junction (1981-1984), Teslin (1982-1984), and Lorne Mountain (1980-1983) areas declined by 42%, 24%, and 58% respectively during this study (Table 5). However, only the Haines Junction estimates were significantly ($P < 0.10$) different. Mean population estimates in Rose Lake (1982-1986) and the Auriol Range (1980-1987) increased by 23% and 27%, respectively (Table 5). The increase in Rose Lake was not significantly ($P > 0.10$) different and the increase in the Auriol range was not statistically tested as population values were based on total area counts rather than random samples.

The effects of wolf reduction on moose numbers could only be assessed in the Rose Lake experimental area. A moose estimate was not obtained in either Haines Junction or Lorne Mountain after wolf populations were reduced for more than 1 year (Appendix 5). The moose population in Rose Lake did not increase significantly between the fall of 1982 (pre-reduction) and the fall of 1986 (post-reduction) which represents a 66% reduction in wolf numbers (Table 5). Moose population trends increased in the Auriol control and decreased in the Teslin control over similar time periods.

Composition in both the experimental and control areas were similar throughout the study period (Table 5). Cows ($\geq$18 months) represented 62% of the fall population in the experimental areas between 1981-86 and 57% in the control areas over the same period. Bulls ($\geq$18 months) represented 25% of the experimental and 29% of the control areas. Calves represented 14% (range 2%-21%) of the fall population in both the experimental and control areas.

Productivity and Calf Sex Ratios

One hundred and fifteen of the 129 (89%) females ($\geq$34 months) diagnosed in the 3 experimental and Teslin control areas were pregnant, with an average (1983-85) birth rate (calves born per pregnant and non-pregnant female) of 112 calves/100 females. Twins were observed with 46 of 173 (27%) pregnant females. Calving occurred over 25 days with 71% of the calves born over a 10 day period (20 May - 29 May) (Figure 3). The median calving date was 25 May.

The sex ratio of collared calves at birth (34 females:22 males) in Rose Lake in 1985 was skewed in favor of females and was significantly different (x^2=5.29, $P<0.05$) from a 100:100 ratio. Verification of sex (presence of antlers) in 16 calves which survived for over 1 year indicated that 1 male or 6% of the calves were incorrectly sexed at birth.

Cow Age, Causes and Rates of Cow Mortality

The mean (±SE) age of females (N=124) in the study area was 8 years (±0.3) with 84% of the females between 5 and 13 years. No differences were found in female age among areas although Teslin had a skewed distribution with a higher (9.6 years) mean age compared to the other 3 areas (Figure 4).

Of the 134 females captured in the 3 experimental and Teslin control areas, and monitored between 1983-88, 10 probably died from drug-related causes within 3 weeks of handling, contact was lost with 13, and 1 was known to have been killed by native hunters (Appendix 6). Forty-six of the remaining 110 females died, however, the proximate cause of mortality was determined in only 16 cases (35%, Appendix 6). The cause of mortality was not usually determined, either because a visual sighting was not attempted (N=12), or because no sign was observed when the site was investigated from the air (N=18). Of the 16 females that died from known causes, 8 (50%) were killed by wolves, 4 (25%) by grizzly bears, 2 (12.5%) by either wolves or grizzly bears, and 2 (12.5%) from unknown predators.

The average annual survival rate of radio-collared females in the study area was 89% between 1983-88 (Table 6). No significant differences were found in annual female survivorship among years (P=0.92) or among areas (P=0.81). There was no difference (P=0.30) in the mean annual female survival rate (92%) in the areas and years of wolf reduction (Haines Junction 1984 through 1986, Rose Lake 1983 through 1987, and Lorne Mountain 1985 through 1987) compared to mean survival rate (88%) in the non-reduction area (Teslin 1983 through 1988). The data was insufficient to test for differences in female survivorship between pre-reduction and reduction periods within the same area.

No significant correlations were found between annual cow survivorship in the 3 experimental areas combined and annual pre-reduction wolf numbers (r^2=0.007, P=0.93), annual post-reduction wolf numbers (r^2=0.001, P=0.91) or % cumulative wolf reduction (r^2=0.004, P=0.83). We have concluded that annual cow survival rates did not change significantly as a result of the levels of wolf reductions achieved.

Causes and Rates of Calf Mortality

In 1983, 76 newborn calves were radiocollared in Rose Lake and Teslin, and in 1985, 59 were collared in Rose Lake. Two died from capture and contact was lost with another in the first 12 months. Of the remaining 132 collared calves 96 (73%) died within 6 months and 105 (80%) within 12 months of birth. Of the 105 deaths, 12 died from unknown causes. Of the remaining 93, predators accounted for 86 (92%) of the combined calf deaths (Table 7). Grizzly bears were the major proximate known cause of annual calf mortality, accounting for 54 of the 93 deaths (58%), wolves 25/93 (27%), black bears 4/93 (4%) and unknown predators 3/93 (3%) (Figure 5, Table 7). Non-predator causes, such as drowning and exposure, accounted for the remaining 7/93 (8%) deaths. The majority (93%) of radio-collared calves which died over 1 year died between birth and 1 November. Ninety-five percent of the calves which were killed by grizzly bears over 1 year died within the first 8 weeks after parturition (Figure 5). Wolf predation, although significant in the spring, continued throughout the year. No statistical differences were found among the known causes of calf mortality between the 2 studies in the Rose Lake experimental area (P=0.34) or among the experimental and the Teslin control areas (P=0.23), although some predator reductions had occurred prior to and during the Rose Lake studies (Table 7).

A discrepancy occurred between the 2 techniques used to estimate calf survival to 6 months of age. We documented a higher ($P>0.05$) calf survival rate using the radio-collar method compared to the aerial census method in the Teslin area in 1983 and 1984, however, no significant differences were found in the Rose Lake area in 1983 and 1986 (Table 8).

The reason for the discrepancy between areas was unclear, although it may be due to differences in observability, monitoring techniques or sample sizes. The terrain in the Teslin area was less precipitous and the vegetation denser in comparison to Rose Lake, and most of the monitoring of collared moose in Teslin was done by a different person than in the remaining areas. Collared calf sample sizes in Rose Lake, for the combined 2 year comparison, were twice as high (N=66) compared to Teslin (N=32).

Because of this potential bias, only the aerial census calf survival rates were used in our analysis. We assumed that survival rates based on the large sample from the aerial census would provide the most accurate estimate of survival rates. Also, because of this potential bias we questioned the validity of the radio-collared survival rates in other years. Calf survival rates to 6 months based on only the radio-collar technique were determined for the Haines Junction and Lorne Mountain areas for 1985 and 1986. The Haines Junction data were used as moose observations made on wolf surveys in November of 1986 agreed with telemetry survival results during the same period (R. D. Hayes, unpubl. data). However, we did not use the 1985 and 1986 Lorne Mountain calf survival data, as there were no other survey results for comparison.

Wolf reduction significantly increased calf survival to 6 months of age. Mean calf survivorship to 6 months of age was higher ($P=0.06$) in the wolf reduction areas (Haines Junction 1984 to 1986, Rose Lake 1983 to 1986 - 31%) compared to the control areas (Teslin 1983 to 1984, Auriol Range 1983 to 1987 - 21%) during the same time period. Mean calf survival rates were also significantly greater (P=0.03) in the same areas during the reduction period (31%) compared to the non-reduction period (17%) in the same areas (Haines Junction 1981-83, Rose Lake 1981-82, Lorne Mountain 1980-83).

Calf survivorship to November in the 3 prescription areas was not correlated with the number of wolves in the fall (prior to annual reductions; r^2=0.02, P=0.52) or to wolf numbers in late winter (after annual reductions and prior to calving; r^2=0.05, P=0.52). There was, however, a positive correlation (r^2=0.44, P=0.02) between calf survival rates to 6 months and % cumulative wolf reduction rates in the winter prior to calving.

Multiple regression results between calf survivorship to 6 months of age in the 3 prescription areas, predator numbers, and weather parameters, indicate that a combination of fall wolf numbers, grizzly bear numbers, and snow depths the preceding winter, best explained the variation in calf survival rates (Table 9). Model 3 was the best predictive model, explaining 66% of the variation. The prescription area had minimal effect on the model, explaining only 1% of the variation. Mean spring temperature had no effect on the model.

Multiple regression analyses were then used to separately analyze the Rose Lake prescription area (Table 10). The best grizzly bear population data, the most extensive moose population data, and over half (6/11) of the cells in the above multi-area analysis, were from the Rose Lake area. Three separate models were run, using different combinations of variables. Generally, all 3 Rose Lake models had higher R-square and lower P values compared to the multi-area model (Table 9), suggesting a stronger relationships existed with these variables in the Rose Lake area compared to the combined areas. This stronger relationship was most evident with variables describing wolf abundance (% cumulative wolf reduction) prior to calving (model A-1), wolf population size in the fall (model B-1), and wolf population size in the winter preceding birth (model C-1). Maximum snow depths and grizzly population size explained some of the variation in calf survival.

Mean calf survivorship to 10 months was significantly higher (P=0.02) in the Teslin control area (1984 to 1987 - 36%) compared to the wolf reduction area (21%) during the same time period (Haines Junction 1985-86, Rose Lake 1983-87, Lorne Mountain 1985-87). We were not able to make a temporal comparison of calf survival rates to 10 months of age within the experimental areas due to the lack of data. Calf survivorship to 10 months was not correlated with wolf numbers present earlier in the same winter (r^2=0.13, P=0.29), or to wolf numbers in late winter (after annual reductions and prior to calving) (r^2=0.05, P=0.52), within the experimental areas. These results suggest that the level of wolf reduction achieved had no measurable effects on calf survival to 10 months of age.

Range Fidelity and Condition of Moose

Based on 3156 relocations of radio-collared female moose between May 1983 and March 1987, the study animals were confined largely within the prescription areas (Figure 7). The 1 exception was the Haines Junction area where 18 out of the 29 (62%) collared moose stayed within the prescription area while 11/29 (38%) occupied both the prescription and control (Auriol Range) areas. Utilization of the Auriol Range varied from seasonal to prolonged periods of time. Of the 11 females using both areas, all but 2 moved annually between the areas. Two females moved from the prescription to the control area after collaring, and stayed in the control area from 2-3 years before dying. We speculate that the annual movement out of the Auriol Range in winter was triggered by excessive snow fall at higher elevations. Moose traditionally wintered at lower elevations in the southeastern part of the Auriol Range and in the Haines Junction area.

The effects of movement out of the Haines Junction prescription area on annual female and 6 month calf survivorship were assessed. The average (1984-86) survivorship of females (91%) confined to the Haines Junction area was not significantly different from females (93%) that utilized both areas. We conclude that female survival in Haines Junction was not biased due to the movement of animals into the Auriol Range. Calf survivorship to 6 months in the Haines Junction area (30%) was not significantly different than that of calves, with collared females, which inhabit both areas (24%). Although the survivorship of calves with collared females was not different between areas, calf survivorship trends based on the fall census data were different. As survival increased in Haines Junction between 1984-86, it decreased in the Auriol Range (Table 8, Figure 6). Based on these data, calf survivorship may have been affected by the area they inhabited. In order to minimize any potential biases, calf survival analysis in the Haines Junction area was based on only those animals which stayed within the Haines Junction prescription area.

Moose killed by wolves in late winter were not severely malnourished, based on bone marrow fat content. The mean ($\pm$SE) fat content for calves (n=9) and adults (n=27) was 55% $\pm$ 5.9 and 77% $\pm$ 3.4 respectively. Both were greater than the levels indicative of starving moose (Franzmann and Arneson 1976). Cow moose were judged to be in good body condition in late winter, based on external examination. Pack cell volume levels were similar (41.6% SD ± 5.4, Glover and Larsen 1988) to levels reported from moose in good condition in Alaska (47.9% - 49.1%) as reported by Franzmann and LeResche (1978) and Franzmann et al (1987).

Weather

Snow conditions were similar throughout the study area over the past 2 decades, with excessive snow accumulations (≥80 cm) occurring in 1971/72, 1975/76, and 1982/83 (Figure 8). Mean maximum snow depths and mean winter severity index (WSI) were not significantly different ($P>0.05$) among the Haines Junction, Whitehorse, and Teslin weather stations. However, Teslin recorded higher mean maximum snow depths (53.4 cm) than either Haines Junction (46.9 cm) or Whitehorse (43.8 cm). Above average WSI occurred in Haines Junction (1968/69, 1982/83), Teslin (1971/72, 1975/76) and Whitehorse (1971/72, 1978/79).

Mean calf survival to 6 months of age based on the proportion of live to dead calves, was significantly ($P=0.05$) higher (22%) in the areas where the maximum snow depth was <80 cm in the year preceding birth, compared to survivorship in the areas where the snow depth was ≥80 cm (11%). Calf survival rates from Haines Junction (1983), the Auriol Range (1983), and Teslin (1976) represented survival following winters of deep snow, while Haines Junction (1981-82) Auriol Range (1980, 1981, 1984-87) and Teslin (1974, 1978-86) represented survival rates in years following winters with <80 cm of snow. Years in which survival rates could have potentially been affected by the wolf reduction program were excluded from the above analyses (Appendix 5).

Mean calving/postcalving (May 1 - July 31) temperatures were similar between the Haines Junction (9.4°± 0.25 SE), Whitehorse (10.6°± 0.16 SE), and Teslin (10.1°± 0.15 SE) weather stations. Below average temperatures occurred in Whitehorse (1974) and Teslin (1974, 1976). Insufficient data were available on calf survivorship during below average years to adequately test for its affects.

Calf survivorship to 6 months of age based on regression analysis throughout the study area (excluding areas and years with wolf reduction) was correlated with WSI prior to birth (r^2=0.11, P=0.10), but not with maximum snow depths in the winter prior to birth (r^2=0.11, P=0.17), using a 0.10 alpha level. Given the small sample sizes, the latter was likely biologically significant. Spring temperature during and following calving was not correlated with calf survivorship (r^2=0.003, P=0.82). In addition to single year effects, we tested for the effects of cumulative maximum snow depths for 3 years prior to birth on calf survival, but found no relationship (r^2=0.02, P=0.63).

We were not able to adequately test for the effects of weather on female survivorship, because either wolf reduction programs were being carried out (except for Teslin) concurrently, or severe winters did not occur during the period when female survivorship was measured (appendix 5).

The relative size of the female cohorts, as represented by the radio-collared female sample (Figure 4), can be used to assess the historical effects of weather on those cohorts during their birth year (1974-83), if we assume that survival was consistent among cohorts after they reached 1 year of age. The current numbers of female moose in each cohort was not affected by recent wolf reduction programs, as female ages were collected prior to reductions. Females older than 10 years were not included in this analysis due to the potential effects of poisoning programs on predators in the 1960's (Smith 1983). Simple regression analysis between the current number of female moose in each cohort and WSI of their birth year (r^2=0.05, P=0.19), and maximum snow depths during the year of birth (r^2=0.02, P=0.35) failed to explain the variation in the number of moose.

Population Models

Population models can be used as management tools to clarify and interpret data, as well as predict the likely responses of populations to hypothetical management strategies. Models used to predict the effects of predator reductions are appropriate in this study as many of the limitation tests were weak or inadequate, due to the lack of predator reduction (especially bears) and lack of post-reduction monitoring of the moose population.

Our first population model predicted a slowly declining (1% per year) moose population (Table 11). For practical purposes we can assume that this population is stable as rates of change of this magnitude would not be detected for decades using current census techniques. For example, a decline of over 40% was required in Haines Junction before it was statistically significant.

Based on the model, grizzly bears were the major proximate cause of moose mortality (natural and man induced) in the southwest Yukon. Grizzly bears were responsible for 937 of the 1943 (48%) deaths in this population, wolves 568 (29%) and Indian and non-Indian hunting 179 (9%) (Table 11). These are considered minimum values as 259 (13%) natural mortalities were not assigned to a known cause of death. Also, we have stated earlier that our data on hunting were preliminary due to lack of extensive Indian harvest data. However, even if we double the reported Indian harvest from 1988, hunting remains substantially less important compared to grizzly bear and wolf predation. If 120 moose were killed by Indians instead of the 60 used in the model, then 2,003 moose would have died in this population over 1 year (1943 + 60 = 2,003, Table 11). With a total harvest of 239 moose (179 + 60) hunting would represent 12% of the overall deaths, wolves 28%, and grizzly bears 47%.

In addition to the relative significance of grizzly bears to other causes of mortality, the model demonstrates the magnitude of grizzly bear predation. In the 3 prescription and Teslin control areas, grizzly bears killed 850 moose calves (Table 11) with the majority (95%) of these dying in the first 8 weeks after parturition (Figure 5).

The model was then used to predict the effects of improved calf survivorship between 1984-86 on moose population densities in areas where population monitoring was discontinued early in the study (i.e. Haines Junction and Teslin). Calf survivorship was between 35-40% in Haines Junction in 1985 and Teslin in 1985 and 1984, respectively. If summer calf survivorship was increased in the model from 22% to 40%, the result would be an annual moose population increase of 9% (Table 11). At this rate, it would take 4 years before the population would increase by 40% (i.e. the approximate level of increase required in Haines Junction before population increases could be detected). Based on these predictions, and the assumption that calf survivorship to November continued around 40% after 1985, we speculate that the Haines Junction and Teslin populations would have increased significantly by 1988 or 1989.

The second model predicted a post-hunt population in 1986 that was within the confidence intervals of the observed post-hunt population in 1986 (Table 12). This result suggests that the demographic parameters measured in this study were reasonably accurate, lending some credence to the conclusions drawn from the first model.

The effects of selected management scenarios on moose numbers were predicted using the results from the first model (Table 13). The most effective scenario for increasing moose numbers, over the shortest time period was achieved through concurrent and severe reductions in hunting, wolf numbers and grizzly bear number. The least effective scenario was through the reduction of only hunting. The remaining 3 scenarios which involved the elimination of hunting, along with the reduction of either grizzly bears or wolves resulted in similar moose recovery periods. We emphasize that these conclusions may be affected by compensation in predation rates among and between predator species after reduction.

DISCUSSION AND MANAGEMENT IMPLICATIONS

Limiting Factors

We accept that wolves were a major limiting factor to moose population growth because: 1) there was a significant increase in calf survival to 6 months between the pre- and post-wolf reduction periods, 2) calf survival to 6 months of age increased significantly between the experimental wolf reduction and control areas; 3) there was a significant correlation between the percentage of wolf reduction and calf survival to 6 months of age in the experimental areas, and 4) wolves were the primary cause of female moose mortality.

Contrary to the above results: 1) wolves accounted for only 29% of all deaths in the moose population over 1 year; 2) wolves were identified as the second most important source of calf mortality, accounting for 27% of calf deaths; 3) moose numbers did not increase significantly between the pre- and post-wolf reduction periods in the Rose Lake area; 4) there was no significant difference between female survival in the experimental wolf reduction and control areas; and 5) no correlations were found between calf survival to 6 months, and wolf numbers in the fall or late winter. Although wolf predation was not the major limiting factor, it was obviously a very important source of mortality.

We accept that grizzly bears predation was the major limiting factor to moose population growth because: 1) grizzly bears were responsible for the largest proportion (48%) of all moose deaths over one year; and, 2) grizzly bears were identified as the primary source of mortality of radio-collared calves (58%) and the second most important cause of female mortality.

We reject that the harvest was a primary limiting factor to moose population growth but hunting was an important source of mortality. Rejection was based on the fact that hunting was responsible for only 9% of the annual deaths in the moose population. It is important to note that this conclusion is based on harvest data which is partially tentative in nature (i.e. Indian harvest). The following results support rejection. Hunting of bulls has not resulted in low pregnancy rates (89%) and calving occurred within a relatively short period (i.e. over 25 days, with 71% of calves born over a 10 day period), indicating that most females were bred over several weeks (i.e. one estrus cycle). These data suggest that the skewed number of males present in the fall did not result in lower productivity of the population, and was therefore not a major limiting factor to population growth.

We reject that climate was a major limiting factor to moose population growth, but snow conditions may have influenced calf survival rates. Rejection was based on the fact that calf survival to 6 months was relatively low (22%) following winters with normal snowfall, as well as in years with abnormally high snowfall (11%). Although neither of the above survival rates are high, snowfall the preceding year had a significant effect on calf survival. Calf survival was correlated with snow depths the year preceeding birth, but not with maximum snow depth in the 3 years preceding birth or with calving/post-calving temperatures. We were not able to test the effects of snow depths during the calves' first winter on its survival or compare survival rates in years of abnormal calving/post-calving temperatures to years with normal temperatures.

No data were collected on forage which would allow us to either accept or reject this hypothesis; however, the following results suggest that forage was likely not limiting: 1) adult pregnancy rate was 89%, birth rate was 112 calves/100 adults ($\geq$2 years), and the twinning rate was 27%; 2) the mean bone marrow fat content was 55% for wolf killed calves and 77% for wolf-killed adults; and, 3) adult female moose in late winter were judged to be in good physical condition by a veterinarian and P.C.V. levels were not low enough to suggest moose were in poor condition.

Finally, emigration did not likely affect moose numbers throughout the study area because movements did not occur away from the majority of the prescription and control areas. The exception to this was in the Haines Junction and Auriol Range areas, however the effects there were minimal as movements did not result in a long term absence from the area.

Effects of Wolf Removal

The level of wolf reduction (62% between 1983-86) in Rose Lake may or may not have affected moose numbers over the duration of this study. The apparent increase in the mean number of moose was not statistically significant, but may have some biological basis, given that wolves were the second most important predator on moose calves and the primary predator on females. As well, modeling the population suggested that moose numbers would likely increase with higher levels of wolf reduction over a longer time period. We suggest that wolf reduction may have stimulated population growth, but that it was not carried out long enough to allow for a significant increase in moose numbers. This supposition is supported by the fact that calf survival to 6 month did increase as a result of wolf reduction.

The results of the multiple regression models also support the suggestion that wolf reduction stimulated moose population growth. The regression models using the Rose Lake data showed stronger relationships between calf survival and wolf parameters (Table 10) compared to the data from the combined areas (Table 9). This may be due to the influence of wolves on calf survival in Rose Lake compared to the other areas, or that the effects of wolves were altered more substantially in Rose Lake (62% mean cumulative reduction) compared to the combined areas (52% mean cumulative reduction).

Our results are similar to those reported by Ballard et al. (1987) from a multipredator program system in Alaska, where predation by grizzly bears was thought to be the primary limiting factor to moose population growth. In that study, wolf densities were reduced to between 1.7 and 3.2 wolves /1000 Km^2. A significant increase in calf survivorship resulted, however, they were unable to show an increase in moose population size. Ballard suggests that this lack of response was partially because wolves were not the primary cause of death (grizzly bear predation was more significant) and partly due to inadequate monitoring of the moose population prior to wolf control.

Effects of Grizzly Bear Removal

We have stated that grizzly bear reduction levels in this study were insufficient to increase moose numbers and thus test the limitation hypothesis. Ballard et al. (1980, 1981) and Ballard and Miller (1989) reported that a 60% removal of grizzly bears in one year reduced calf mortality by 78% in southcentral Alaska. Modeling results in our study (Tables 11 and 13) also suggest that large numbers of bears would have to be removed to substantially increase calf survival over the short term.

Although we believe that insufficient numbers of bears were removed to stimulate moose population growth, we are uncertain of the precise long term effects of removal on the bear population. This is primary due to the limited demographic information on this bear population (Pearson 1975, Larsen and Markel 1989), and our poor understanding of factors regulating bear densities. However, several factors should be considered when evaluating both the short and long term effects of bear reduction achieved in this study.

The direct effects of hunting on grizzly bear populations are obscured by the difficulty in obtaining accurate population estimates and the general lack of information on productivity, survival and natural mortality of the study population. Population models are commonly used to help assess the effects of hunting. Bunnell and Tait (1981) constructed a model to predict maximum sustained mortality from hunting and natural causes for grizzly bear populations with different natality rates. Using a natality rate of $\leq$0.51 and a mean age of first litter of 7.8 years (calculated from Pearson's 1975 Yukon data), their model would predict a maximum sustained total mortality of approximately 9% per year for the study population. McCullough (1981) also used a model to estimate maximum sustained yield for grizzly bears, based on balancing recruitment of 4-year-olds with adult mortality. In this model, the maximum number of bears that could be removed from all causes was 13% of the total population. Sidorowicz and Gilbert (1981) suggested an annual sport harvest of 2-3% would maintain a stable grizzly bear population in the Yukon. Grizzly bears in the Yukon are currently managed at an assumed sustainable harvest rate of 4% (6% for males and 2% for females, Smith and Pelchat 1989).

Sustainable harvest models may be confounded by the density dependent relationship between the proportion of adults (primarily mature males) in a population, and recruitment. Both the reproductive potential of adult females and survivorship of subadults have been negatively correlated with the proportion of adult males in both grizzly and black bear populations (McCullough 1981, Bunnell and Tait 1981, Kemp 1972, 1976, Shaffer 1983, Stringham 1980, Young and Ruff 1982). The regulatory mechanisms involved are not clear, but it is generally agreed they include direct predation on young bears, forced egress of subadults, decreased ingress of potential immigrants, and monopolization of productive foraging habitats (Bunnell and Tait 1981, McCullough 1981, Stringham 1980). Between 1984-87, 53% (32) of the bears removed and aged from Haines Junction, Rose Lake, Lorne Mountain and Teslin were males, and 65% of the males were $\geq$6 years of age. It is possible that the removal of these males may have stimulated the population rather than reduced it. If this was the case, reduction levels reported in this paper were an overestimation of the actual removal rate.

Although limited information on sustainable harvest rates for grizzly bears exists, average rates of 4% reported for our study population would likely have minimal effect on the bear population over the short term duration of this study. A higher level of reduction, directed at both sexes, would be required to reduce the bear population sufficiently to cause a measurable change in moose survivorship over the short term. As well, we do not feel that the levels of reduction achieved in this study would likely affect moose survivorship significantly over the long term. However, long term reduction programs, directed equally towards both sexes, would require close monitoring of the population. The intent of such a program would be to reduce, not extirpate, local bear populations.

Effects of Hunting

Hunting was not the primary limiting factor to moose population growth in the southwest Yukon. This implies that the number of moose dying from hunting was not as great as the number dying from predation. It doesn't imply that hunting was insignificant in terms of the additive effects of hunting along with other limiting factors.

The effects of hunting will depend largely on the status of the moose population. If the population is stable without hunting, the addition of hunting will cause a decline. This occurs because recruitment is not high enough to replace adults which are being removed by both hunting and natural forces. In the southwest Yukon, recruitment was low primarily because of high grizzly bear predation on calves. Neonatal losses due to predation are numerically much greater than adult losses due to hunting. Therefore, it is predation, not hunting, which drives this population, however, in areas with high predation, hunting becomes an increasingly important (depensatory) factor. If a moose population is either increasing or decreasing without hunting, then the addition of hunting will likely slow down the increase or speed up the decline. As in the stable population, hunting would not be the primary driving force regulating moose numbers in declining or increasing populations subject to high predation.

Moose populations in the southwest Yukon are likely either stable or decreasing without hunting. Hunting of these populations over long periods of time primarily along transportation corridors, have depressed moose densities in accessible areas. This is clearly demonstrated by the lack of moose adjacent to most major and secondary highways. We believe that moose populations which are subject to high predation, especially along transportation corridors, would not normally be able to support any additional mortality from hunting.

For the remaining moose population in the southwest Yukon, an acceptable level of annual harvest (i.e. within sustainable yield) over the past 10 years would have been approximately 4% of the pre-hunt fall population (including calves). Based on our population model (Table 11) a harvest level of 179 moose, or 6% of the pre-hunt population, would result in a slowly declining population. By changing the harvest level in the model to 4% the population would stabilize or slowly increase. The harvest rate in the study area since 1979 was estimated to be between 6.6-8.5%. These rates were in excess of the allowable harvest, given the high rate of natural mortality by predators. It should be noted that the model was based on average moose survival rates from populations which were declining and from populations which were stable. Clearly, a 4% rate would be excessive if the population was declining. The 4% harvest rate should, in the future, be adjusted to the status of the individual population.

The allowable harvest levels over the next 10 years will be determined by a combination of public policy and moose demography. Future allowable harvest levels will be determined by the number of moose the public desires in the area, the time period to achieve that number (in areas where populations are below the desired levels), the specific demographic parameters for each moose population, and the acceptance of manipulative techniques needed to enhance populations. The proposed management objective in those areas where moose have declined (Haines Junction and Lorne Mountain) is to double those populations over the next 5 - 10 years (1993-1998). Enhancement is to be affected by using a combination of severe restrictions on hunting, followed by wolf and grizzly bear reduction programs. If these objectives are sanctioned, hunting should be completely eliminated, or at least restricted to 1 - 2% of the population until the management targets are achieved. In the areas where the population has not declined, the harvest should be restricted to approximately 4% of the population.

Hunting mortality is usually considered the easiest of the major mortality factors to manipulate in order to increase moose numbers. Therefore, it is often the primary tool used in managing moose populations. This strategy may be appropriate for many areas, however, in some situations it may be inadequate. For example, if hunting was a minor source of mortality such that manipulating the harvest alone would not achieve the management objective. This situation occurs in the southwest Yukon where it is predicted that 16 years of no hunting would be required to achieve the management objective of doubling the moose population. It is clear that other limiting factors must be manipulated concurrently with hunting if the objective is to be realized.

The decline in moose harvest by non-Indian residents was primarily the result of either a decline in the availability of moose or a self-imposed reduction in hunting effort. Government imposed hunting restrictions appeared to have minimal effect on the harvest. In all four prescription areas which were hunted, the decline in the harvest began prior to restrictive hunting regulations (Figure 2). The only evidence that hunting regulations may have decreased the harvest was in Haines Junction between 1983 and 1984 when a sharp decline in the harvest occurred with a change to more restrictive regulations. The decline in Haines Junction, however, also corresponded to a decline in the moose population. This was also the case in Lorne Mountain. In Rose Lake and Teslin the moose population has remained stable, yet the harvest has declined (Table 5). The reduction in harvest in these areas suggest that hunting pressure was self regulated.

We had inadequate data to test the effects of reduced harvest on the moose population. Population estimates were obtained in only one area (Rose Lake) after significant harvest reductions (Appendix 5).

Concern has been expressed over the potential effects of a male only hunting season on moose demography. The average adult male:female ratio in the 3 prescription and Teslin control (except 1974-1980) areas was 41:100. Selective hunting of males can affect the population by either reducing the overall density of a population which would in turn increase predation on the remaining population or by reducing productivity and calf viability. The latter would occur if a substantial number of females were bred during their last estrous period, as the result of insufficient numbers of bulls to breed the majority of females in the peak estrous period (late September). Females which were bred late would give birth late in the spring. Late born calves may not survive the winter as well as peak born calves. Our results suggest that despite the skewed sex ratio in the study area, most of the females were fertilized over a short period, as the majority of calves were born over a 10 day period. We attribute this high reproductive success to the clumped distribution of moose in these areas during the rut. Larsen (1982) estimated that 65% of the southwest Yukon moose utilized 12% of the habitable moose range during the post-rut period (November - December).

Effects of Weather

Winter weather can potentially affect moose survival in several ways. Moose follow an annual weight cycle, where they gain weight during the snow-free periods and lose weight during the winter (Gasaway and Coady 1974, Franzmann and LeResche 1978). Weight loss is brought about by the decreased availability of browse due to deep snow or reduced mobility. The loss of body weight over the winter could potentially affect moose by causing starvation, increased vulnerability to predators (Peterson and Allen 1974), and decreased productivity or calf viability (Peterson and Allen 1974, Markgren 1969, Thompson 1980, Rolley and Keith 1980, Peterson et al. 1982). Snow depth may influence vulnerability to predation by either restricting mobility of moose and increasing mobility of wolves or restricting mobility of moose, thus increasing energy costs. Mech et al. (1987) reported on the cumulative effects of winters to moose vulnerability and survival. The results of that study suggested that the nutritional status of the females may be determined by the cumulative effects of the preceding winters, and that the nutritional status of the female in turn affects fecundity and calf survival.

The effects of weather on moose calf survivorship presented in this paper are considered preliminary because 1) the study was conducted over a short time period, thus reducing the full range of weather conditions which would likely occur over a longer period; 2) the wolf reduction program potentially confounded any relationships between survivorship and weather; 3) any relationships with weather may have been masked by the extensive mortality of calves due to predation during the first 2 months after parturition (in some years, few calves survived long enough to be affected by winter weather) and 4) we were not able to test the effects of winter weather on calves during their first year due to inadequate winter survival data.

Given the above limitations, our tentative conclusion was that snow depths in the winter prior to birth may have influenced calf survival to 6 months of age.

Calf survival was higher in areas with average or below average snow depths, compared to areas with above average snow depths. This relationship does not appear to be strong, however, as only 11% of the variation in calf survival was explained by snow depths the preceding winter, and no relationship was found between calf survival and the cumulative snow depths the preceding 3 winters. The low survival rate (22%) in areas with average snow suggest that other factors (i.e. predation) were driving calf survival.

Physical Condition of Moose

We conclude that moose killed by wolves in the experimental area were not starving, based on high calf (55%) and adult (77%) bone marrow fat content. Franzmann and Arneson (1976) considered adult moose with 10% marrow fat to be in a severe malnourished state, while Peterson et al. (1984) used a value of 20%. The latter authors reported that calves generally have less fat reserves than adults in winter due to growth requirements. If predators select the most vulnerable prey, and if vulnerability is determined by the physical condition of the prey, then moose killed by wolves in winter should represent that segment of the population in the worst condition. By inference, the remaining moose population were in healthy condition. Further evidence that moose in the study area were not starving was based on the good body condition of females in the late winter, the packed cell volume levels in females in late winter, and the moderate to high productivity of this population (Blood 1974).

Implication of a Skewed Calf Sex Ratio

We have tentatively concluded that the primary sex ratio of moose calves in the southwest Yukon was skewed in favor of females. These results must be considered preliminary as they were based on a small sample (56 calves) collected in 1 area (Rose Lake), over 1 year (1985). The number of reported studies in which moose calf sex ratios deviate from the theoretical 1:1 are rare. However, ratios favoring females have been reported from central Canada by Eason (1986) and Crichton (Manitoba Fish and Wildlife, pers. comm.), and sex ratios favoring males from Alaska by Franzmann (cited in Verme and Ozoga 1981) and C. Schwartz (Alaska Fish and Game, pers. comm.).

If sex ratios are skewed towards female calves, it would confound interpretations of adult sex ratios. The high proportion of adult females in the Rose Lake population may be due not only to the selective harvesting of males, but also a higher proportion of female calves at birth. The neonatal sex ratio in 1985, was only slightly lower (61%) than the mean proportion of females (79%) in the adult population (≥18 months) in the same area in 1986 (Table 5). Over the past decade the harvest was directed primarily towards bulls, although a short (10 day) female season was in effect prior to 1982 (Appendix 2). Without knowledge of the skewed calf sex ratio, one would immediately conclude that the skewed adult ratio was solely a function of a selective harvest strategy. Considering the potentially skewed sex ratio at birth, this conclusion should be further evaluated with additional information on calf sex ratios in the future.

Study Approaches and Future Considerations

Both inductive (radio-telemetry and population models) and deductive (predator manipulation) study approaches were used to assess the effects of predators on changes in moose survival and population size in the southwest Yukon. The radio-telemetry results strongly suggest that grizzly bears and wolves were significant proximate causes of moose mortality. In contrast, results from the wolf reduction experiment were somewhat equivocal.

Results from the 2 study approaches may seem to contradict one another, but we suggest they in fact are in agreement. We believe that the lack of a clear response to predator manipulation was due mainly to the lack of reduction of the primary predator (grizzly bear) and an insufficient reduction of the secondary predator (wolves). The level of wolf reduction achieved in this study was likely sufficient to increase moose numbers in a single predator system subject to high wolf predation. It was not sufficient to increase moose numbers in a multi-predator system where wolves were the secondary predator. Wolves were not reduced to the level required to bring about a dramatic, and thus clear, change in moose density over the duration of our study. We believe that significant levels of wolf reduction ($\geq$ 70%) over a minimum of 5-6 years would result in an increase in moose numbers.

Insufficient predator removal levels, or in some cases removing the wrong predator, was recognized as a serious problem by Connolly (1978). He suggested that the lack of sufficient removal may be one of the reasons why any desired view of predation could be reinforced by a selective review of the literature. The insufficient reduction of either the primary or secondary predators on moose has now been suggested by several studies (Gasaway et al. 1986a , Ballard et al. 1987, Crete and Jolicoeur 1987, and this study). Our study suggests that if predator reduction is used as a management tool to enhance moose populations in grizzly bear/wolf systems where wolves are the secondary predator, a measurable change in the prey population would not occur unless wolf manipulations were done over a longer ($\geq$ 5 years) time period, and with a higher level ($\geq$70%) of continuous reduction (Larsen and Gauthier 1985). Lower levels of reduction or interrupted reduction programs may result in conflicting data which is difficult to interpret. If long term recovery programs are acceptable, lower levels of predator reduction would be possible.

We feel that short term (3-5 year) enhancement programs are preferable over long term programs in the southwest Yukon as: 1) moose in this area are old and a severe winter may result in substantial losses to the population, unless large cohorts of younger animals are recruited into the population; 2) recovery of an extremely low density moose population will take longer than the recovery of a low to moderate density moose population; and, 3) temporal changes in confounding effects are less likely to occur in short term experiments.

The current study reinforces the concern raised by Larsen and Gauthier (1985) that substantial reduction in grizzly bear densities in the southwest Yukon would not occur over the short term unless hunting regulations were grossly liberalized, or bears were directly removed through government programs (eg. translocation). We suspect that gross liberalization of hunting would also be necessary to achieve a moderate to substantial (25% - 50%) reduction of grizzly bear numbers over the longer term (5-10 years).

If predator reduction programs are used as management tools, they should be implemented as effectively and expeditiously as possible. The financial (Appendix 7) and public relations cost of this project far outweighed the benefits, in terms of increased numbers of moose. Much controversy surrounded this project from 1982 to 1989. Most of the controversy was focused on the proposed removal of grizzly bears, which in the end did not occur. We suggest if grizzlies were removed to the level, and within the 2 year time period originally proposed, the benefits to the moose population would have been apparent immediately. However, because of the restraints placed on the study, the controversy was prolonged and few benefits were realized.

We believe that if predator reduction is used as a management tool, in a multi-predator system, both wolves and grizzly bears number should be reduced concurrently for the following reasons. Firstly, compensation in predation among and within predator species may occur. A reduction in grizzly bear numbers would increase the availability of calves to wolves. If the additional calves were killed by wolves, it would offset the benefits of removing grizzly bears. The removal of a small portion of the grizzly bear population could result in the remaining grizzly bears or black bears taking proportionally more calves per bear. The removal of only wolves could result in an increased availability of calves which then could be compensated by increased grizzly bear and black bear predation. We were unable to find evidence from other studies which would support or reject our speculations about compensation. It is clear that compensatory predation in multi-predator systems requires further study. We suggest a multi-prescription study design (Larsen and Gauthier 1985) would help to clarify this issue.

Secondly, extensive reduction of one predator would be required to substantially increase moose numbers. Massive reduction of either predator may be unacceptable, however, moderate reduction of both may be less contentious. Reducing grizzly bear populations is considered more drastic a measure compared to reducing wolf populations. This is primarily due to the low reproductive rates of bears, their relative low numbers world wide, their value to sport hunters, and the disproportional expense of measuring the effects of a reduction program on bears, as compared to wolves (Gasaway et al. In prep.).

Grizzly bears and wolves are likely the primary reason for low moose numbers over an area much larger than the current study. Both predators have been identified as major sources of moose mortality in the southwest Yukon (current study), and west of the Alaska-Yukon border (Boertje et al. 1985). Low density moose populations are common in the area between these 2 studies (Larsen 1982; Markel and Larsen 1983, 1988; Gauthier 1984; Boertje et al. 1985; Gasaway et al in prep; and this study). We agree with Gasaway et at (in prep) that the low moose densities throughout this larger area are the result of near natural densities of grizzly bears and wolves.

In addition to the benefit of higher moose numbers for consumptive and non-consumptive uses, moose populations should be maintained at reasonably high densities for several reasons. Firstly, predator populations (especially wolves) would, over the long term, be more abundant. Temporary wolf reduction programs could therefore benefit both wolf and moose populations. Secondly, reasonable densities of these two species will in turn benefit grizzly bear and other wildlife species in this area by elevating wildlife values which can then be used to oppose resource activities such as mining which potentially destroy habitat.

Thirdly, if moose populations are allowed to decline to extremely low levels, rehabilitation efforts would be less effective. A good example is the Dawson Range population (Markel and Larsen 1988). If the objective were to double this population from the existing 0.04 moose/km^2, the density would still be extremely low after rehabilitation. However, if rehabilitation occurred at 0.25 moose/km^2 (Rose Lake) a doubling would result in a reasonable density of moose. If rehabilitation was to be achieved through the translocation of bears, the cost of doubling either density would be similar given the major cost of predator reduction would be finding the bears. Therefore, it is more effective to implement bear reduction before major declines in moose numbers occur. Due to the high cost/benefit ratio of enhancing extremely low density moose populations, these populations will likely be left to natural regulation.

Fourtly, the effects of grizzly bear predation would likely become more pronounced as moose densities declined. Lidicker (1978) argued that the effect of predation increases as prey densities decrease due to a lag in response from the predator ("anti-regulatory control"). This lag should be shorter for an obligate predator, such as wolves, compared to a facultative predator, such as grizzly bears (Gasaway et al. 1983). Where both predators occur, prey populations may be initially reduced by the combined effect of both predators, however, wolves will eventually adjust their numbers to the reduced prey base in single prey systems, but grizzlies will not. As a result of the depressed prey base, high grizzly bear numbers, and the density independent nature of grizzly bear predation (Boertje et al. 1988) grizzly bears would exert proportionately more influence on prey numbers as moose densities declined.

In this section we have raised issues which need to be addressed when developing management objectives for moose in the southwest Yukon, as well as other areas in the Territory. Our recommendations from this study pertain mainly to policy issues surrounding the management of moose and their predators over a wide geographical area. As such, we have not presented specific recommendations from this study. Our recommendations will be presented in a future document dealing with this broader issue.

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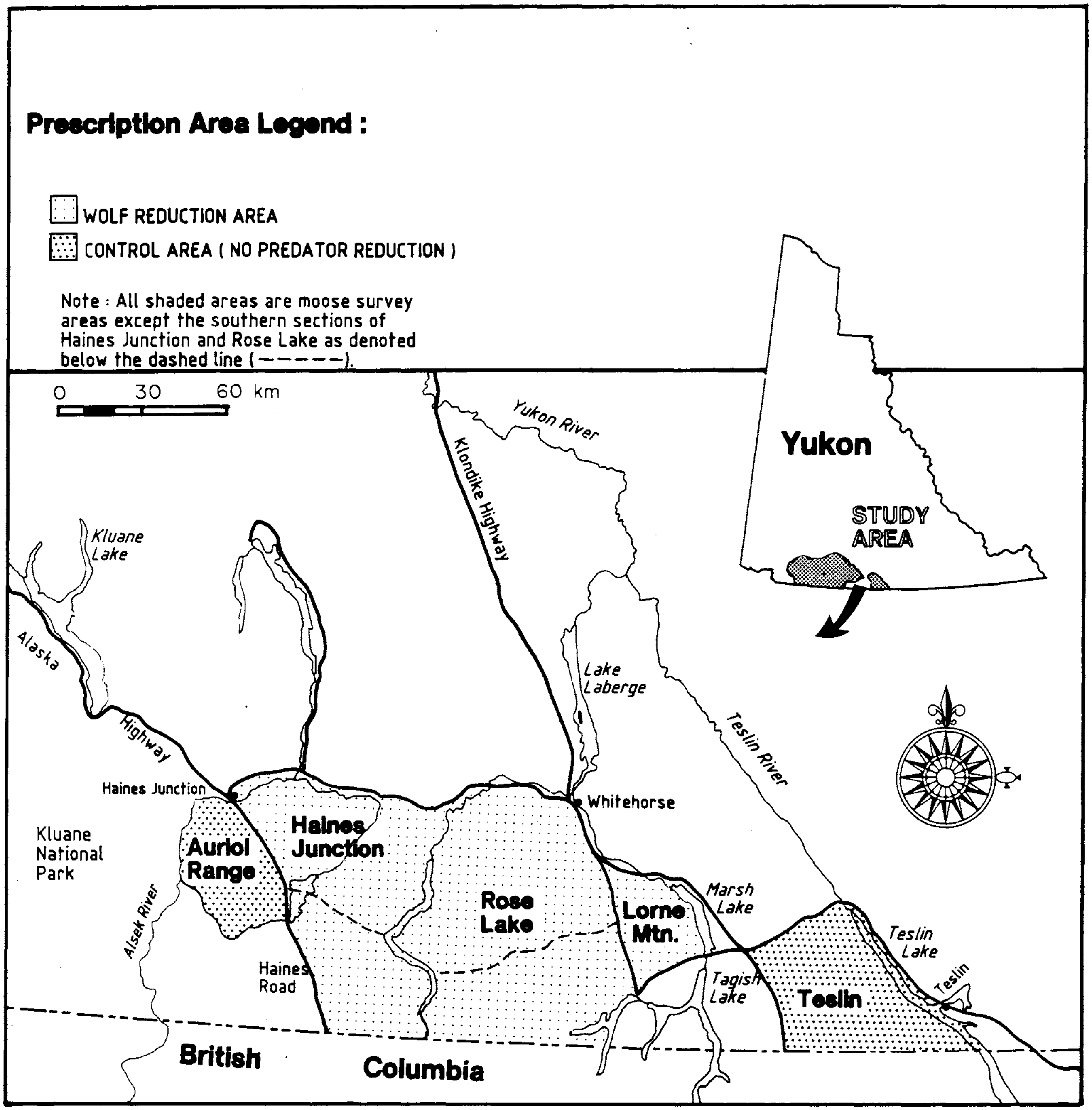
Figure 1. Location of the study area in the southwest Yukon.



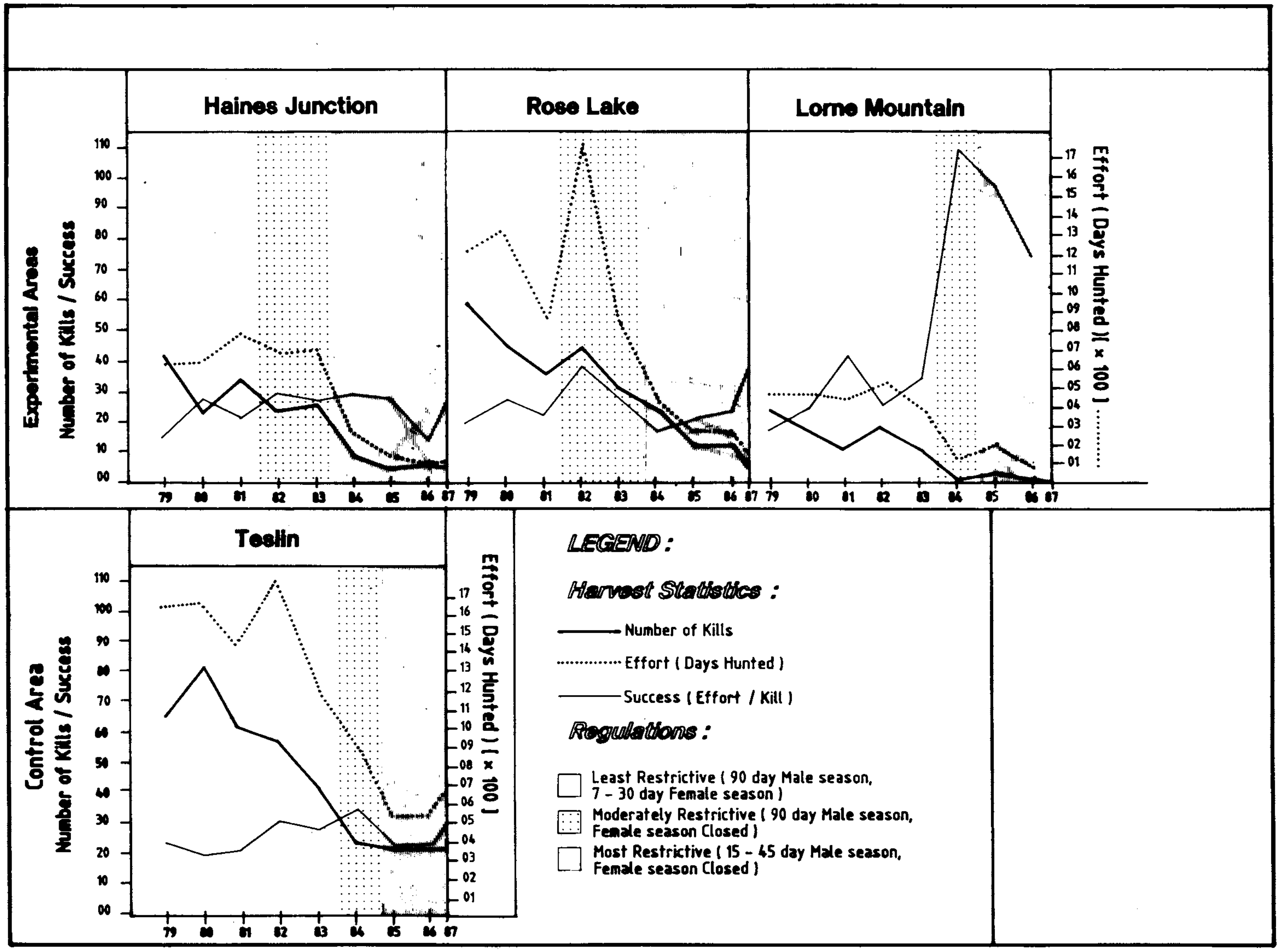


Figure 2. Moose harvest, effort and success rate by resident non-Indians in the southwest Yukon, 1979-1987.

Figure 3. Frequency and timing of parturition for 148 radio-collared cow moose in the experimental area, southwest Yukon, 1983-1985.

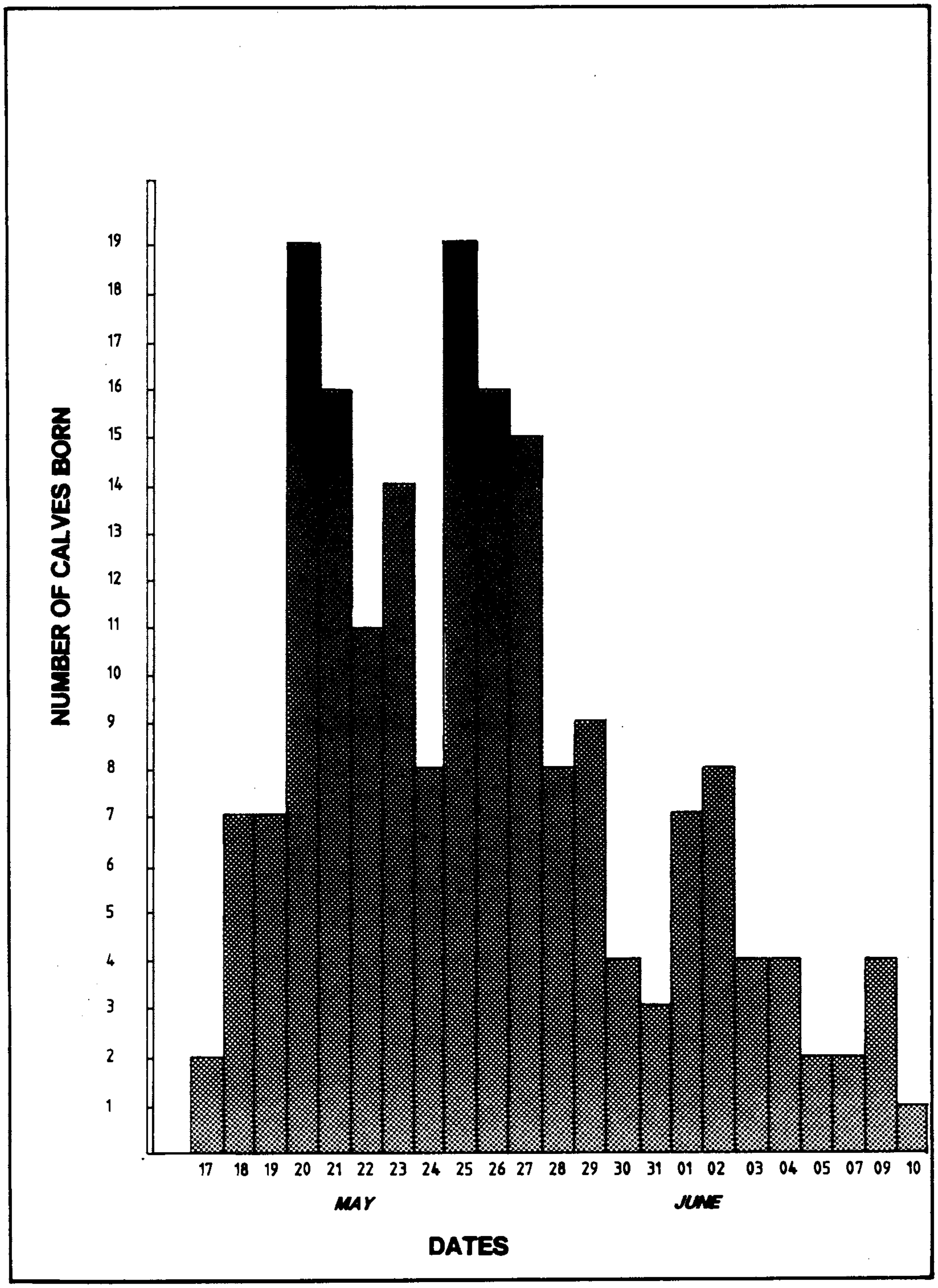


Figure 4. Moose cohorts and ages (1983), based on 124 cows captured between 1983-1985 in the experimental area, southwest Yukon.

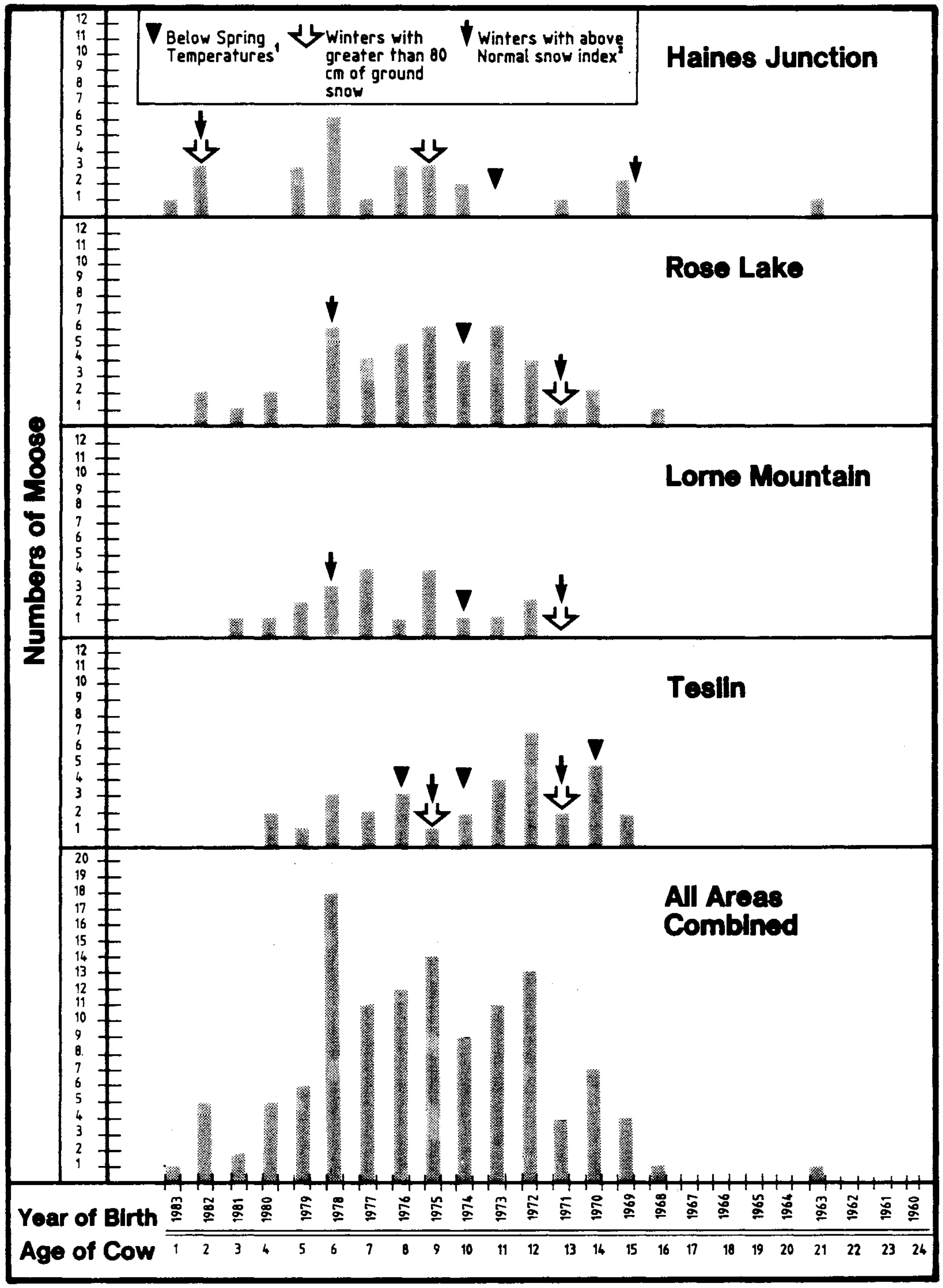
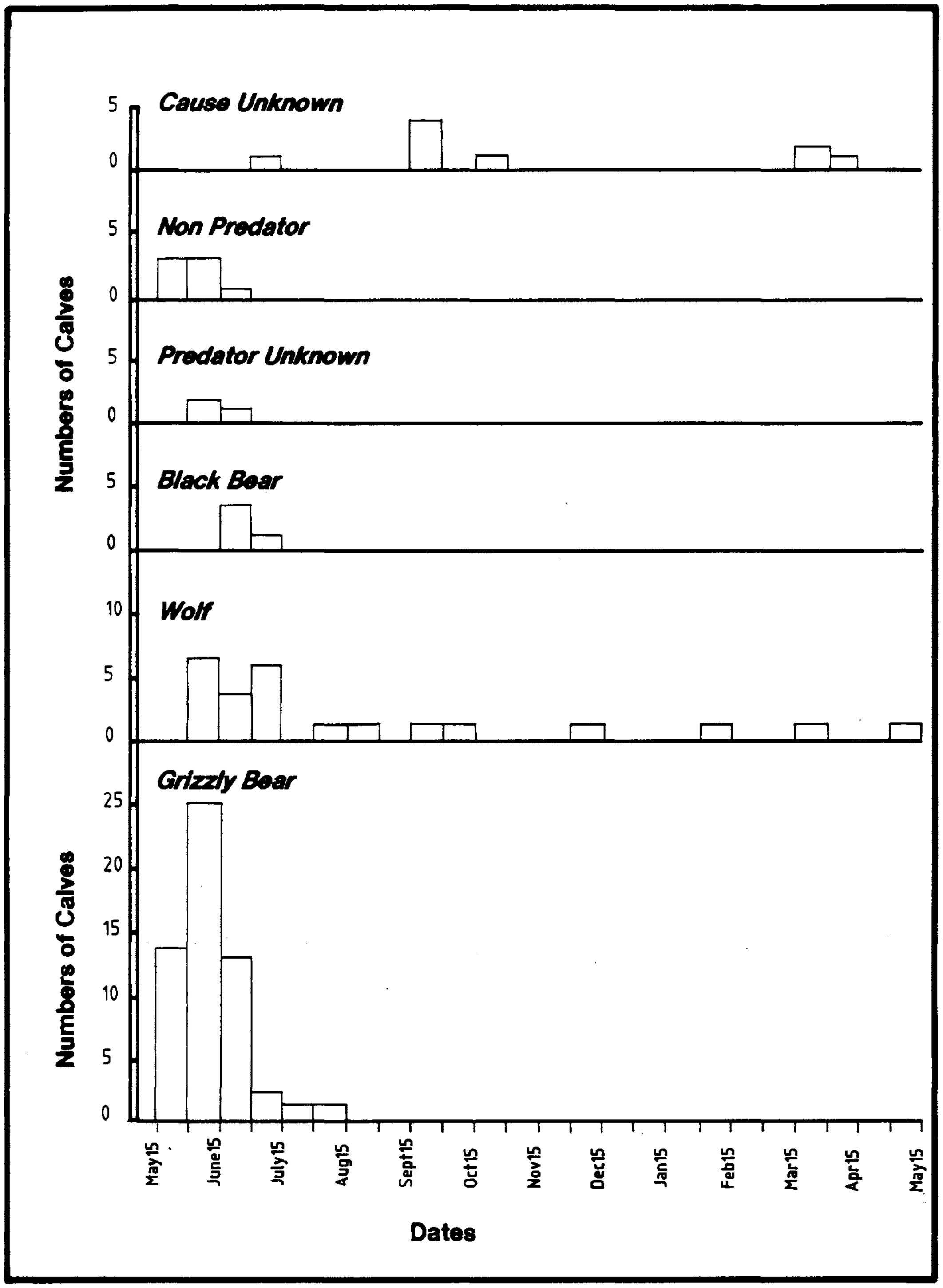


Figure 5. Timing and cause of annual moose calf mortality, based on 105 radio-collared calf deaths in Rose Lake (1983-1985) and Teslin (1983), southwest Yukon.



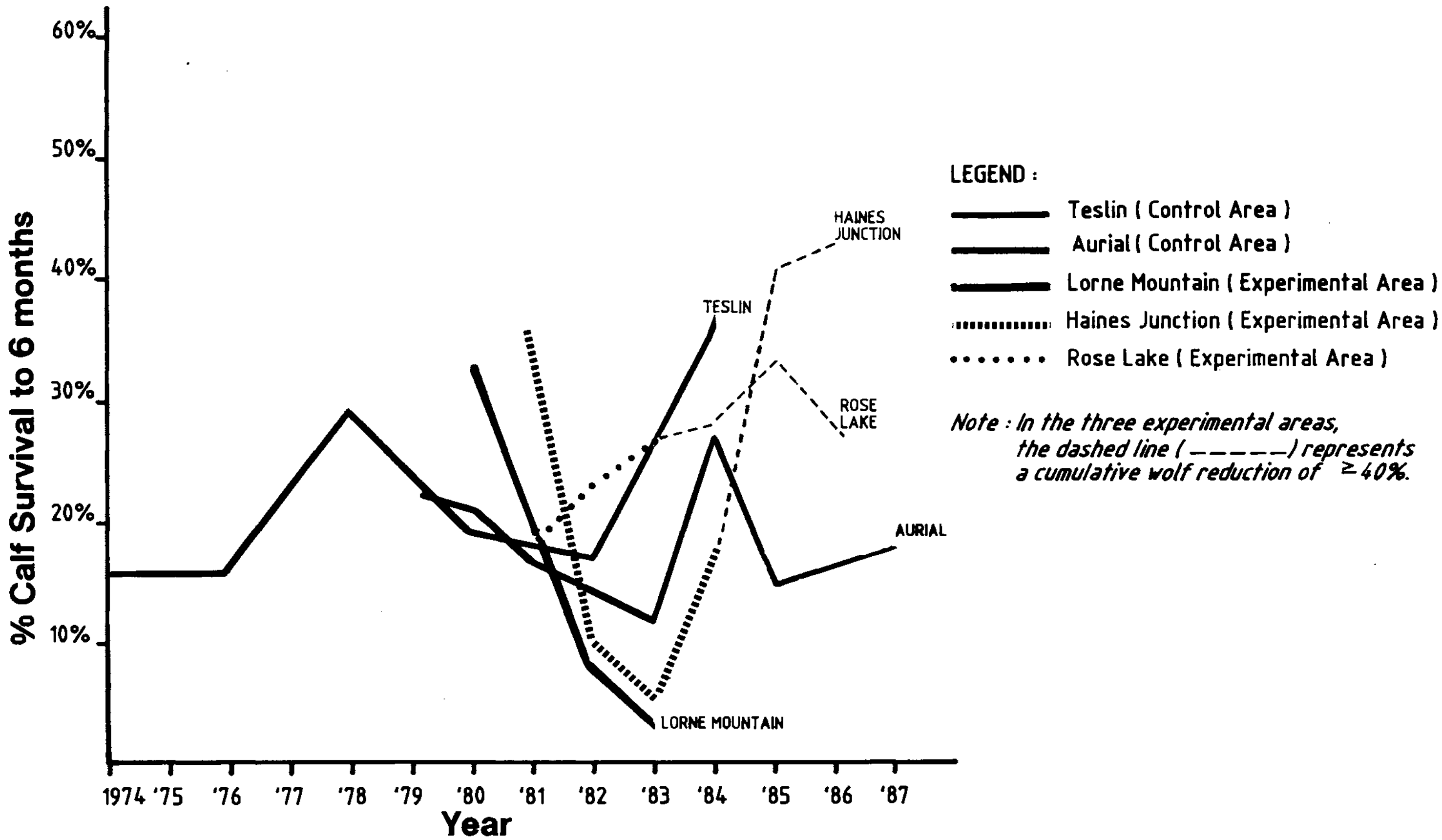
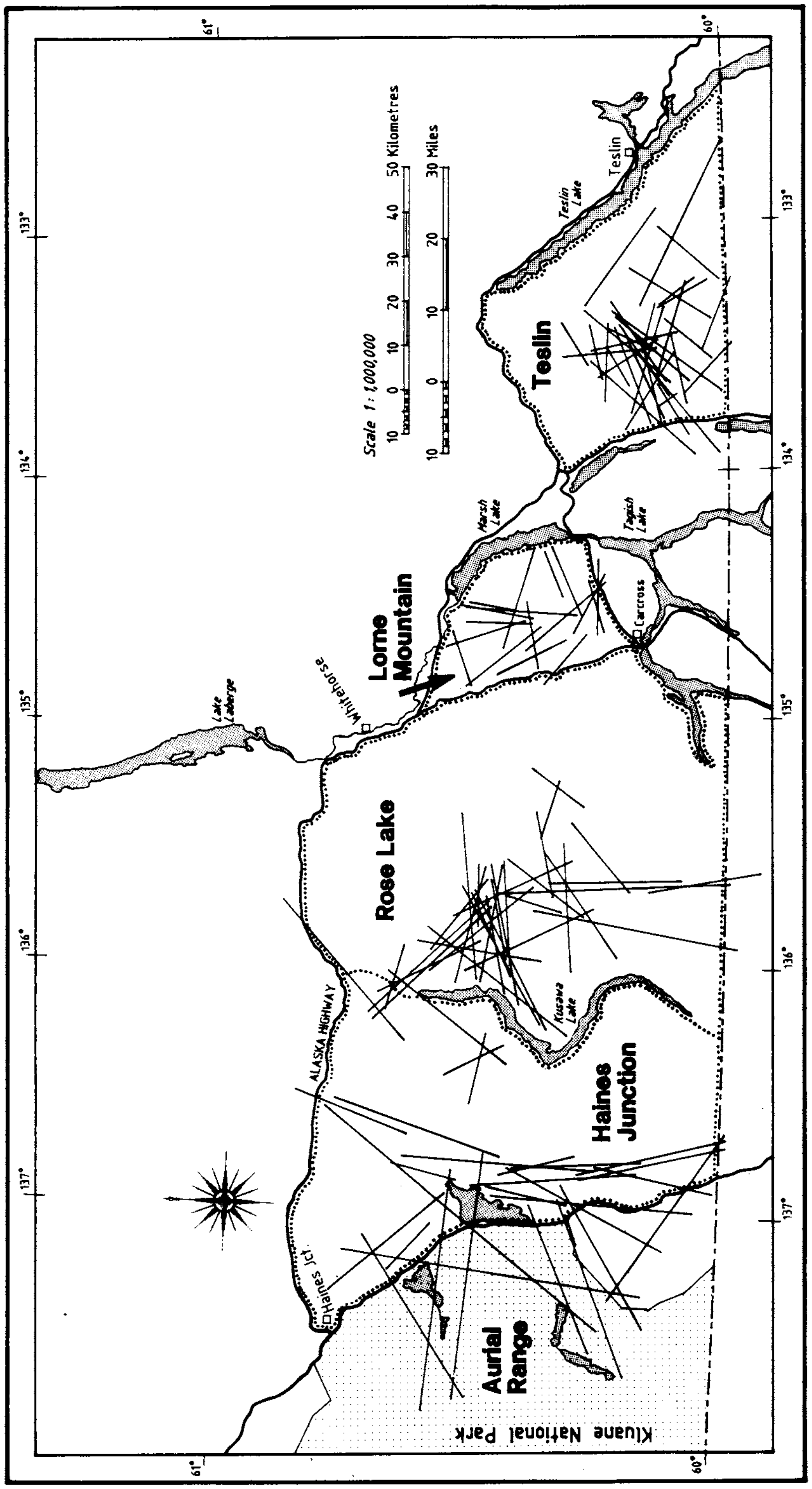


Figure 6. Calf survival rates as determined from aerial surveys and radio-collared moose in the experimental and control areas, southwest Yukon.

Figure 7. Distribution and home ranges (long axis) of 124 radio-collared cows between 1983-1987, southwest Yukon.



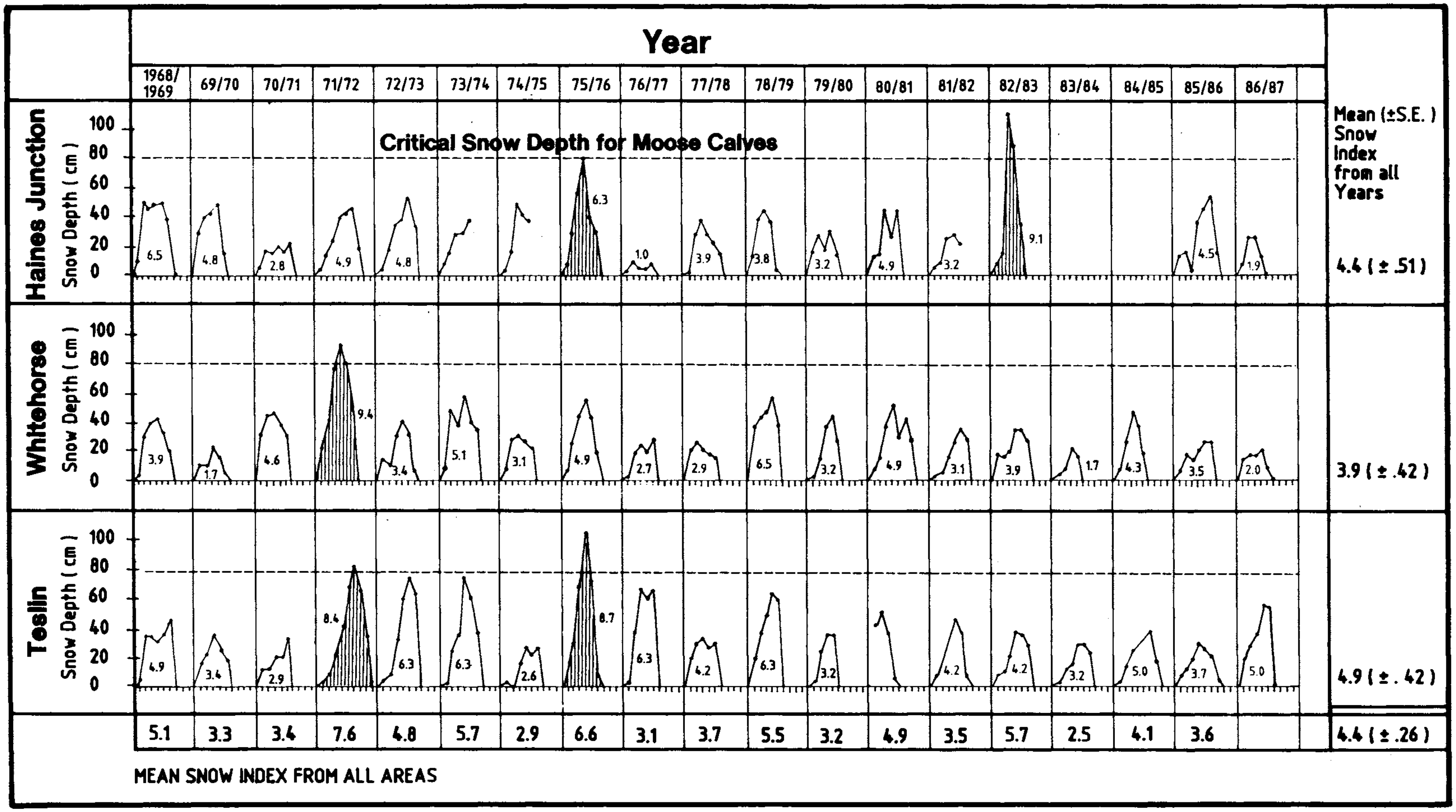


Figure 8. Snow conditions (snow index and maximum snow depth) throughout the study area between 1968-1987 (Shaded areas indicate severe winters).

Table 1. Estimated number of wolves[a] in the experimental wolf reduction areas in the southwest Yukon, 1982-1988.

Sufficient Wolf Reduction[b]

Prescription Areas	1982 fall	1983 late winter	1983 fall	1984 late winter	1984 fall	1985 late winter	1985 fall	1986 late winter	1986 fall	1987 late winter	1987 fall
Haines Junction											
Total Estimated Wolves	62	42	62	35	50	23	39	33	46	38	59
Annual Reduction[c]	32%		44%		54%		15%		17%		
Cumulative Reduction[d]	32%		44%		63%		47%		39%		
Rose Lake											
Total Estimated Wolves	74	37	63	35	54	14	28	16	57	40	55
Annual Reduction	50%		44%		74%		43%		30%		
Cumulative Reduction	50%		53%		81%		78%		46%		
Lorne Mountain[e]											
Total Estimated Wolves	25	20	25	23	33	10	6	3	8	8	27
Annual Reduction	20%		8%		70%		50%		0%		
Cumulative Reduction	20%		8%		60%		88%		68%		

[a] Fall estimates are based on late winter estimates plus wolves that were harvested between fall and the late winter census.

[b] Years in which wolves were reduced by $\geq$40% of their pre-reduction levels.

[c] Number of wolves killed over-winter each year divided by the number of wolves present in the fall of each year.

[d] Difference between the original pre-reduction population and the number alive in late winter divided by the original population.

[e] Wolf population estimates in Lorne Mountain were based on an area (1940km^2) larger than the area used to estimate moose numbers (1020km^2).

Table 2. Estimated number of grizzly bears and proportions removed[a] from the southwest Yukon study area, 1984-1988.

Prescription Area	1984		1985		YEAR 1986		1987		1988
Haines Junction									
Estimated number of bears (post denning)	90		78		76		70		65
Estimated % annual reduction		13%		3%		8%		7%	
Rose Lake[b]									
Estimated number of bears (post denning)	108		100		90		85		78
Estimated % annual reduction		7%		10%		6%		8%	
Lorne Mountain[b]									
Estimated number of bears (post denning)	16		16		16		16		16
Estimated % annual reduction		0%		0%		0%		0%	
Teslin[b]									
Estimated number of bears (post denning)	46		41		39		37		37
Estimated % annual reduction		11%		5%		5%		0%	
Auriol Range					NO REDUCTION				

[a] Grizzly bear abundance was estimated to be 16 bears/1000 km^2 in the Rose Lake area in 1985 (Larsen and Markel in 1989). Grizzly bear abundance in the remaining areas in 1985 were calculated by multiplying areas by the Rose Lake density. Bear population estimates after 1985 were calculated by subtracting the number of bears removed each year through human activity from the 1985 estimates. Estimates prior to 1985 were calculated by adding the number of bears removed each year to the 1985 population estimate. These extrapolations assume that natural mortality equalled recruitment and densities were homogenous throughout all the areas.

[b] Bear reduction areas in which hunting regulations were liberalized to encourage the harvest of grizzly bears by resident and non-resident sport hunters. (Appendix 2).

Table 3. Grizzly bear removal and harvest from the southwest Yukon study area between 1974-1987.

Prescription Area	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	MEANS ± SE 1974-1983	MEANS ± SE 1984-1987
Haines Junction																
-bears removed[b]	1	1	5	4	2	3	5	3	2	3	12	2	6	5	3 ± 0.5	6 ± 2.1
-bears harvested[c]	(1)	(1)	(5)	(4)	(2)	(3)	(5)	(2)	(1)	(3)	(8)	(2)	(5)	(5)	(3 ± 0.5)	(5 ± 1.2)
Rose Lake																
-bears removed	2	0	1	3	0	3	5	3	3	1	8	10	5	7	2 ± 0.5	8 ± 1.0
-bears harvested	(2)	(0)	(1)	(3)	(0)	(3)	(5)	(2)	(3)	(1)	(4)	(2)	(5)	(6)	(2 ± 0.5)	(4 ± 0.9)
Lorne Mountain																
-bears removed	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
-bears harvested	(0)	(0)	(0)	(0)	(1)	(0)	(0)	(0)	(1)	(0)	(0)	(0)	(0)	(0)	(0)	(0)
Teslin																
-bears removed	0	2	0	4	1	5	1	0	0	0	5	2	2	0	1 ± 0.6	2 ± 1.0
-bears harvested	(0)	(2)	(0)	(4)	(1)	(5)	(1)	(0)	(0)	(0)	(5)	(2)	(2)	(0)	(1 ± 0.6)	(2 ± 1.0)
Auriol Range	NO HUNTING														NA	NA

[a] areas in which hunting regulations were liberalized to encourage the harvest of grizzly bears by resident and non-resident sport hunters (Appendix 2).

[b] bears removed by hunting, in defence of life and property, drug complications during bear research, and environmental relocation.

[c] bears harvested (by resident and non-resident hunters).

Table 4. Estimated moose harvest by licensed resident and non-resident hunters in the experimental and control areas in the southwest Yukon between 1979-1987. (Indian harvest not included.)

Prescription Area	Hunter Class	1979	1980	1981	1982	1983	1984	1985	1986	1987	Mean (+ SE)	Mean Harvest Intensity moose/1000km^2
Experimental Areas												
Haines Junction[1]	Non-native	41	23	35	23	25	9	5	7	4	19	
	Non-resident	8	5	5	6	1	3	0	1	1	3	
	Total	**49**	**28**	**40**	**29**	**26**	**12**	**5**	**8**	**5**	**22(5.3)**	**9**
Rose Lake[1]	Non-native	59	46	37	45	32	25	13	12	4	30	
	Non-resident	22	16	7	0	12	6	3	10	9	9	
	Total	**81**	**62**	**44**	**45**	**44**	**31**	**16**	**22**	**13**	**40(7.3)**	**15**
Lorne Mountain	Non-native	25	19	11	19	11	1	2	1	0	10	
	Non-resident	1	0	0	1	0	0	0	0	0	<1	
	Total	**26**	**19**	**11**	**20**	**11**	**1**	**2**	**1**	**0**	**10(3.3)**	**11**
Control Areas												
Teslin	Non-native	67	82	63	57	41	24	22	22	22	44	
	Non-resident	16	0	1	1	0	0	0	0	1	2	
	Total	**83**	**82**	**64**	**58**	**41**	**24**	**22**	**22**	**23**	**47(8.7)**	**19**
Auriol Range						NO HUNTING						

[1] Harvest data was based on moose survey, rather than prescription, areas. (Figure 1).

Table 5. Fall moose population characteristics in the experimental and control areas, southwest Yukon, 1974-1987.

Prescrip. Area - (Habitable Moose Area)	Estimated Abundance[a]		Estimated Composition[a]				Estimated Ratios[a]			
	Mean Estimate ±90% CI	Density (moose/ 1000km^2)[b]	Adult Bulls (>30mo.)	Adult Cows (>30mo.)	Yearlings (18 mo.)	Calves	Bulls/ 100 cows (>30 mo.)	Yrlgs./ 100 cows (>30mo.)	Calves/ 100cows (>30mo.)	% Calves
EXPERIMENTAL AREAS										
Haines Junction (2332km^2)										
1981[d]	570±120	244	100±29	294	57	119±44	34	19	40	21
1982[d]	351±92	151	86±40	233	6	26±18	37	0	11	7
1983	337±91	145	78±32	240	2	17±9	32	1	7	5
1984	329±66	141	85±28	201	2	41±10	43	1	20	13
Rose Lake (2613km^2)										
1981[d]	607±109	232	111±34	338	91	67±22	33	27	20	11
1982[d]	582±163	223	112±35	366	10	94±45	31	2	26	16
1983	651±143	249	153±49	371	16	111±59	42	4	30	17
1986	717±143	274	111±28	406	75	125±28	27	18	31	17
Lorne Mountain (916km^2)										
1980	406±248	443	91±46	177	72	66±66	51	41	37	16
1982[d]	300±174	328	123±107	161	2	14±14	77	1	9	5
1983	171±62	187	54±20	108	5	4±4	51	7	4	2

[a]Population parameters from all areas except for the Auriol Range (1979-1987) and Teslin (1974-1978) were estimated from fall (Nov-Dec) aerial surveys, following the technique described by Gasaway et al. (1986b) and Larsen (1982). Population data from the Auriol Range (1979-1987) and Teslin (1974-1978) was based on moose observed during fall aerial surveys. These surveys were designed to obtain a total count in portions or all of the prescription area.

(continued....)

Table 5 (cont'd...)

Prescrip. Area - Habitable Moose Area	Estimated Abundance[a]		Estimated Composition[a]				Estimated Ratios[a]			
	Total	Density (moose/ 1000km^2)b	Adult Bulls (>30mo.)	Adult Cows (>30mo.)	Yearlings (18 mo.)	Calves	Bulls/ 100 cows (>30 mo.)	Yrlgs./ 100 cows (>30mo.)	Calves/ 100cows (>30mo.)	% Calves in popul.
CONTROL AREAS										
Teslin (2515km^2)										
1974[e]	572	NA	249[c]	273[c]	NA	50	91	NA	18	9
1976[e]	380	NA	109[c]	230[c]	NA	41	47	NA	18	11
1978	923	NA	288[c]	478[c]	NA	157	60	NA	33	7
1980[e]	882	NA	291[c]	488[c]	NA	103	60	NA	21	12
1982[d]	1383±484	550	316±139	816	94	157±58	39	12	19	11
1983[e]	472±127	431	88±40	293	4	87±28	30	1	30	18
1984	1049±189	417	316±70	482	63	188±39	65	13	39	18
Auriol Range										
1979[e]	75	NA	35[c]	32[c]	NA	8	109	NA	25	11
1980	140	NA	40[c]	81[c]	NA	19	49	NA	23	14
1981	152	NA	53[c]	83[c]	NA	16	64	NA	19	11
1983	170	NA	57[c]	100[c]	NA	13	57	NA	13	8
1984	201	NA	63[c]	106[c]	NA	32	59	NA	30	16
1985	207	NA	78[c]	111[c]	NA	18	70	NA	16	9
1986	190	NA	69[c]	103[c]	NA	18	67	NA	17	9
1987	193	NA	79[c]	95[c]	NA	19	83	NA	20	10

[b] Density was calculated on habitable moose range (Larsen, 1982).

[c] Adult bull and cow categories include all animals $\geq$18 mo.

[d] Survey results were initially calculated from larger areas then recalculated for smaller areas which were comparable to survey areas in subsequent years (see methods).

[e] The 1979 survey in the Auriol Range and the 1974, 1976, 1980 and 1983 surveys in Teslin were flown in an area smaller than in subsequent years, therefore, population estimates are not comparable with other years but ratio estimates are comparable.

Table 6. Annual survival rates of collared cows in the southwest Yukon study area, 1983-1988.

Prescription Area	1983-1984	1984-1985	1985-1986	1986-1987	1987-1988	Combined
Haines Junction	-	100(22/22)	83(24/29)	83(20/24)	94(16/17)	89(82/92)
Rose Lake	88(29/33)	94(32/34)	94(30/32)	87(26/30)	91(20/22)	91(137/151)
Lorne Mountain	-	61(11/18)	100(11/11)	91(10/11)	90(9/10)	82(41/50)
Teslin	92(23/25)	94(30/32)	93(28/30)	85(23/27)	76(16/21)	89(120/135)
All Areas	90(52/58)	90(95/106)	91(93/102)	86(79/92)	87(61/70)	89(380/428)

Table 7. Extent and known causes of annual moose calf mortality in a control and an experimental area, southwest Yukon 1983 and 1985 (based on 135 radio-collared calves).

	Experimental Area Rose Lake 1983	**Experimental Area** Rose Lake 1985	**Control Area** Teslin 1983	Combined
Captured:				
Collared	60	59	16	135
Capture-related death	0	1	1	2
Lost Contact	0	1	1	2
Remaining	60	57	14	131
Natural Causes:				
Known Causes				
Grizzly	34(61%)	15(50%)	5(56%)	54(58%)
Wolf	14(25%)	7(23%)	4(44%)	25(27%)
Blk. Bear	1(2%)	3(10%)	-	4(4%)
Pred. Unk.	2(3%)	1(3%)	-	3(3%)
Non-Predator	3(5%)	4(13%)	-	7(8%)
Total	**54(100%)**	**30(100%)**	**9(100%)**	**93(100%)**

Table 8. Percent Calf survival (n) by time period and year in the experimental and control areas between 1974 and 1988, southwest Yukon.

Time Period	Year	Experimental Areas: Haines Jct.	Experimental Areas: Rose Lake	Experimental Areas: Lorne Mtn.	Control Areas: Teslin	Control Areas: Auriol Range	Age of Cohort
	1974				16(50/306)[c]		
	1976				16(41/258)[c]		
	1977						
	1978				29(157/535)[c]		
	1979					22(8/36)[c]	
	1980			33(66/198)	19(103/547)[c]	21(19/91)[c]	
	1981	36(119/329)	18(67/379)			17(16/93)[c]	
Summer[a]	1982	10(26/261)	23(94/410)	8(14/180)	17(157/914)		
(17 May	1983	6(17/269)	27(111/416)	3(4/121)	27(87/328)	12(13/112)[c]	6 mo.
to			23(9/39)[b]		43(3/7)[b]		
01 Nov.)	1984	18(41/225)	28(10/36)[b]		35(188/540)	27(32/119)[c]	
					56(14/25)[b]		
	1985	40(6/15)[b]	33(12/36)[b]	18(2/12)[b]	55(16/29)[b]	15(18/124)[c]	
	1986	42(5/12)[b]	27(125/455)	50(6/12)[b]	46(11/24)[b]	16(18/115)[c]	
			33(9/27)[b]				
	1987					18(19/106)	
Winter[d]	1983/84		78(7/9)		100(3/3)		
(02 Nov.	1984/85		100(10/10)		94(17/18)		
to	1985/86	83(5/6)	100(11/11)		100(14/14)		
01 Mar.)	1986/87		100(7/7)	100(6/6)	100(6/6)		
	1983/84		18(7/39)		43(3/7)		
Annual[b]	1984/85		28(10/36)		55(12/22)		
(17 May	1985/86	33(5/15)	32(10/31)	9(1/11)	29(8/28)		10 mo.
to	1986/87	13(2/16)	28(8/29)	18(2/11)	38(9/24)		
01 Mar.)	1987/88	22(4/18)	20(5/25)	10(1/10)	17(3/18)		

Table 8 cont.

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[a] Summer calf survival rates were estimated by comparing the predicted calf population at birth to the calf population observed on aerial surveys in November. The predicted spring calf population was estimated by multiplying the number of cows ($\geq$ 30 mo.) in the fall aerial census times the average (1983-85) birth rate (112 calves/100 adult cows).

[b] Calf survival rates were estimated by comparing the number of calves with collared cows in November and in March with the predicted number of calves born in May. The predicted number of calves born was calculated by multiplying the number of collared cows times the average birth rate (112 calves/100 cows). This method was not used in the year the cow was immobilized due to the negative effect on post natal calf survivorship (Larsen and Gauthier 1989). In Rose Lake and Teslin 1983, uncollared cows with collared calves were used instead of collared cows.

[c] Calf survival rates in these areas and years were calculated as in (a) except adult cows were $\geq$ 18 months.

[d] Winter calf survivorship was estimated by comparing the number of calves with collared cows alive in November to the number alive in March. In 1983 collared calves with uncollared cows were used. Winter was restricted to a 4 month time period (November-March) as contact with uncollared calves was not consistently maintained passed 1 March.

Table 9. Best predictive models of moose calf survivorship to six months of age, based on stepwise multiple regression analyses and R-square and Mallow's (p) criteria for selection, in the Rose Lake, Haines Junction, and Lorne Mountain experimental areas, Southwest Yukon.

Model Number	Model Variables[a]	R-square	C(p)	P
1	grizzly pop.	0.40	2.14	0.04
2	grizzly pop. fall wolf pop.	0.56	1.71	0.04
3	grizzly pop. fall wolf pop. max. snow depth	0.66	2.19	0.05
4	grizzly pop. fall wolf. pop. max. snow. depth mean temp.	0.66	4.10	0.11
5	grizzly pop. fall wolf pop. max. snow depth mean temp. perscription area	0.67	6.00	0.23

[a] grizzly pop. = grizzly population size in the year the calves were born.

fall wolf pop. = wolf population size in the fall of the calves birth year.

max. snow depth = maximum snow depth in the winter preceeding calving.

mean temp. = mean temperature between 1 May - 31 July of the year the calves were born.

Table 10. Best predictive models of moose calf survivorship to six months of age, based on stepwise multiple regression analyses and R-square and Mallow's C(p) criteria for selection, in the Rose Lake experimental area, Southwest Yukon.

Model	Model Number	Model Variables[a]	R-square	C(p)	P
A.	1	cum. w. red. p.	0.77	-0.09	0.02
	2	cum. w. red. p. cum. g. red.	0.80	1.70	0.09
	3	cum. w. red. p. cum. g. red. temp.	0.88	3.00	0.18
	4	cum. w. red. p. cum. g. red. temp. max. snow p.	0.88	5.00	0.50
B.	1	f. w. pop.	0.82	8.68	0.01
	2	f. w. pop. max. snow p.	0.94	3.65	0.02
	3	f. w. pop. max. snow p. temp.	0.97	3.90	0.05
	4	f. w. pop. max. snow p. temp. gr. pop.	0.98	5.00	0.19
C.	1	w. wolf pop.	0.77	-0.29	0.02
	2	w. wolf pop. gr. pop.	0.83	1.28	0.07
	3	w. wolf pop. gr. pop. temp.	0.85	3.07	0.21

.../2

Table 10 continued...

Model	Model Number	Model Variables[a]	R-square	C(p)	P
	4	w. wolf pop. gr. pop. temp. max. snow p.	0.86	5.00	0.53

[a] gr. pop. = grizzly population size in the year the calves were born.

f. w. pop. = wolf population size in the fall of the calves birth year.

max. snow p. = maximum snow depth in the winter preceeding calving.

temp. = mean temperature between 1 May - 31 July of the year the calves were born.

cum. w. red. p. = % cumulative wolf reduction in late winter, prior to calving.

cum. g. red. = % cumulative grizzly reduction in the same year as calving.

w. wolf pop. = wolf population size in late winter prior to calving.

Table 11. Projections of the study area moose population based on average composition, productivity rates and causes of mortality in Southwest Yukon

a. Population Status	Estimated Population[a] (November) Year One	Winter Survival Rate[b]		Predicted pre-calving population		Birth Rate[c]	Predicted calving population[d]		Summer Survival Rate[b]		Predicted prehunt population		Hunting Survival Rate[e]		Predicted Population (November) Year Two
Adult ♀	1710	x .945	=	1616	x	1.12	1701	x	.945	=	1607	x	.996	=	1601
Adult ♂	690	x .945	=	652			737	x	.945	=	696	x	.756	=	526
Yearling ♀	90	x .945	=	85			202	x	.945	=	191	x	1.0	=	191
Yearling ♂	90	x .945	=	85	x	1.12	202	x	.945	=	191	x	1.0	=	191
Calves	420	x .960	=	403			1905	x	.220	=	457	x	.996	=	455
Total	3000			2841			4747				3142				2964

			Natural Mortality[f]			+ Hunting Mortality	= Total Mortality of Adults and Calves		
b. Total Annual Mortality and Causes	Moose Age/Sex Group	Number of Deaths[g]	Causes	%	Number	Number	Causes		Number
	Adults and Yearlings	= 299	Grizzly Bears	x .29	= 87	177	Grizzly Bears	=	937
			Wolves	x .58	= 173		Wolves	=	568
			Unknown/Other	x .13	= 39		Unknown/Other	=	259
	Calves	= 1465	Grizzly Bears	x .58	= 850	2	Hunting	=	179
			Wolves	x .27	= 395		Total	=	1943
			Unknown/Other	x .15	= 220				

Table 11 continued ...

[a] Population size was the sum of the study area (excluding the Auriol Range) moose population estimates in November - December in the first year censused (Table 5) i.e. 570 (HJ81) + 607 (RL81) + 406 (LM80) + 1383 (Tes82) = 2966 (rounded off to 3000). Average composition from moose population estimates between 1980-1986:

Adult females:	57% x 3000 = 1710
Adult males:	23% x 3000 = 690
Yearlings: (assumed equal proportions of ♂ to ♀)	6% x 3000 = 180
Calves:	14% x 3000 = 420

[b] Adult survival rates were originally assessed on an annual basis (89%). For this analysis we have assumed equal rates of survival between summer and winter and, therefore, divided the annual rate between these periods. Adult survival rates were based on radio-collared cows between 1983-1988 in the three experimental and one of the control (Teslin) areas (Table 6). Calf survival rates (summer = 22%, winter = 96%) were estimated from fall aerial surveys, and radio-collared cows and calves (Table 8), from 1974-1988.

[c] Productivity: 112 calves born/100 cows $\geq$24 mo. (pregnant and non-pregnant)

[d] The calving population was estimated by: adding the pre-calving long yearlings to the adult cohorts; dividing the pre-calving short yearlings (November calves) equally into the male and female yearling cohorts, and multiplying the pre-calving adult and yearling cows by the average birth rate to obtain the calf cohort.

[e] The average Indian and non-Indian harvest was 179 moose/year, of which 95% were males (170), 4% were females (7), and 1% were calves (2). Therefore, the harvest survival rate = the prehunt population, minus the harvest, divided by the prehunt population (eg. adult cow harvest survival rate = (1607 -7) ÷ 1607 = .996). **Note that the model uses the average (1979-1987) harvest, which is substantially higher than the harvest in recent years.**

[f] Causes of adult/yearling mortality were assessed from 16 collared cows that died from known causes between 1983-1986 in the three experimental and one of the control (Teslin) areas (Appendix 6). Only the two major sources of natural mortality (grizzly bears and wolves) were used. The known causes of collared cow mortality were originally assessed as: wolf (50%), grizzly (25%), and either wolf or grizzly (15.5%). The dual predator group was divided between the two single groups according to the proportions of the single groups. We assumed that yearlings (male and female) and adult male moose died from the same causes as adult female moose.

Causes of calf mortality were assessed from 93 radio-collared neonates that died from known causes in Rose Lake and Teslin in 1983 and 1985 (Table 7).

[g] Total numbers of deaths over one year was calculated by adding the number of animals within each age/sex class which was lost during the winter and summer periods. Age/sex subtotals were then added together (eg. adult cows: winter losses (1710 - 1616 = 94) + summer losses (1701 - 1606 = 94) = 188.

Table 12. Projections of the moose population between November 1983-November 1986, in the Rose Lake area, southwwest Yukon.

	Estimated post hunt population Nov. 1983[a]	Winter Survival 1983/1984[b]	Predicted pre-calving population 1984	Birth Rate[c]	Predicted Calving Population 1984	Summer Survival 1984[b]	Predicted pre-hunt population 1984	Hunting Survival 1984[b]	Predicted post hunt population Nov. 1984	Winter Survival 1984/1985	Predicted pre calving population 1985	Birth Rate	Predicted Calving population 1985
Adult ♀	371	x 1.0	= 371	x 1.12	424	x .94	= 399	x 1.0	= 399	x 1.0	= 399	x 1.12	440
Adult ♂	153	x 1.0	= 153		161	x .94	= 151	x .56	= 85	x 1.0	= 85		126
Yrlg. ♂	8	x 1.0	= 8		44	x .94	= 41	x 1.0	= 41	x 1.0	= 41		60
Yrlg. ♀	8	x 1.0	= 8	x 1.12	44	x .94	= 41	x 1.0	= 41	x 1.0	= 41	x 1.12	60
Calvs.	111	x .78	= 87		425	x .28	= 119	x 1.0	= 119	x 1.0	= 119		493
TOTAL	651	± 22%	627		1098		751		685		685		1179

	Summer Survival 1985	Predicted pre-hunt population 1985	Hunting Survival 1985	Predicted post hunt population 1985	Winter Survival 1985/1986	Predicted pre calving population 1986	Birth Rate	Predicted Calving population 1986	Summer Survival 1986	Predicted pre hunt population 1986	Hunting Survival 1986	**Predicted post hunt population Nov. 1986**	**Estimated post hunt population Nov. 1986[a]**
	x .95	= 418	x 1.0	= 418	x .95	= 397	x 1.12	451	x .95	= 428	x 1.0	= 428	406
	x .95	= 120	x .60	= 72	x .95	= 68		122	x .95	= 116	x .53	= 61	111
	x .95	= 57	x 1.0	= 57	x .95	= 54		82	x .95	= 78	x 1.0	= 78	37
	x .95	= 57	x 1.0	= 57	x .95	= 54	x 1.12	82	x .95	= 78	x 1.0	= 78	37
	x .33	= 163	x 1.0	= 163	x 1.0	= 163		505	x .27	= 136	x 1.0	= 136	125
TOTAL		815		767		736		1242		836		781	717 ± 20%

Table 12 (con´t.)

[a] Population estimates were obtained from aerial surveys using a stratified random sampling procedure (Gasaway et al 1986, Larsen 1982).

[b] Survival data specific to the Rose Lake area was used in this model, rather than average survival rates for the study area. Winter and summer female survival rates for Rose Lake were from Larsen et al (1989). We assumed males died at the same rate as females, except for hunting. Hunting survival was calculated by adding the non-Indian harvest for each year (Table 4) to the midpoint (32) of the range (20-44) of Indian harvest from Rose Lake in 1988 (Quock - unpubl. data).

[c] Birth rates were from the overall study area.

Table 13. Management scenarios and predicted effects[a] on moose demography, southwest Yukon.

Management Scenarios	Calculations	Predicted Annual Growth Rate	Predicted Number of Years to Double the Population[b]
Status quo (maintain harvest[c] and some predator reduction)[d].	Population year 1 = 3000 Population year 2 = 2964 for a loss of 36 moose.	-1.2%	N/A
Remove 100% of the harvest with no predator removal.	Hunting mortalities (179) + year 2 population (2964) = 3143. An additional 143 moose (3143-3000) would be added to the population.	+4.8%	16
Remove 100% of the harvest and 25% of the grizzlies.	Hunting mortalities (179) + grizzly mortalities (.25 x 937 = 234) + year 2 moose population (2964) = 3377. An additional 377 moose would be added to the population.	+12.6%	6
Remove 100% of the harvest and 50% of the grizzlies.	Hunting mortalities (179) + grizzly mortalities (.50 x 937 = 469) + year 2 population (2964) = 3612 An addition of 612 moose to the population.	+20.4%	4
Remove 100% of the harvest and 70% of the wolves.	Hunting mortalities (179) + wolf mortalities (.70 x 568 = 398) + year 2 population (2964) = 3541. An addition of 541 moose to the population.	+18.0%	5
Remove 100% of the harvest, 70% of the wolves, and 25% of the grizzlies.	Hunting mortalities (179) + wolf mortalities (398) + grizzly mortalities (234) + year 2 population (2964) = 3775. An additional 775 moose to the population.	+25.8%	3

[a] Predicted effects are based on the assumption that no compensation occurs between or within predator species after reduction.

[b] The current direction is to rebuild moose populations to their 1981 levels. In the Lorne Mountain and Haines Junction areas, populations must be doubled to achieve that objective.

Table 13 (con't.)

[c] The average (1979-1987) harvest from Larsen et al. (1989a) was used in this model.

[d] Calf moose survival values used in these predictions were average survival rates over the pre-reduction, reduction, and post-reduction periods, as well as from the experimental and control areas. Adult survival values were average rates over the reduction and post-reduction period in both the experimental and control areas. As such, the effects of predator reduction, albeit minor, that were achieved in this study, are reflected in these figures. Therefore, the growth rates and thus the number of years to double the moose population should be viewed as minimal values.

APPENDICES

Appendix 1. Estimated density[1] (animals/1000 km^2) of predator and prey species in the study area prior to or during the reduction programs, Southwest Yukon.

	Experimental Areas			Control Areas	
Species	Haines Junction	Rose Lake	Lorne Mtn.	Teslin	Auriol Range
Moose[2]	163	129	398	536	128
Caribou[3]	0	16	59	39	0
Sheep[4]	164	657	0	0	348
Goats[5]	10	16	0	0	41
Wolves[6]	13	12	13	18	12
Grizzly Bears[7]	16	16	16	16	40
Black Bears	unk.	unk.	unk.	unk.	unk.

1 Densities were based on total land area within the entire prescription area.

2 Moose estimates in the Auriol Range were from a total count in 1981 (Parks Canada, unpubl. data); Haines Junction, and Rose Lake, from a stratified aerial survey technique used in 1981 (Larsen 1982); Lorne Mtn. from aerial surveys in 1980 (Larsen and Nette 1980); and Teslin from aerial surveys in 1982.

3 Caribou estimates in Rose Lake (Farnell, pers. comm.), Lorne Mtn. (Larsen and Nette 1980) and Teslin (Yukon Fish and Wildlife, unpubl. data).

4 Sheep estimates in all areas except the Auriol Range were from total cumulative counts between 1974 and 1986 (Hoefs, 1974, 1975, Yukon Fish and Wildlife, unpubl. data). Estimates from the Auriol range were the average total counts between 1978-84 (Parks Canada, unpubl. data).

5 Goats estimated in the Auriol Range were the average total counts between 1977-83 (Parks Canada, unpubl. data). Goats in the remaining areas were estimated from complete counts on aerial surveys (Yukon Fish and Wildlife, unpubl. data).

Appendix 1 cont.

6 Wolf estimates in Haines Junction, Rose Lake, Lorne Mtn., and Teslin were based on pre-reduction (fall 1982) survey results (Hayes *et al.* 1983, Hayes and Baer 1986). Wolves in the Auriol Range were assumed to be similar to the Haines Junction densities (R.D. Hayes, pers. comm.).

7 Grizzly bear densities in the Auriol Range were estimated at 40 bears/1000 km^2 by Pearson (1975), and in the Rose Lake area in 1985 at 16 bears/1000 km^2 by Larsen and Markel (1989). Grizzly bear densities in the remaining areas were assumed to be similar to density reported for Rose Lake.

Appendix 2. Summary of the hunting regulations in the experimental and control areas between 1978-1987, Southwest Yukon.

Prescription Area	Species[1]	YEAR 1979	1980	1981	1982	1983	1984	1985	1986	1987
Haines Junction	Moose	- one moose/year								
		- ♂ 90 day season					15 to 90 days	15 days		
		- ♀ 7 day season		10 days	closed					
	Grizzly Bear	- 1 bear/lifetime for nonresidents					1 bear/2 yrs.	1 bear/3 yrs		
		- 1 bear/yr for residents				1 bear/4 yrs	1 bear/2 yrs	1 bear/3 yrs		
		- 60 day fall season					0-90 days	50-90 days		55-90
		- spring season closed				10-20 days	10-60 days	40-60 days		45-60
		- non resident hunting allowed								
	Black Bear	- 1 bear/year (res & nonres)				1to2 bears/yr	2 bears/yr			
		- 90 day fall season								
		- 45 days season			60 days					
	Wolf	no limit								
		9 month season			11 months					
Rose Lake	Moose	same regulations as in Haines Junction (above)								
	Grizzly bear						Reduction area			
		- 1 bear/lifetime for non residents					1 bear/yr			
		- 1 bear/year for residents				1 bear/4 yrs.	1 bear/yr			
		- 60 day fall season				0-55 days	105 days			
		- spring season closed		0-30 days	0-45 days	0-20 days	80 days	65 days		

Appendix 2 cont.

Prescription Area	Species[1]	1979	1980	1981	1982	1983	1984	1985	1986	1987
		- Non resident hunting in Northen half, southern half closed					nonres hunting in N. and 8 permits in S. South	nonres hunting in North and 26 permits in	nonres hunting for N and no permits in S.	5 permits
	Black Bear	- 1 bear/year (res & nonres)				1to2 bears/yr	3 bears/yr	2 bears/yr		
		- 90 day fall season					all year			
		- 45 day spring season		60 days			all year			
	Wolf	Same regulations as in Haines Junction (above)								
Lorne Mtn.	Moose	- one moose/year								
		♂ 90 day season					closed	15 days		
		♀ 30 day season								
								Reduction area		
	Grizzly Bear	- 1 bear/lifetime for non residents					1 bear/2 yrs	1 bear/yr		
		- 1 bear/year for residents				1 bear/4 yrs	1 bear/2 yrs	1 bear/yr		
		60 day fall season				55 days	closed	105 days		
		spring season closed			15 days	10 days		65 days		
		Non resident hunting closed						5 non res permits	no permits	
	Black Bear	- 1 bear/yr (res & non res)				1to 2 bear/yr	2 bear/yr			
		90 day fall season						all year		
		45 day spring season		60 days				all year		

Appendix 2 cont.

Prescription Area	Species[1]	1979	1980	1981	1982	1983	1984	1985	1986	1987
Lorne Mtn cont´d	Wolf	Same regulations as in Haines Junction (above)	——	——	——	——	——	——	——	——
Teslin	Moose	1 moose/year	——	——	——	——	——	——	——	——
		♂ 90 day season	——	——	——	——	——	15 days	45 days	
		♀ 30 day season	——	——	——	——	Closed	——	——	——
							Reduction area			
	Grizzly Bear	1 bear/lifetime for non residents	——	——	——	——	1 bear/yr.	——	——	——
		1 bear/year for residents	——	——	——	1bear/4 yrs.	1 bear/yr.	——	——	——
		60 day fall season	——	——	——	55 days	105 days	——	——	——
		spring season closed	——	——	15 days	20 days	80 days	65 days	——	——
		non resident hunting closed	——	——	——	——	10 non res permits	24 non res permits	No permits	
	Black Bear	1 bear/yr. (res & non res)	——	——	——	——	1to2 bears/yr	3 bears/yr	2 bears/yr	——
		90 day fall season	——	60 days	90 days	——		all year	——	——
		45 day spring season	——	60 days	——	——		all year	——	——
	Wolf	same regulations as in Haines Junction (above)	——	——	——	——	——	——	——	——

Appendix 2 cont.

Prescription Area	Species[1]	1979	1980	1981	1982	1983	1984	1985	1986	1987
					YEAR					
Auriol Range		NO HUNTING								

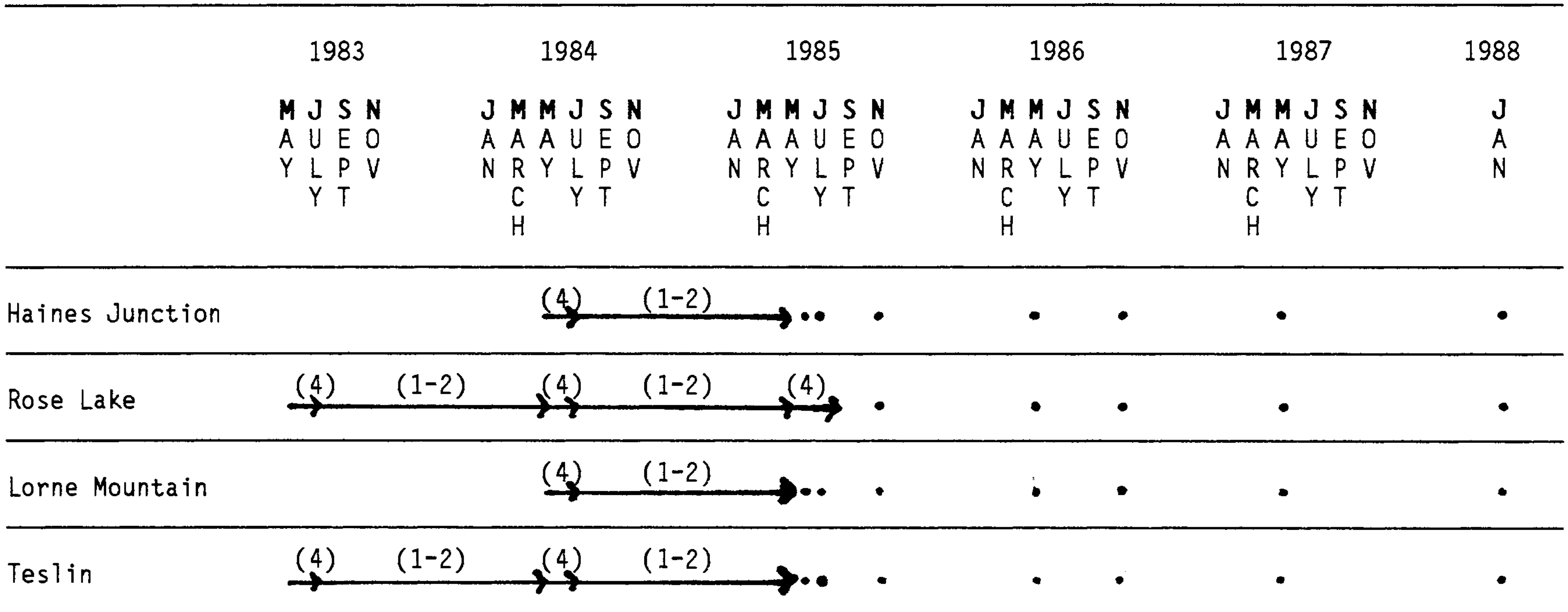
1. The following regulations remained unchanged between 1978 and 1986:

	moose	grizzly bear	black bear	wolf
a. resident seal fees	$5	$25	$5	NA
non resident trophy fees	$150	♂ $500 ♀ $750	$ 75	$ 75

b. female bears with young and the young were protected

c. non resident hunting occurred in Haines Junction, Aishihik, Whitehorse north, and the northern half of Rose Lake between 1978 and 1986. Non resident hunting did not occur in the southern half of Rose Lake, Lorne Mtn. and Teslin between 1978 and 1983, but was allowed in these areas through special non resident permits between 1984 and 1986.

Appendix 3. Frequency of monitoring radio-collared cow moose (flights/month) in the Southwest Yukon experimental areas. 1983-1988.

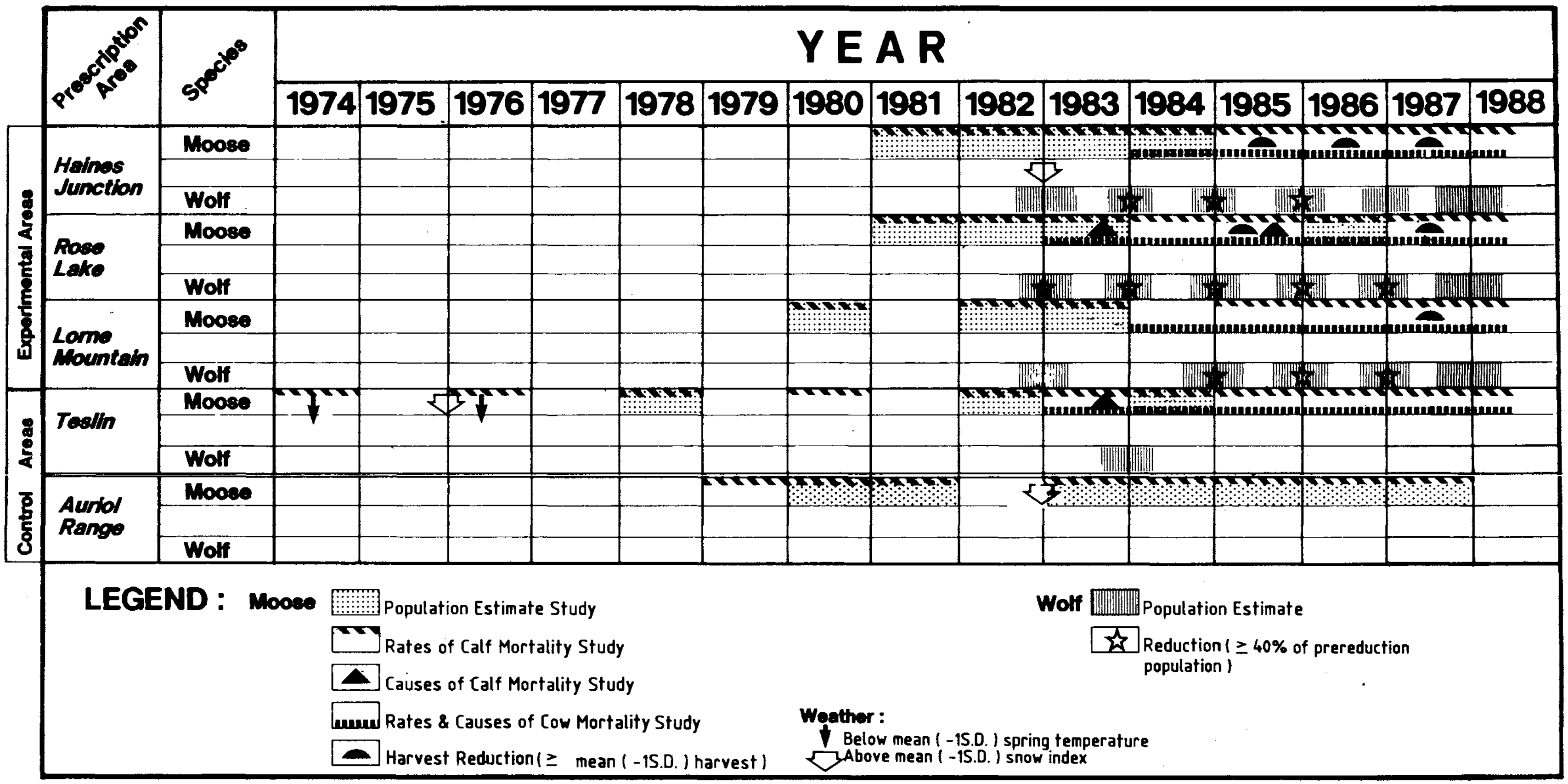


Decimals represent 1 monitoring flight.

Appendix 4. Numbers of moose calves by calf/cow collar combinations in the Southwest Yukon experimental area, 1983-1986.

Experimental Area	Year	Radio-Collar Combinations			Total
		Collared Calf/ Collared Cow	Collared Calf/ Uncollared Cow	Uncollared Calf/ Collared Cow	
Haines	1983	-	-	-	-
Junction	1984	-	-	17	17
	1985	-	-	24	24
	1986	-	-	5	5
Rose	1983	21	39	15	83
Lake	1984	-	-	38	38
	1985	19	40	18	77
	1986	-	-	7	7
Lorne	1983	-	-	-	-
Mtn.	1984	-	-	11	11
	1985	-	-	5	5
	1986	-	-	6	6
Teslin	1983	9	7	13	29
	1984	-	-	34	34
	1985	-	-	21	21
	1986	-	-	6	6
Total		49	86	220	363

Appendix 5. Chronology of data collected and reduction programs in the Southwest Yukon.



Appendix 6. Annual[1] causes of collared cow mortality (March 1983-March 1988) in the experimental and Teslin control areas, southwest Yukon.

Prescription Area	Status	1983-1984	1984-1985	1985-1986	1986-1987	1987-1988	Combined
A. Haines Junction	Captured	-	26	8	-	-	34
	Lost Contact	-	-	-	-	5	5
	Unnatural Causes:						
	Drugging	-	3	1	-	-	4
	Hunting	-	1	-	-	-	1
	Remaining[2]	-	22	29	24	17	92
	Natural Known Causes	-	-	-	-	-	-
	Unknown causes[3]	-	-	5	2	1	8
	Total	**-**	**-**	**5**	**2**	**1**	**8**
B. Rose Lake	Captured	39	5	-	-	-	44
	Lost Contact	1	-	-	-	4	5
	Unnatural Causes:						
	Drugging	2	-	-	-	-	2
	Hunting	-	-	-	-	-	-
	Not Collared	3	-	-	-	-	3
	Remaining[2]	33	34	32	30	22	151
	Natural Known Causes:						
	Grizzly	1	1	1	-	-	3
	Wolf	2	-	-	-	-	2
	Grizzly/Wolf	1	-	-	-	-	1
	Pred. Unknown	-	-	1	-	-	1
	Unknown Causes[3]	-	1	-	4	2	7
	Total	**4**	**2**	**2**	**4**	**2**	**14**

(continued...)

Appendix 6. (cont'd...)

Prescription Area	Status	1983-1984	1984-1985	1985-1986	1986-1987	1987-1988	Combined
C. Lorne Mtn.	Captured	-	20	-	-	-	20
	Lost Contact	-	-	-	-	-	1
	Unnatural Causes:						
	Drugging	-	2	-	-	-	2
	Hunting	-	-	-	-	-	-
	Remaining[2]	-	18	11	11	10	50
	Natural Known Causes:						
	Wolf	-	3	-	-	-	3
	Grizzly/Wolf	-	1	-	-	-	1
	Pred. Unknown	-	1	-	-	-	1
	Unknown Causes[3]	-	2	-	1	1	4
	Total	-	7	-	1	1	9
D. Teslin	Captured	27	9	-	-	-	36
	Lost Contact	-	-	-	1	2	3
	Unnatural Causes:						
	Drugging	2	-	-	-	-	2
	Hunting	-	-	-	-	-	-
	Remaining[2]	25	32	30	27	21	136
	Natural Known Causes:						
	Grizzly	-	1	-	-	-	1
	Wolf	2	1	-	-	-	3
	Unknown causes[3]	-		2	4	5	11
	Total	**2**	**2**	**2**	**4**	**5**	**15**

(continued...)

Appendix 6. (cont'd...)

Prescription Area	Status	1983-1984	1984-1985	1985-1986	1986-1987	1987-1988	Combined
E. **All Areas combined**	Captured	66	60	8	-	-	134
	Lost Contact	1	-	-	1	11	13
	Unnatural Causes:						
	Drugging	4	5	1	-	-	10
	Hunting	-	1	-	-	-	1
	Not Collared	3	-	-	-	-	3
	Remaining[2]	58	54	7	-	-	107
	Natural Known Causes:						
	Grizzly	1	2	1	-	-	4
	Wolf	4	4	-	-	-	8
	Grizzly/Wolf	1	1	-	-	-	2
	Pred. Unknown	-	1	1	-	-	2
	Unknown Causes[3]	-	3	7	11	9	30
	Total	6	11	9	11	9	46

[1] Annual mortality period was from March 1 of Year 1 to February 28 of Year 2.

[2] Cows remaining represents the cumulative number of collared cows present, i.e. collared cows which survived from previous years plus cows captured.

[3] Unknown causes (N=30) of cow mortality resulted from a) mortality signals detected from aircraft but not investigated (N=12), or b) mortality signals detected from the air and mortality sites investigated from aircraft (N=17).

Appendix 7. Approximate program costs (x $1000) for moose-predator work in the southwest Yukon, 1981-1987.

	MOOSE	WOLF		GRIZZLY BEAR
Year	Fall Surveys Cow & Calf Mortality Studies	Research	Reductions	Research
1981	55	-	-	-
1982	150	90	-	-
1983	300	55	35	-
1984	160	30	50	-
1985	190	80	-	98
1986	6	40	-	-
1987	6	30	-	-
TOTAL	867	325	85	98