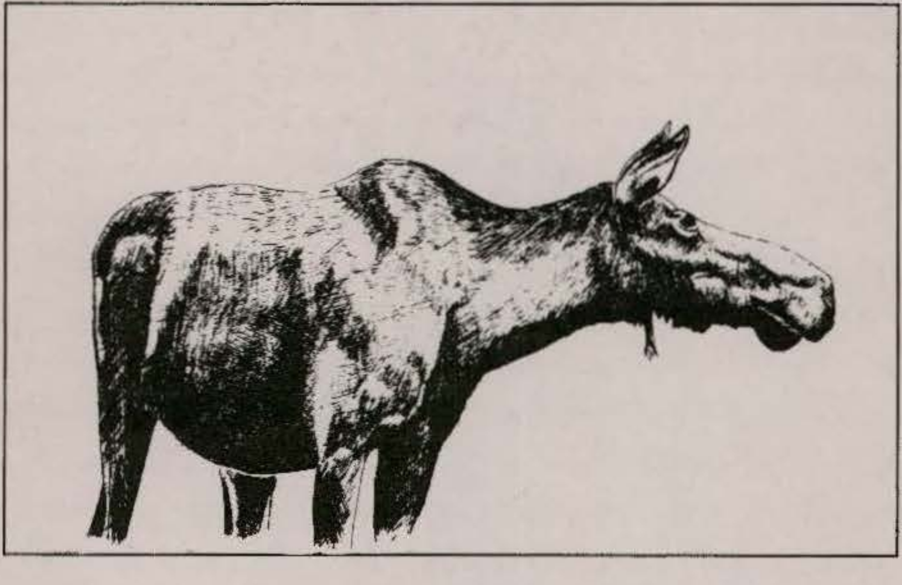
Alaska Department of Fish and Game
Division of Game
Federal Aid in Wildlife Restoration
Research Progress Report

FACTORS LIMITING MOOSE POPULATION GROWTH IN SUBUNIT 20E



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PROGRESS REPORT (RESEARCH)

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Job No.: 1.37R Job Title: Factors Limiting Moose Population Growth in Subunit 20E

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(Includes data through 30 November 1987)

SUMMARY

Moose (*Alces alces*) population density in Game Management Subunit 20E declined drastically from the mid-1960's through the mid-1970's and has since remained low. In 1981 the density was 86 moose/1,000 km^2 ± 23 moose (90% CI)--the lowest density recorded in Alaska using the stratified random-sampling technique.

Two hypotheses were tested: (1) food limits moose population growth, and (2) predation limits moose population growth in Subunit 20E. Data presented in this and previous reports (Boertje et al. 1985, 1987; Gasaway et al. 1986*b*) support rejection of the food-limiting hypothesis. Data presented in this and previous reports (Boertje et al. 1985, 1987; Gasaway et al. 1986*b*) strongly support acceptance of the hypothesis that predation by grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) is limiting moose population growth in Subunit 20E. Predation was the largest source of mortality for calf and adult moose.

Harvest of grizzlies increased substantially after 1980; however, recent attempts by the Alaska Board of Game and Alaska Department of Fish and Game have failed to further increase the recreational harvest of grizzly bears. Preliminary harvest for Subunit 20E during 1987 totaled 21 grizzlies, similar to harvests in recent years: 21 in 1986, 12 in 1985, 22 in 1984, 24 in 1983, and 23 in 1982. No major short-term decline in the grizzly bear population is expected from these harvests, but we have inadequate data to assess the precise effects of these harvests.

Key Words: Alaska, grizzly bears, moose, moose mortality, predation, wolves.

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BACKGROUND

Moose (*Alces alces*), caribou (*Rangifer tarandus*), and the predators and scavengers that depend on them, e.g., wolves (*Canis lupus*) and wolverines (*Gulo gulo*), continue to remain at low densities throughout much of Interior Alaska. In the short term, low densities of wildlife deprive the state of a potentially valuable renewable resource. More importantly in the long term, public expectations and demands for effective management decline. Many past management actions, such as shortening or eliminating hunting seasons, have been ineffective at increasing numbers of moose and caribou, the primary or secondary food base for many carnivores. Yet, increased abundance of these ungulates and carnivores is important to many Alaskans because it can result in an increase in hunting, aesthetic, and trapping opportunities as well as an increase in revenues from tourists and nonlocal and out-of-state hunters. Indeed, moose, caribou, wolves, grizzly bears (*Ursus arctos*), and wolverines are synonymous with the concept of Alaskan wilderness. Management actions that would increase ungulate populations have significant impacts on the livelihoods and quality of life of many Alaskans.

Intensive studies of ungulate-browse-predator interrelationships provide an understanding of the factors that limit growth of ungulate and predator populations. Knowledge gained from these studies in specific areas allows more accurate predictions of effective management actions in similar ecosystems where information is less complete. Additionally, intensive studies provide insights on how to increase low-density animal populations and, most important, how to prevent populations from declining to low densities. Increasing low-density animal populations can be costly because extreme or long-term management actions may be required. Only by preventing populations from reaching low densities can we enjoy moderate sustained benefits from wildlife.

Game Management Subunit 20E in eastcentral Alaska is one of the areas in the Interior where moose, caribou, wolverines, and wolves declined to low densities during the 1970's. Moose and caribou in Subunit 20E prospered during and shortly after a predator poisoning program during the years 1948-1959 (Davis et al. 1978). Poisoning was aimed at reducing wolf predation; however, grizzly and black (*Ursus americanus*) bears were also killed. Moose and caribou had declined to a low density by 1976; the early part of this decline in the mid-1960's corresponded to a period of high wolf density (Davis et al. 1978). Wolf abundance declined during the mid-1970's when prey was at a low density (D. Grangaard, pers. observ.).

Moose-predator relationships in Subunit 20E contrast sharply with moose-predator relationships studied elsewhere in Alaska, particularly in regard to the relatively low moose density and moose:predator ratios in Subunit 20E. We estimated that 646 moose ± 27% (90% CI) occupied 7,500 km^2 of moose habitat in the southwest quarter of Subunit 20E during fall 1981. The mean moose density was 86 moose/1,000 km^2, which is the lowest density recorded in 15 locations in Alaska using a stratified random-sampling technique (Gasaway et al. 1986*a*). This low density and continued poor recruitment stimulated the Alaska Board of Game to authorize wolf removal during November 1981. In other areas of Alaska where predators were removed to increase moose numbers (i.e., Game Management Unit 13 and Subunit 20A), moose densities were initially 10 and 3 times greater, respectively, than in Subunit 20E, but recruitment was similarly poor (Ballard et al. 1981, Gasaway et al. 1983).

We proposed to test hypotheses about factors currently limiting moose population growth in Subunit 20E through actions that would lead directly to their acceptance or rejection. Since predator removal (Bergerud 1971, Ballard et al. 1980, Gasaway et al. 1983) had allowed a more rapid and accurate assessment of factors limiting ungulates than the "collar-and-watch" approach, we planned to rely heavily on that method to provide definitive tests of the hypotheses. However, the Alaska Board of Game withdrew authorization to reduce wolf abundance soon after this research began, and the liberalized hunting regulations for grizzly bears have not yet caused a significant reduction in grizzly bear predation in most of the area. Therefore, tests involving reductions in wolf predation are incomplete and reductions in grizzly predation have only begun.

The proposed tests of 2 hypotheses (H_1 and H_2) concerning factors limiting moose population growth are outlined below. Most aspects of these tests were reported in previous progress reports (Boertje et al. 1985, 1987; Gasaway et al. 1986b) and in Boertje et al. (in review), which has been submitted to the Canadian Journal of Zoology (Appendix A).

H_1: Predation Limits Moose Population Growth

Actions taken, actions to be taken, and tests of the hypothesis:

1. Assess effects of ADF&G wolf-removal programs (Nov 1981-Oct 1983) in and adjacent to the experimental area. Control areas (without wolf removal) are in the nearby Ladue River, Sixtymile River, and Washington Creek drainages.
    a. Supports acceptance of H_1 if calf survival and numbers of moose increase in response to wolf removal by fall 1985.
    b. Rejection of H_1 not possible if no positive population response. Assess bear predation.
2. Radio-collar 30 calf moose in experimental area during 1984 to assess bear predation and remaining wolf predation.
    a. Supports acceptance of H_1 if predation was a large mortality source.
    b. Supports rejection of H_1 if little predation occurred.

3. Radio-collar 15 grizzly bears to determine predation rates on adult moose in 1985-86.

    a. Supports acceptance of H_1 if grizzly bears regularly kill adult moose.

    b. Supports rejection of H_1 if grizzly bears kill few moose.

4. If grizzly bears are implicated, reduce grizzly bear predation in experimental area during the years 1987 through 1989.

    a. Supports acceptance of H_1 if moose survival increases and population grows.

    b. Supports rejection of H_1 if no change in numbers of moose occurs and if black bears are not implicated as major predators on calves.

5. If black bears are a major predator on calves and there was little response by moose to wolf and grizzly reductions, reduce black bear abundance.

    a. Supports acceptance of H_1 if moose survival increases and population grows.

    b. Supports rejection of H_1 if no change in moose survival.

H_2: Winter Food Limits Moose Population Growth

Actions taken, actions to be taken, and tests of the hypothesis:

1. Estimate browse availability and utilization in the experimental area.

    a. Supports acceptance of H_2 if there is very high browse utilization.

    b. Supports rejection of H_2 if there is adequate browse and low rates of use.

2. Measure moose population trend and calf survival in experimental and control areas after adequately reducing predation.

    a. Supports acceptance of H_2 if no positive moose population response.

    b. Supports rejection of H_2 if population increases in experimental area with no improvement in vegetation.

3. Assess condition of live cow moose by blood chemistry, physical status, and morphometric measurement.

    a. Supports acceptance of H_2 if moose are in poor condition during a winter of normal weather.

    b. Supports rejection of H_2 if moose are in good condition as determined by standards set by Franzmann and LeResche (1978) and Franzmann and Schwartz (1983).

4. Estimate pregnancy and twinning rates in 1984.

    a. Supports acceptance of H_2 if rates are low ($\leq$80% pregnancy rate for females $\geq$2 years old and $\leq$20% twinning rate).

    b. Supports rejection of H_2 if rates are average or above average.

5. Estimate marrow fat content of adult moose found dead.

    a. Supports acceptance of H_2 if fat content is consistently low ($\leq$20%) for adult moose.

    b. Supports rejection of H_2 if average fat content is $\geq$50%.

Tests of these hypotheses were originally proposed during 1981. Tests involving reductions in wolf predation were altered as the study progressed because the program to reduce the wolf population was discontinued.

In this brief progress report, we provide data that were collected during the past year and point out continuing trends and significant changes based on conclusions presented in last year's extensive progress report (Boertje et al. 1987). The final report (due 1 January 1989) will provide a complete analysis of limiting factors for moose in the study area.

OBJECTIVES

To determine if either predation or food limit the low-density moose population in Subunit 20E, and if predation is limiting, to determine how much control managers need to exert over wolf and bear populations to allow a low-density moose population to recover.

To correlate moose:predator ratios and moose population dynamics.

To apply findings to the management of other moose and predator populations in Interior Alaska as appropriate.

STUDY AREA

The study area (Fig. 1) was described by Boertje et al. (1987).

METHODS

Methods for all aspects of the study were described by Boertje et al. (1987).

RESULTS AND DISCUSSION

Testing the Predator-limiting Hypothesis

Wolf Population Status:

Historical Wolf Abundance. Details of wolf abundance during 1968-76 were gathered during this reporting period (Fig. 2). J. Terwilliger (a trapper, pers. comm.) reported extremely high wolf densities along the Taylor Highway from the mid-1960's through the mid-1970's; he trapped 27 wolves during winter 1968-69 in this area. Wolves began declining during winter 1974-75 and especially during winter 1975-76, although harvest by some trappers remained high because of increased trapping experience and the resulting increased vulnerability of wolves. For example, D. Grangaard trapped 32 wolves (SD = 12, *n* = 5) annually during the period 1971-76 on the same line he currently traps in the experimental area. The number of wolves trapped annually declined to 15 during winter 1976-77 and remained low ($\bar{x}$ = 6, SD = 4, *n* = 4) through fall 1981, at which time we initiated the wolf population estimates (Fig. 2).

Population Size and Harvest, 1986-87. Wolves with territories in or partially in the experimental area numbered 114 in fall 1986; therefore, wolves have not regained the numbers observed in the area prior to ADF&G wolf removal (125 wolves in fall 1981, Table 1). ADF&G ceased wolf removal during October 1983 (Table 1). The harvest and natural mortality accounted for 32 wolves (28% of the study population) during winter 1986-87 (Table 1), including six taken by ADF&G for radiocesium analysis.

Distribution. As in previous years, several wolf packs shifted or enlarged winter territories (Boertje et al. 1987; Fig. 3).

Winter Food Habits. Stomach contents and radiocesium analyses of 30 wolf carcasses necropsied during this reporting period will assist in assessing wolf food habits in the study area. In the final report, radiocesium analyses (Table 2) will be calibrated to a single time period to help approximate the proportions of moose and caribou in the wolves' diets.

Productivity, Age Structure, and Nutritional Condition. Productivity of female wolves ≥2 years old in the experimental area between 1981 and 1987 was comparable to values in Subunit 20A when prey was scarce (1976-79) and markedly lower than that found in Interior Alaska between 1957 and 1966 when prey was abundant (Table 3). Similarly, the percentage of reproductively active females ≥2 years old was only 74% (17 of 23 wolves) in the study population and 71% (15 of 21 wolves) in Subunit 20A in 1976 (Gasaway et al. 1983), compared with 89% in a previous statewide sample (Rausch 1967).

Data on nutritional condition of necropsied wolves (e.g., body weight and length and weight of fat deposits) from the experimental area (Table 2) will be compared in subsequent reports with wolf condition data from areas of high prey densities. Body length of pups may be the best relative indicator of general nutritional condition, because total weight and fat deposits can change rapidly if a temporary food shortage occurs; e.g., if animals are trapped.

Grizzly Bear Population Status:

Harvest. The Alaska Board of Game's recent liberalization of grizzly bear hunting seasons and bag limits and the Game Division's promotion of bear hunting in Subunit 20E during 1987 were unsuccessful in increasing the number of grizzly bears harvested. As detailed in Boertje et al. (1987), no major short-term declines in the grizzly bear population are expected from these harvests (4-8% of the estimated population), although we have inadequate data to assess the precise effects of them. In order to increase harvest rates and, in turn, reduce numbers of grizzly bears and predation on moose, a prolonged program of encouraging bear hunting will be required.

Moose Population Status:

Population Trend. Early winter moose surveys suggest the moose population in the experimental area may have increased slightly from the low densities during the 1970's. This interpretation is based on 3 survey areas where the index of moose/hr indicated an increase and 1 survey area that indicated no detectable trend (Fig. 4). Also, in one of the 2 trend areas where total moose observed was the index, a weak increasing trend in the population was indicated (Telegraph Creek, $\underline{P} < 0.1$, linear correlation); no trend ($\underline{P} > 0.1$) can be inferred from the initial 1982 count of the north Mount Fairplay area (Fig. 5).

No significant ($\underline{P} > 0.1$, linear regression) trend in numbers of moose was observed from 1982 to 1987 in 3 survey areas within the 2 control areas (Figs. 1, 6). However, following inspection of the trend data (Fig. 6), we concluded, as did Boertje et al. (1987), that the number of moose in the control survey areas (Fig. 4) was more likely stationary or slightly increasing rather than declining.

Calf Moose Mortality:

The pattern of high prewinter moose calf mortality continued during 1987 in the experimental area (Tables 4 and 5) and in the 3 control survey areas (Table 6).

Adult Moose Mortality:

A 6% mean annual natural (not human-caused) mortality rate was estimated for 39 radio-collared moose from 21 March 1984 to 10 March 1987. Predation remains the primary cause of death for yearling and adult moose. Cause of death was determined for 47 yearling and adult moose from 1981 through 30 November 1987: 41 (87%) were killed by predators, four (9%) died from antler wounds or locked antlers, one (2%) drowned, and one (2%) was shot (Appendix B). Based on these causes of mortality, predators probably killed 5 additional moose that we investigated, but cause of death could not be confirmed because too much time had elapsed between death of the moose and discovery of the carcass; i.e., evidence of cause of death had been obscured by predators and/or scavengers.

Testing the Food-limiting Hypothesis

Data presented by Boertje et al. (1985, 1987) and Gasaway et al. (1986b) supported rejection of the hypothesis that food limits moose population growth in the experimental area: (1) low use (<5%) of annual browse production, (2) high pregnancy rate (100%) among 27 adult female moose examined, (3) high twinning frequency (52%) among cows giving birth, (4) large morphometric measurements for adult female moose, (5) moderate-to-high condition indices for adult moose, and (6) moderate percentage of marrow fat in predator-killed adult moose.

Additional data on marrow fat content in 4 dead moose found during 1986-87 continue to support rejection of the food-limiting hypothesis. None of these moose had <20% marrow fat (Appendix B), confirming that few moose in the population were in a severely malnourished state (Franzmann and Arneson 1976, Peterson et al. 1984).

Conclusions

Conclusions from Boertje et al. (1987) that remain appropriate are repeated below:

1. We reject the hypothesis that food was limiting moose population growth in Subunit 20E, based on measurements of browse availability and use and on moose reproductive and nutritional status.

2. To date, we have no unequivocal test of the predation-limiting hypothesis. Only by reducing the effect of a potential limiting factor and measuring the change in moose abundance will we be able to make an unequivocal test. However, the mortality data presented make a strong case for predation limiting this moose population at its low density.

3. After wolf numbers were reduced by 20-40%, grizzly bear predation had a greater effect on moose population dynamics than wolf predation. Data were unavailable to determine which predator had a greater impact on moose prior to the reduction in wolf numbers.

4. The effects of a slowly increasing migratory caribou herd on short-term moose-predator relationships are likely both beneficial and detrimental to moose, depending on when and how long caribou are present in the predator's home range. When both caribou and moose are present in a wolf pack's territory, wolves often kill caribou rather than adult moose (Gasaway and Boertje, unpubl. data); therefore, the moose population benefits. However, a short-term abundance of caribou may allow wolves and, possibly, grizzly bears to maintain greater densities than if only moose occur. When caribou leave the predator's home range, the increased predator population preys primarily on moose--to the added detriment of the moose population.

Alternatively, moose, as a widely distributed resident prey base, sustain predators throughout all seasonal ranges of the Fortymile Caribou Herd, thus causing higher rates of predation on caribou than if no moose were present (Bergerud 1978). Moose, therefore, have primarily detrimental effects on caribou population dynamics (Bergerud 1978).

RECOMMENDATIONS

The Alaska Board of Game, Alaska Department of Fish and Game (ADF&G), and local advisory committees support general goals of increasing numbers of moose, caribou, and wolves in Subunit 20E. Debate continues on how best to accomplish these goals, and no specific goals or implemental plans have been approved by the Alaska Board of Game or local advisory committees. We recommend a management options plan be prepared by the Division of Game and approved by the Alaska Board of Game so that there are clear goals and approved methods for achieving those goals. The planning procedure will reduce the controversy on management actions and goals in Subunit 20E.

Long-term monitoring of moose, caribou, wolves, and grizzly bears in Subunit 20E should be continued to determine how long the naturally regulated and lightly exploited predator and prey populations will remain at low densities. Specifically, ADF&G should continue to monitor (1) moose and caribou population trend, size, and recruitment; (2) wolf population size and the effect of harvest on wolf population growth rate; (3) wolf food habits, productivity, and condition; and (4) grizzly bear harvest and its potential effect on grizzly bear abundance and moose population growth. Additionally, data from these studies should be presented in publishable manuscript form.

ACKNOWLEDGMENTS

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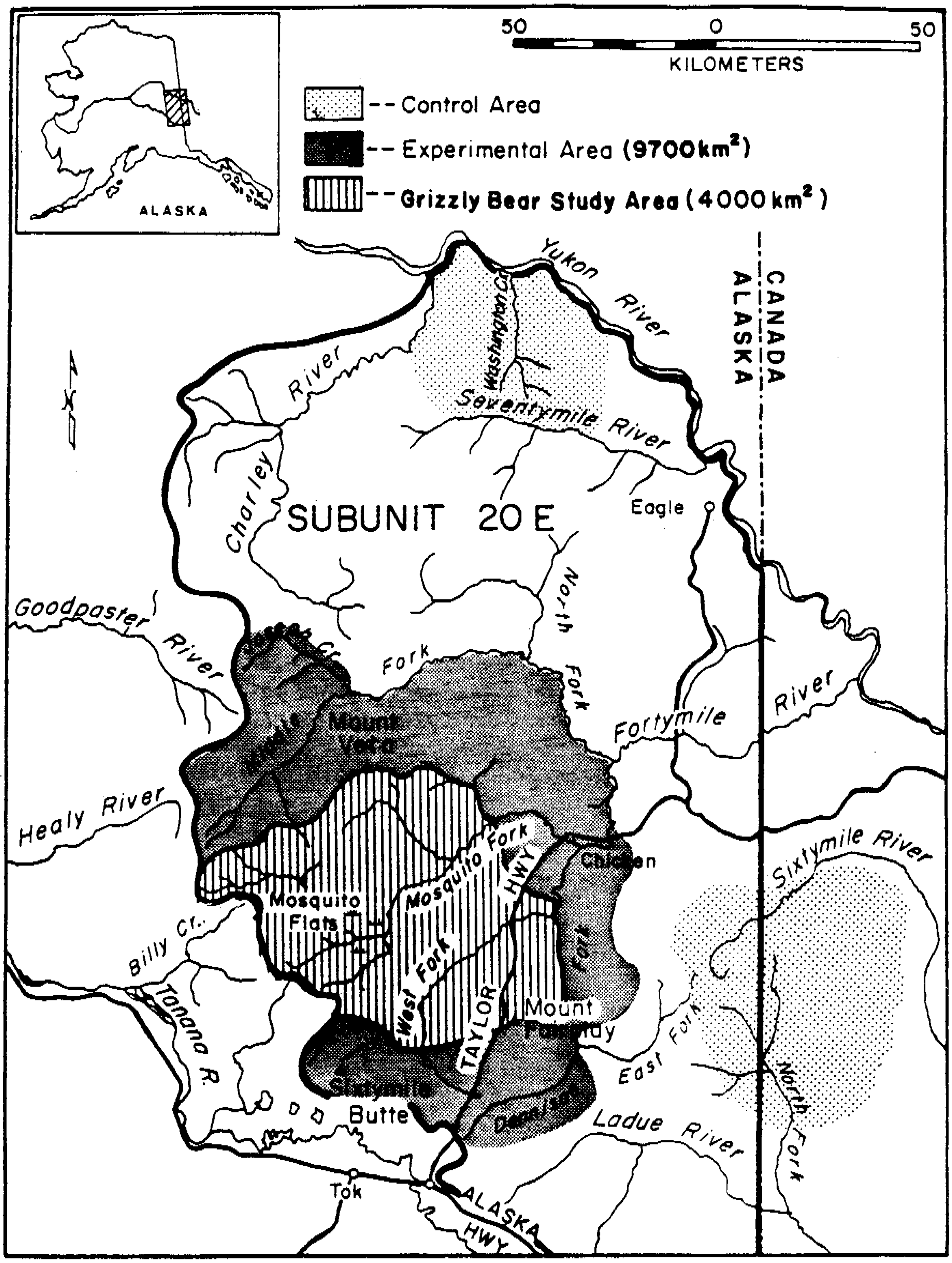

Fig. 1. Experimental area (with wolf removal), control areas (without wolf removal), and grizzly bear study area in Subunit 20E, Alaska, and adjacent Yukon Territory, Canada.

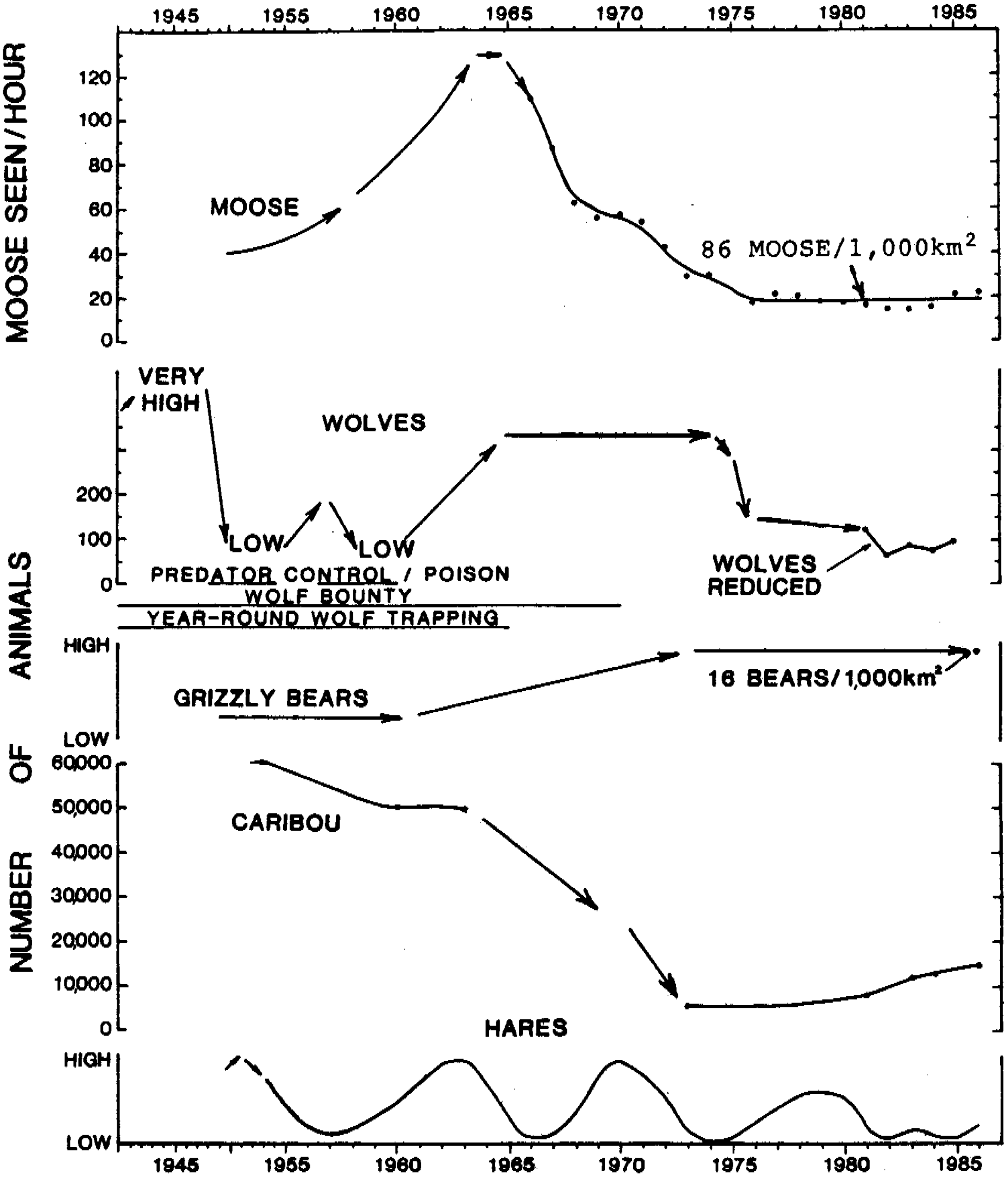

Fig. 2. Estimated and relative numbers of moose, wolves, grizzly bears, caribou, and hares in the experimental area of Subunit 20E, Alaska, 1940-86. Dots indicate estimated values; arrows indicate trends and approximate relative abundance based on qualitative observations.

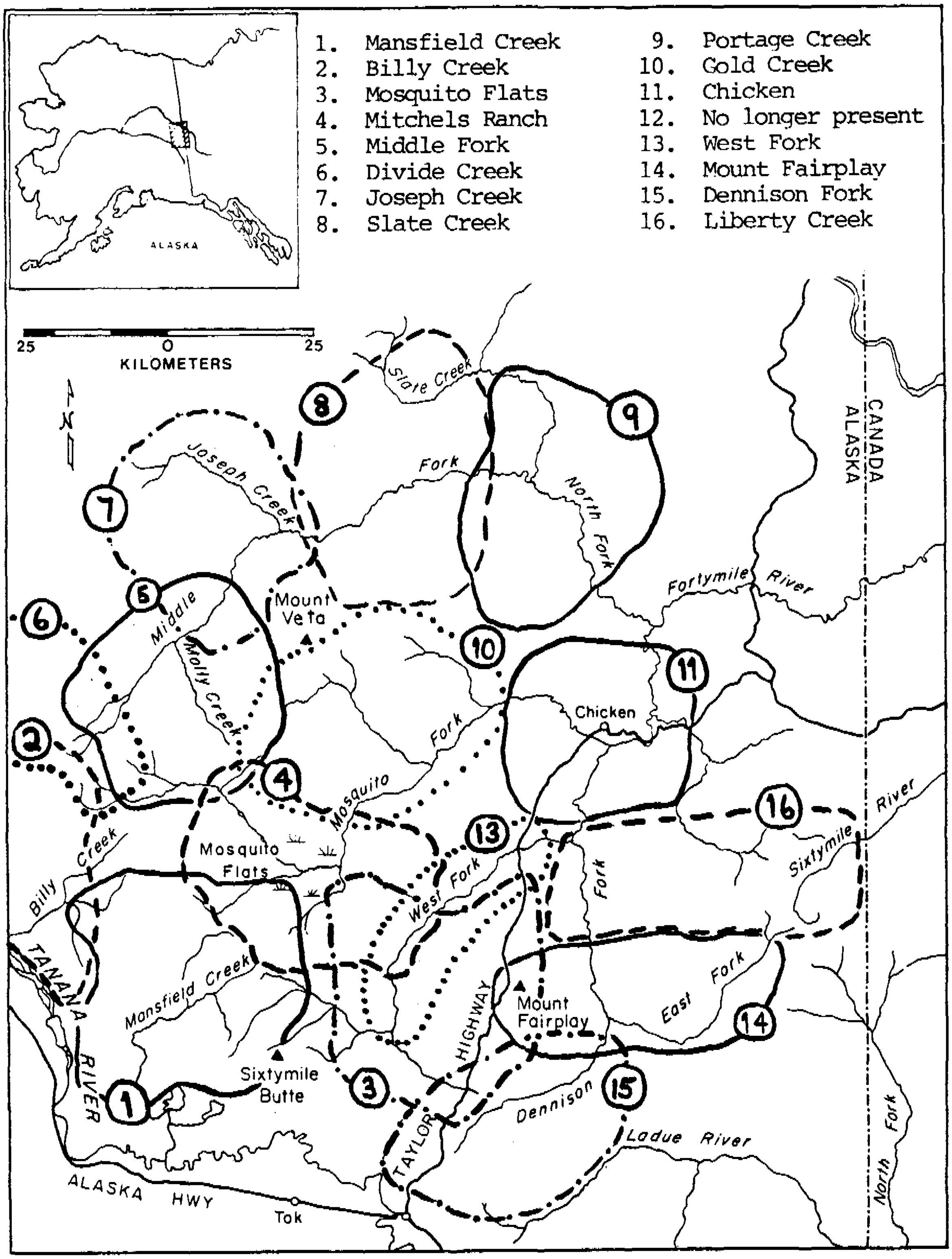

Fig. 3. Location and minimum size of wolf pack territories in and overlapping into the experimental area of Subunit 20E, Alaska 1986-87.

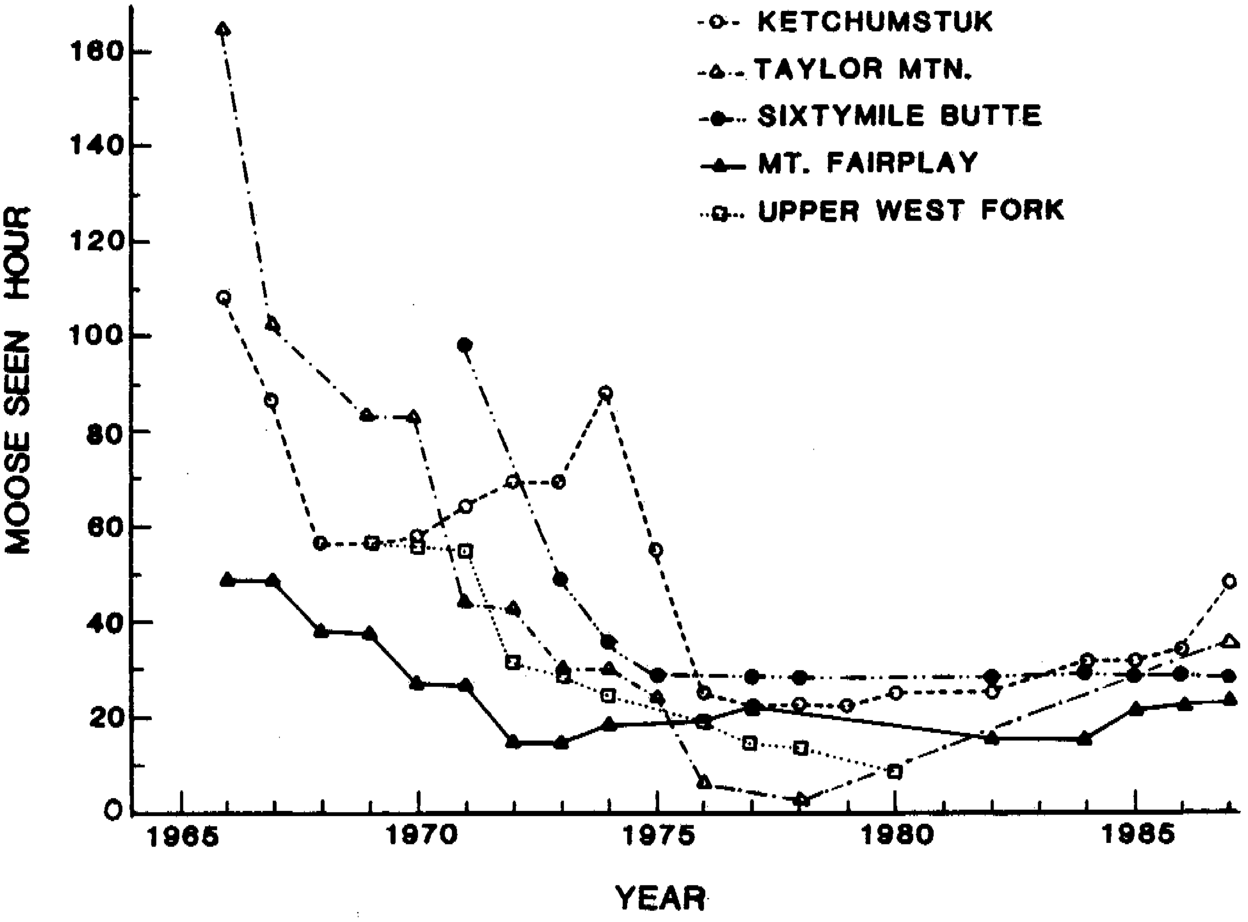

Fig. 4. Trends in number of moose seen per hour in 5 aerial survey areas in the experimental area of Subunit 20E, Alaska, 1966-87.

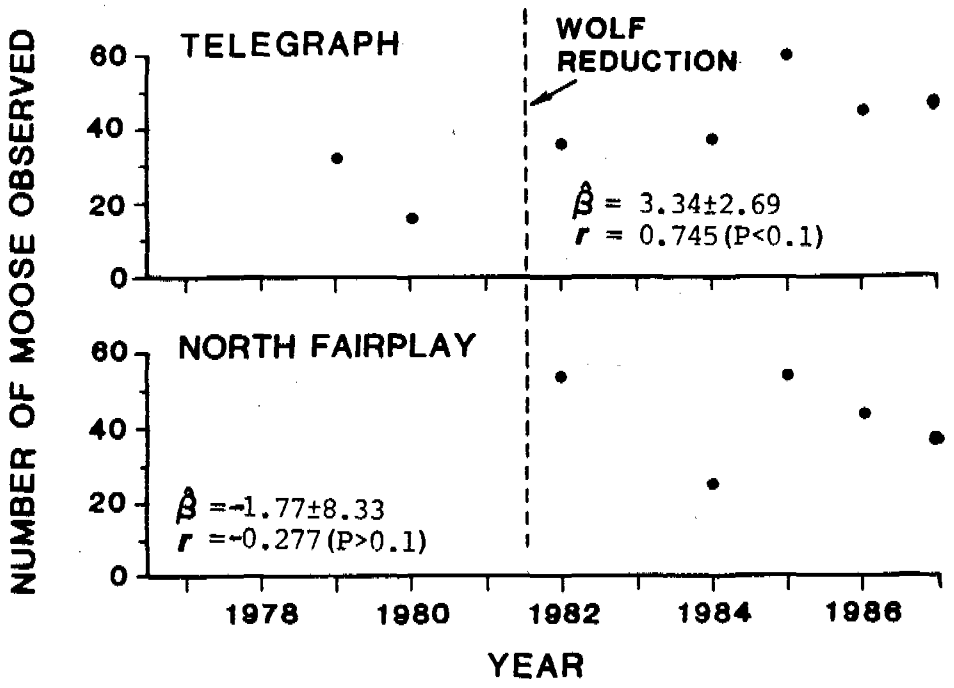

Fig. 5. Trends in number of moose observed in 2 aerial survey areas in the experimental area of Subunit 20E, Alaska, 1979-87. ± 90% CI equals the estimated slope of the linear regression line, and r equals the correlation coefficient.

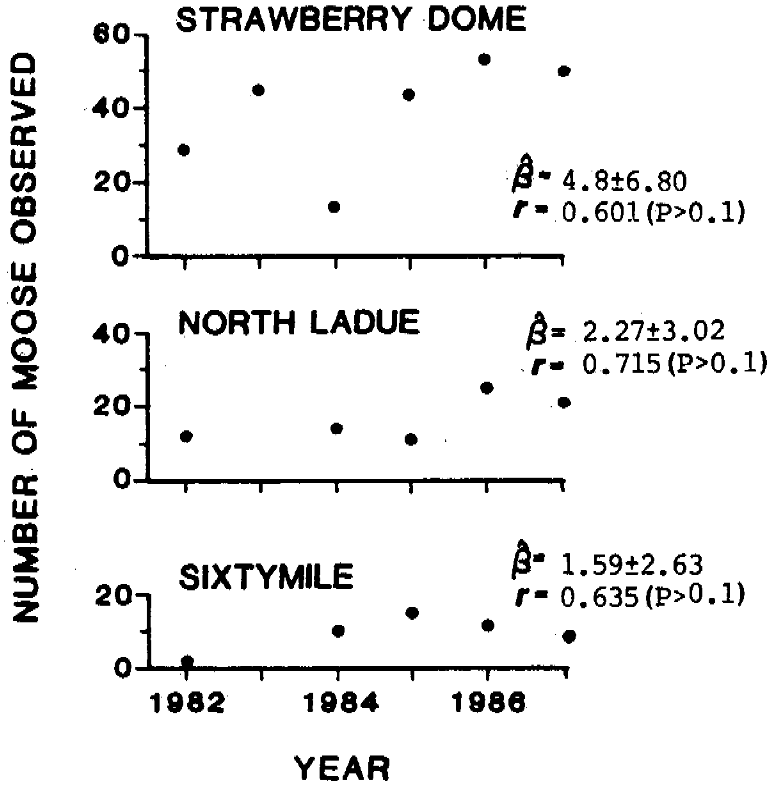

Fig. 6. Trends in number of moose observed in 3 aerial survey areas in the 2 control areas of Subunit 20E, Alaska, and adjacent Yukon Territory, Canada, 1982-87. ± 90% CI equals the estimated slope of the linear regression line, and r equals the correlation coefficient.

Table 1. Estimated numbers of wolves and wolf pack names in a 15,500-km^2 area, including the experimental area and adjacent areas of Subunit 20E, Alaska, fall 1981-spring 1987.

Pack No.	Pack name	Before wolf removal	After wolf removal[a]											
			1982		1983		1984		1985		1986		1987
		fall 1981	spring	fall	spring	fall	spring	fall	spring	fall	spring	fall	spring
1	Mansfield Creek	9	2	10[b]	1	5	3	4	3	6	6	12	8
2	Billy Creek	9[d]	2[b]	2[b]	1	8	8[c]	8[c]	2	8	4	10	3
3	Mosquito Flats	0	0	0	0	8	4	5	5	7	7	5	2
4	Mitchels Ranch	15[c]	2	2	2	4	2[b]	5	5[b]	7[b]	6[c]	8[b]	5
5	Middle Fork	11[d]	2	3	3	5[b]	2	5	4	6	4	5	4
6	Divide	8	0	0	0	0	0	0	0	0	0	2	2
7	Joseph Creek	6	2	2	2	6	3[b]	3[b]	2	2	2	5	5
8	Slate Creek	0	0	0	0	6	6	6	4	8	8	14	13
9	Portage Creek	12[b]	4[b]	4[b]	0	9	8[b]	9[b]	9	12	10	13	10
10	Gold Creek	5[b]	0	0	0	3	3	8	8[b]	11[c]	8[c]	10[c]	6[c]
11	Chicken	7	3	5	4	8	4	5	5	4	3	7	3
12	Ketchumstuk	3	3	5[b]	2	1	1[b]	0	0	2	1	0	0
13	West Fork	10	2	4	2	3	2	2	2	2	2	2	2
14	Mount Fairplay	2	2	2	2	2	2	2	0	3	2	2	0
15	Dennison Fork	9	9	11	1	1	1	3	3	3	1	3	3
16	Liberty Creek	8	8	8	8	10	6[b]	6[b]	6	7	5	6	6
	Lone wolves	11	11	6	6	8	8	7	7	9	9	10	10
Total wolf numbers		125	52	64	34	87	63	78	65	97	78	114	82
Percentage change			-58%	+23%	-47%	+156%	-28%	+24%	-17%	+49%	-20%	+46%	-28%
Density (wolves/1,000 km^2)		8	3	4	2	6	4	5	4	6	5	7	5

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[a] Department wolf take was 9 during winter 1980-81, 56 during 1981-82, 15 during 1982-83, and 7 during October 1983. The remaining wolf mortality includes some natural mortality and harvest by private trappers and hunters.

[b] One wolf had a functioning radio collar.

[c] Two wolves had functioning radio collars.

[d] Three wolves had functioning radio collars.

Table 2. Necropsy data from 122 wolves killed in and adjacent to the experimental area of Subunit 20E, Alaska, during winters 1980-87.

Pack name	Date	Age (yr)	Sex	Total weight (kg)	Xiphoid fat(g)	Kidney fat(g)	Subcu. fat(mm)	Body length (cm)	Radio-cesium[a]
Mansfield Creek	3/16/81	2	F	40	--	87	16	132	639
Mansfield Creek	3/16/81	2	M	43	--	112	33	130	546
Mansfield Creek	10/10/82	1	M	27	125	--	5	106	490
Mansfield Creek	10/10/82	1	M	25	10	20	0	106	528
Mansfield Creek	10/10/82	3	F	48	144	--	43	127	--
Mansfield Creek	10/10/82	--	M	50	85	--	14	133	--
Mansfield Creek	10/10/82	4	M	56	230	--	55	133	--
Mansfield Creek	2/2/83	4	F	41	145	--	28	129	--
Mansfield Creek	2/19/83	3	M	45	--	--	--	131	--
Mansfield Creek	10/26/83	2	M	40	80	--	28	129	818
Mansfield Creek	11/20/86	1	M	37	25	--	3	122	5,097
Mansfield Creek	12/1/86	Pup	M	34	35	--	23	120	638
Mansfield Creek	3/20/87	1	M	36	--	--	45	123	425
Billy Creek	2/10/81	Pup	M	39	--	81	31	128	5,701
Billy Creek	3/25/81	Pup	F	34	--	75	30	130	7,475
Billy Creek	2/28/82	6	F	36	--	46	6	--	1,691
Billy Creek	3/19/83	2	M	50	137	--	30	134	12,325
Billy Creek	2/85	3	M	36	158	--	19	129	157
Billy Creek	3/85	Pup	M	41	188	--	35	133	178
Billy Creek	3/85	Pup	M	43	173	--	35	133	191
Billy Creek	3/85	Pup	F	34	115	--	32	121	129
Billy Creek	3/18/85	2	F	36	125	--	40	127	126
Billy Creek	3/18/85	Pup	F	30	80	--	22	121	545
Billy Creek	2/25/87	4	M	41	90	--	9	127	283
Billy Creek	1/87	1	F	37	140	--	24	120	705
Billy Creek	1/87	Pup	F	36	157	--	26	124	556
Billy Creek	1/87	Pup	M	43	220	--	37	126	408

Table 2. Continued.

Pack name	Date	Age (yr)	Sex	Total weight (kg)	Xiphoid fat(g)	Kidney fat(g)	Subcu. fat(mm)	Body length (cm)	Radio-cesium[a]
Billy Creek	1/87	1	M	41	220	--	38	124	593
Billy Creek	1/87	Pup	M	44	205	--	40	133	616
Billy Creek	3/87	2	M	40	105	--	9	135	500
Billy Creek	3/87	Pup	F	36	116	--	11	124	446
Mosquito Flats	1/2/87	4	M	38	12	--	0	125	10,270
Mosquito Flats	11/25/86	Pup	F	30	85	--	23	113	4,667
Mosquito Flats	11/25/86	1	F	34	145	--	48	124	749
Mitchels Ranch	3/24/81	Pup	F	37	--	83	33	124	3,203
Mitchels Ranch	3/3/82	Pup	M	39	235	55	43	135	362
Mitchels Ranch	3/28/82	Pup	M	44	167	69	23	127	462
Mitchels Ranch	3/28/82	2	F	40	136	104	18	125	661
Mitchels Ranch	3/28/82	2	F	43	173	81	26	125	718
Mitchels Ranch	3/29/82	1	F	32	135	88	33	--	675
Mitchels Ranch	3/29/82	2	M	50	267	91	42	129	571
Mitchels Ranch	2/16/84	3	F	36	165	--	22	122	4,202
Mitchels Ranch	1/15/86	Pup	F	17	0	--	0	114	7,040
Mitchels Ranch	11/20/87	Pup	M	28	25	--	8	116	3,896
Mitchels Ranch	11/20/87	3	F	36	80	--	23	118	5,353
Middle Fork	4/22/81	Pup	F	36	--	50	12	136	1,984
Middle Fork	4/22/81	1	M	42	--	79	24	142	2,139
Middle Fork	12/15/81	1	M	48	232	69	48	--	5,993
Middle Fork	1/4/82	3	F	36	219	105	27	128	11,246
Middle Fork	3/4/82	Pup	F	34	44	48	21	112	12,377
Middle Fork	3/4/82	Pup	F	30	44	53	21	113	13,356
Middle Fork	3/5/82	2	M	39	100	40	18	118	10,364
Middle Fork	3/5/82	7	F	39	130	102	29	123	20,338

Table 2. Continued.

Pack name	Date	Age (yr)	Sex	Weight (kg)	Xiphoid fat(g)	Kidney fat(g)	Subcu. fat(mm)	Body length (cm)	Radio-cesium[a]
Middle Fork	3/7/82	2	M	50	177	108	27	128	15,718
Middle Fork	3/9/82	1	Unk	34	108	118	26	122	15,532
Middle Fork	3/12/82	Pup	M	29	71	37	18	119	17,380
Middle Fork	10/26/83	2	M	45	140	--	37	130	9,885
Middle Fork	10/30/83	2	F	48	115	--	15	130	13,410
Middle Fork	12/3/83	2	F	43	160	--	36	124	10,060
Middle Fork	12/3/83	4	M	44	168	--	27	118	10,920
Middle Fork	1/10/84	3	M	34	40	--	3	127	14,435
Middle Fork	1/85	Ad	F	39	185	--	40	--	1,890
Middle Fork	12/10/86	Pup	F	23	17	--	6	114	3,077
Divide	12/3/81	4	M	50	265	132	58	130	1,003
Divide	12/81	Pup	--	34	--	--	--	--	1,591
Joseph Creek	2/19/82	Ad	M	52	70	73	39	--	10,860
Joseph Creek	2/28/82	2	M	52	--	--	27	130	7,136
Slate Creek	3/13/87	3	M	47	120	--	39	125	8,131
Portage Creek	1/4/82	3	F	36	219	110	27	128	11,246
Portage Creek	3/5/82	2	M	39	100	43	18	118	10,364
Portage Creek	3/5/82	7	F	36	130	102	29	123	20,338
Portage Creek	3/7/82	2	M	50	177	108	27	128	15,718
Portage Creek	3/9/82	1	Unk	34	108	118	28	122	15,532
Portage Creek	3/11/82	Pup	F	34	--	48	21	--	12,377
Portage Creek	3/12/82	Pup	M	29	--	37	18	--	17,380
Portage Creek	3/20/82	Pup	F	29	44	53	21	--	13,356
Portage Creek	3/8/87	3	M	55	362	--	66	127	1,542
Portage Creek	3/8/87	2	F	40	68	--	76	122	1,576
Portage Creek	3/8/87	Ad	F	47	245	--	55	124	1,586

Table 2. Continued.

Pack name	Date	Age (yr)	Sex	Weight (kg)	Xiphoid fat(g)	Kidney fat(g)	Subcu. fat(mm)	Body length (cm)	Radio-cesium[a]
Gold Creek	1/15/86	Pup	M	23	42	--	8	117	5,440
Gold Creek	1/15/86	Pup	F	24	95	--	26	115	3,290
Gold Creek	1/15/86	Pup	F	30	150	--	35	114	3,250
Gold Creek	11/28/86	Pup	M	29	55	--	17	105	1,764
Gold Creek	3/11/87	4	F	48	128	--	34	118	1,664
Gold Creek	3/11/87	Pup	M	37	65	--	23	117	926
Chicken	10/20/86	Pup	M	30	75	--	29	112	4,360
Chicken	10/20/86	Pup	F	29	60	--	35	108	5,019
Chicken	10/20/86	1	M	46	55	--	4	126	4,601
Chicken	11/5/86	Pup	M	31	45	--	25	105	5,234
Ketchumstuk	3/7/82	4	F	43	95	80	12	128	5,080
Ketchumstuk	3/31/82	3	M	50	186	99	26	129	4,672
Ketchumstuk	3/31/82	4	F	45	125	140	23	128	5,256
Ketchumstuk	4/1/82	Pup	M	29	0	0	0	120	13,092
Ketchumstuk	4/1/82	Pup	M	37	118	139	25	120	5,339
Ketchumstuk	11/17/85	Ad	M	42	--	--	--	--	6,740
West Fork	2/7/82	Pup	F	39	--	--	21	109	5,193
West Fork	2/7/82	Pup	F	29	43	40	13	108	4,996
West Fork	3/31/82	5-9	M	38	117	49	5	132	17,248
West Fork	4/9/82	3	M	41	130	60	22	131	10,047
West Fork	4/9/82	2	F	37	98	54	10	124	15,588
West Fork	11/5/83	3	M	48	130	--	40	126	6,804
Mount Fairplay	11/20/82	Ad	F	39	--	--	22	--	8,231
Mount Fairplay	11/5/86	Pup	M	35	30	--	22	118	458
Mount Fairplay	11/25/86	1	F	37	150	--	26	120	1,168

Table 2. Continued.

Pack name	Date	Age (yr)	Sex	Total weight (kg)	Xiphoid fat(g)	Kidney fat(g)	Subcu. fat(mm)	Body length (cm)	Radio-cesium[a]
Dennison Fork	10/18/82	Pup	M	23	10	13	2	111	457
Dennison Fork	10/29/82	Pup	M	25	41	--	11	113	--
Dennison Fork	11/5/82	1	F	39	51	--	3	124	7,860
Dennison Fork	12/14/82	Pup	F	23	53	--	13	108	5,527
Dennison Fork	12/14/82	Pup	F	26	60	--	24	115	5,315
Dennison Fork	1/83	Pup	F	--	0	--	0	--	8,500
Dennison Fork	1/83	--	--	--	0	--	0	109	7,205
Dennison Fork	1/83	Pup	M	--	0	--	0	117	--
Dennison Fork	3/6/83	2	F	40	272	--	65	119	--
Dennison Fork	3/7/83	Pup	F	32	110	--	23	120	--
Dennison Fork	11/83	4	M	48	110	--	10	131	10,665
Dennison Fork	11/83	4	M	50	80	--	12	132	8,502
Dennison Fork	1/86	Pup	M	19	0	--	0	98	5,010
Dennison Fork	1/86	Pup	F	21	25	--	0	99	4,550
Liberty Creek	3/18/83	1	M	53	175	--	32	135	--
Liberty Creek	3/18/83	1	M	48	210	--	30	137	--
Liberty Creek	12/85	Pup	M	23	12	--	2	106	5,330
Liberty Creek	12/85	Ad	M	39	27	--	1	126	6,620

[a] Cs-137 concentration in pCi/kg wet muscle.

Table 3. Indicators of productivity in female wolves ≥ 3 years old in Interior Alaska, 1957-87.

	Placental scars			Corpora lutea			Fetuses		
Area and year	No. of wolves	$\bar{x}$	95% CI	No. of wolves	$\bar{x}$	95% CI	No. of wolves	$\bar{x}$	95% CI
Interior Alaska 1957-66 (Rausch 1967)	45	7.1		56	6.8		18	6.6	
Subunit 20A 1976-79 (Gasaway et al. 1983)	7	4.3	±0.9	9	5.4	±0.8	5	4.6	±0.7
Subunit 20E experimental area 1981-85	10	4.9	±1.0	7	4.9	±1.2	2	4.5	±2.2

Table 4. Offspring:cow ratios for 1955-87 cohorts at 6 and 18 months of age, as determined from aerial surveys in the experimental area of Subunit 20E, Alaska.

		Age of cohort in months					
		6			18		
Birth year for cohort	No. moose classified	No. cows ≥2 yrs old	Calves: 100 cows ≥2 yrs old	Calves as % of adults ≥2 yrs old	No. cows ≥2 yrs old	Yrlg: 100 cows ≥2 yrs old	Yrlgs as % of adults ≥2 yrs old
1955	--	--	--	--	50	36[a]	23
1956	129	50	62	39	47	51	27
1957	140	47	57	30	48	58	38
1958	129	48	58	38	53	162	76
1959	253	53	100	47	123	55	26
1960	390	123	43	20	--	--	--
1961	--	--	--	--	--	--	--
1962	--	--	--	--	--	--	--
1963[b]	151	--	54[c]	--	--	--	--
1964[b]	271	--	49[c]	--	--	--	--
1965	--	--	--	--	242	34	22
1966	509	242	24	16	284	27[a]	20
1967	498	284	8	6	209	9	5
1968	389	209	13	8	177	25	17
1969	365	177	28	19	191	19	13
1970	386	191	26	19	132	15	11
1971	238	132	20	15	228	8[a]	6
1972	363	228	17	13	169	15	11
1973	269	169	8	6	238	7	5
1974	361	238	8	6	110	4[a]	3
1975	168	110	8	6	84	7	5
1976	124	84	2	2	124	21	15
1977	235	124	7	5	84	29	17
1978	175	84	14	9	50	8[a]	7
1979	73	50	20	17	45	27	14
1980	108	45	22	12	75	35	19
1981	184	75	24	13	110	36[a]	20
1982	255[d]	110	17	10	--	--	--
1983[b]	215[d]	--	13[c]	--	122	18	10
1984	271[d]	122	25	14	145	29	15
1985	342[d]	145	19	10	187	16	9
1986	396[d]	187	25	14	209	22	12
1987	479[d]	209	22	12	--	--	--

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[a] Relatively deep snow occurred during cohort's 1st winter.

[b] Surveys delayed until January-February; therefore, sex identification was not possible.

[c] Estimated from regression of percentage calves vs. calves:100 cows ≥2 years old in the experimental area.

[d] New survey areas were added within the experimental area to increase sample size for composition.

Table 5. Offspring:cow ratios and percentage calves for 1978-87 cohorts at 6 and 18 months of age, as determined by aerial moose surveys in the Mount Veta-Mosquito Flats moose survey area in Subunit 20E, Alaska, before (1978-81) and after (1982-86) wolf removal. n = total number of moose classified.

	Age of cohort in months					
	6				18	
Birth year for cohort	n[a]	No. of cows ≥2 yrs old	Calves: 100 cows ≥2 yrs old	% Calves in total sample	No. of cows ≥2 yrs old	Yearlings: 100 cows ≥2 yrs old[b]
1978	112	58	14	7	46	9
1979	67	46	17	12	24	33
1980	59	24	21	8	72	33
					Yearlings: after wolf removal	
1981[c]		72	26	12	55	18
		Calves: after wolf removal				
1982	119	55	16	8	--	--
1983	70[d]	--	--	9	61	20
1984	119	61	13	7	78	10
1985	160	78	21	10	91	26
1986	203	91	26	12	103	31
1987	259	103	23	9	--	--

[a] Numbers of moose observed cannot be used to estimate population trend because size of survey area and search effort varied among years.

[b] Yearling males are doubled to estimate total yearlings.

[c] Data from 1981 moose population estimate in experimental area west of the Taylor Highway (Fig. 1).

[d] Survey flown during January 1984 after initiation of antler drop; therefore, sex and some age data were not collected.

Table 6. Offspring:cow ratios for 1981-87 cohorts at 6 and 18 months of age, as determined from aerial surveys in 3 control areas in Subunit 20E, Alaska, and the adjacent Yukon Territory. n equals the number of moose classified.

Birth year for cohort	n	Density (moose/ km^2)	Age of cohort in months					
			6			18		
			No. of cows ≥2 yrs old	Calves: 100 cows ≥2 yrs old	Calves as % of adults ≥2 yrs old	No. of cows ≥2 yrs old	Yearlings: 100 cows ≥2 yrs old[b]	Yearlings as % of adults ≥2 yrs old
1981	--	--	--	--	--	18	33	22
1982	43	0.10	18	39	26	20[a]	30	19
1983	42[a]	--	20[a]	20	12	16	0	0
1984	37	0.09	16	12	6	30	20	11
1985	69	0.17	30	23	12	32	50	25
1986	90	0.22	32	31	16	28	50	27
1987	80	0.19	28	25	13	--	--	--

[a] Only a portion of 1 of 3 control areas was surveyed because of shallow snow.

[b] Numbers of yearling males are doubled to estimate total yearlings.

Appendix A. This manuscript "Predation on moose and caribou by radio-collared grizzly bears in eastcentral Alaska" was submitted to the Canadian Journal of Zoology in December 1987.

Predation on moose and caribou by radio-collared grizzly bears in eastcentral Alaska

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Abstract:

Radio-collared grizzly bears (*Ursus arctos*) were sighted daily for approximately 1-month periods during spring, summer, and fall to estimate predation rates on moose (*Alces alces*) and caribou (*Rangifer tarandus*) in eastcentral Alaska. Predation rates on adult moose were highest in spring, lowest in summer, and intermediate in fall. Adult male grizzly bears killed adult moose significantly more ($P < 0.1$) often than adult female grizzlies without cub(s) of the year. We estimated that each adult male grizzly would kill 3.3-3.9 adult moose annually, each female without cubs would kill 0.6-0.8 adult moose and 0.9-1.0 adult caribou annually, and each adult bear would kill at least 5.4 moose calves annually. The minimum spring predation rate on moose calves was 7 bear-days/calf kill. This predation rate was independent of moose density, based on a comparable study of a high-density moose population. Implications are that managers should not allow moose densities to decline to low levels, because grizzlies can have a greater relative impact on low than high moose density populations and because grizzly predation can be difficult to reduce. In respect to ungulates, grizzly bears were primarily predators, not scavengers, in this area of low prey availability (11 moose/grizzly bear); bears killed four times more animal biomass than they scavenged.

Introduction

Quantitative studies on the predatory nature of grizzlies are clearly lacking. Brown or grizzly bears (*Ursus arctos*) have been implicated as major predators on radio-collared moose (*Alces alces*) calves ≤ 6 weeks old in southcentral Alaska (Ballard et al. 1981; Ballard et al., in press) and the southern Yukon Territory (Larsen et al. 1987). Prior to these studies, grizzly bears in North America were often considered primarily scavengers of ungulates (Craighead and Craighead 1972; Jonkel 1978), although considerable circumstantial evidence and anecdotal accounts of grizzly bears killing livestock or wild ungulates are reported in the literature, as reviewed by Haglund (1974) and Ballard and Larsen (in press). No previous study of collared grizzly bears distinguished grizzly predation from scavenging on adult ungulates, nor has grizzly bear activity previously been monitored daily during extended spring, summer, and fall periods.

The present study is part of an investigation of the factors limiting moose population growth in the Fortymile River drainage and adjacent areas of eastcentral Alaska (Boertje et al. 1985, 1987; Gasaway et al. 1986). Low moose densities, 86 ± 23 moose (90% CI)/1000 km^2 in 7500 km^2 during 1981, have prevailed in the area since the mid-1970's despite low moose harvest rates, low or moderate snow depths, and abundant browse. A moose calf mortality study during 1984 revealed that grizzly bears were major predators in this ecosystem; they killed 52% of 33 collared calves.

The objectives of this paper are to: (1) report estimated grizzly bear predation and scavenging rates on moose and caribou (*Rangifer tarandus*), (2) contribute to niche identification of the grizzly bear, and (3) discuss implications of grizzly predation on moose management.

Site description

The grizzly bear study area (4000 km^2), located in eastcentral Alaska north of Tok (Fig. 1), consists of rolling hills and seven subalpine and alpine mountains (1400-1800 m) largely covered with mature black and white spruce (*Picea* spp.) overstory below treeline (1000 m elevation). Subalpine vegetation consists primarily of dwarf birch (*B. nana*) and willow (*Salix* spp.), interspersed with willow-lined drainages. Additionally, there are shrub-dominated burned areas;a 200-km^2 poorly drained shrub-dominated flat (700 m); and meandering drainages bordered by willow, shrub birch (*Betula* spp.), alder (*Alnus* spp.), white birch (*B. papyrifera*), and white spruce (*P. glauca*). A wide diversity of berries is available at all but the highest elevations. The predominant berry species are *Vaccinium uliginosum*, *V. vitis-idaea*, *Empetrum nigrum*, *Arctostaphylos uva-ursi*, *A. alpina*, *A. rubra*, *Viburnum edule*, *Shepherdia canadensis*, *Cornus canadensis*, *Andromeda polifolia*, and *Oxycoccus microcarpus*.

The climate is subarctic and continental. Leaves emerged on a majority of shrubs during June 1-7 in 1983-86, and leaf senescence occurred during the last 2 weeks of August. The average annual temperature near Tok (Fig. 1) is -4C, and total annual precipitation averages 24 cm (National Climatic Data Center, Asheville, North Carolina).

Large carnivores inhabiting the study area include wolves (*Canis lupus*), black bears (*Ursus americanus*), and grizzly bears. Their prey include moose, caribou, beaver (*Castor canadensis*), snowshoe hares (*Lepus americanus*), and hoary marmots (*Marmota caligata*). Arctic ground squirrels (*Citellus parryi*) and salmon (*Oncorhynchus* spp.) are absent from the study area, and snowshoe hares have not been abundant in the study area since the early 1970's. Seasonal and annual distribution of the Fortymile Caribou Herd varies, but usually 300-7500 caribou are in the study area; calving does not occur in the study area.

Methods

Locating, capturing, and radio-collaring grizzly bears and wolves

Boertje et al. (1987) detail methods.

Estimating predation rates on moose and caribou ≥1 year old

Spring, summer, and fall predation rates (number of bear-days/number of kills) were calculated from daily observations (except 5 days) during radio-tracking flights from April 30 through June 10, 1986, July 9 through August 10, 1986, and September 18 through October 18, 1985, respectively. Of the 5 days not flown, no 2 days were consecutive; therefore, based on observations of the length of time bears spent on yearling and adult kills, we included these 5 days when totaling the number of bear-days. Data were also included from five instances when individual bears were obscured by fog or dense vegetation; however, the obscured bear was always sighted the following day to confirm whether a kill had been made. Bear-days excluded from the calculation of predation rates included: (1) the first 5 days following immobilization because daily movements were obviously reduced for 4 days, and (2) days that bears spent in or near dens (i.e., <200 m from dens). The two-tailed Student's *t*-test was used to test for differences in predation rates among seasons and among males and females.

On all flights, an observer accompanied the same pilot in a Piper Super Cub. In a majority of cases, bears were sighted on the first pass or circle. If bears were traveling when first observed, we searched the expected preceding travel path for carcasses and then relocated the bear before departing.

To determine cause of death, we necropsied moose and caribou carcasses within 36 hours of when carcasses were sighted. The site was examined for evidence of a struggle and other sign.

Femurs and lower incisors were collected from each carcass when possible.

To estimate annual grizzly predation rates, we extrapolated data from the three seasonal radio-tracking periods to May 1 through October 15 (168 days), based on mean den exit and entrance dates in the study area. A maximum annual kill rate was derived by minimizing the summer extrapolation to 56 days (June 26 through August 20); conversely, a minimum annual kill rate was derived by maximizing the summer extrapolation to 84 days (June 14 through September 5). Maximum and minimum annual kill rates were calculated because of confusion over when to begin and end the three extrapolations. Dates are based on phenology, bear breeding behavior, and chronology of breeding (J. Hechtel, unpublished data). Data on den exit and entrance dates were only from bears for which annual predation rates were calculated, i.e., male bears and females without cub(s) of the year (hereafter females WOC). The term "females WOC" includes lone females, females with yearlings, and females with 2-year-olds. These were pooled because predatory behavior was relatively similar (Spraker et al. 1981; Miller 1985, 1986). Females with cub(s) of the year (hereafter females WC) were treated separately because of their restricted movement patterns.

Derivation of ratios

Ratios of moose:grizzly bear were derived using moose densities from fall 1987 and grizzly bear densities from May 1, 1986 (Boertje et al. 1987). We estimated a moose population of 700 based on 475 moose counted during low intensity searches with a Super Cub plus an estimate of 225 moose missed in surveyed areas and in areas not surveyed.

Estimating minimum predation rates on calves

We estimated minimum bear predation rates on calves from observations of radio-collared bears feeding on calf carcasses. We made observations during the same flights used to estimate predation rates on moose and caribou ≥ 1 year old. Since calves were not regularly observed until May 22 in 1986, we calculated minimum spring predation rates only for May 22 through June 10.

We did not land at all calf carcasses, but assumed calves attended by radio-collared bears were killed by the bears. This assumption is based on data from necropsied calves attended by bears in 1984 (Boertje et al. 1985) and 1986 and direct aerial observations in 1985 and 1986 of bears killing and subsequently feeding on calves. We found no evidence from our study of radio-collared calves that grizzly bears were consuming calves that died from other causes; this agrees with other studies (Ballard et al. 1981, Franzmann et al. 1980).

Results

Predation on moose and caribou ≥1 year old

Predation rates by male bears were highest during spring (1 kill/26 bear-days), lowest during summer (1 kill/132 bear-days), and intermediate during fall (1 kill/43 bear-days), but rates were not significantly different ($P > 0.1$, Table 1). Extrapolated annual kill rates for an adult male bear ranged from 3.3 to 3.9 adult moose with 0.8 and 6.6 the extremes of 90% confidence intervals.

Estimated seasonal predation rates for female bears WOC were not significantly different ($P > 0.1$, Table 1). The extrapolated average annual kill rates for an adult female grizzly WOC ranged from 0.6 to 0.8 adult moose and 0.9 to 1.0 caribou ≥1 year old. Extremes of 90% confidence intervals on these averages were 0.1 and 1.4 for moose and 0 and 2.2 for caribou. Predation rates of the various reproductive classes of females WOC were as follows: females with yearlings made 0 kills during 22 bear-days during fall, lone females made (four kills during 467 bear-days, and females with 2-year-old(s) made two kills during 72 bear-days during spring and summer.

Females WC killed no moose or caribou ≥1 year old during 117 bear-days in spring and summer. Lack of kills was probably due in part to restricted movements and low prey densities (Boertje et al. 1987).

Adult male bears ≥8 years old killed adult moose at significantly greater rates ($P < 0.1$) than female bears ≥4 years old WOC, when data were combined for the three observation periods (Table 1). Differences in these kill rates may be due to age-specific differences between bears sampled. However, when predation data on moose and caribou ≥1 year old were combined, no differences ($0.1 < P < 0.2$) in predation rates were found between male and female grizzlies WOC. Only female grizzlies killed caribou ≥1 year old.

Data suggest that a majority of male grizzlies ≥8 years old kill adult moose annually and that some males are particularly predatory (Fig. 2). However, no male bears were observed for twice the 42-day average interval between adult moose kills, which was the subjectively determined minimum interval required for assessing if a bear was likely to be a predator of moose ≥1 year old. Nevertheless, four of five male bears that were observed at least 49 days killed adult moose. Two additional male grizzlies that killed no adult moose were tracked only 15 days and 31 days, of which 14 days were spent scavenging an adult moose.

Certain females also killed adult ungulates more often than others. However, because of the long interval between adult kills (94 bear-days/ kill, Table 1) and low number of bear-days sampled ($\underline{n}$ = 561), data are inadequate to assess whether most adult female grizzlies kill adult moose and/or caribou.

Minimum predation rates on calves

The three sex and reproductive classes of bears did not kill calves at significantly different rates ($\underline{P} > 0.1$) when compared within a season or when seasons were combined for each class of bear (Table 2). However, these comparisons may be invalid if, e.g., daily spring observations disproportionately underestimated calf kills by males compared with females; larger bodied males may have consumed small calves more rapidly than lone females.

When all bears were combined, spring predation rates on moose calves (7 bear-days/kill) were significantly greater ($\underline{P} < 0.02$) than summer rates (23 bear-days/kill, Table 2), and no moose calves were killed during 323 fall bear-days (Table 1). However, when classes were treated separately, only females WOC killed significantly more calves ($\underline{P} < 0.1$) during spring than summer. The differences between the spring predation rate for all bears versus the summer or fall predation rate was probably greater than reflected by our estimates (see Biases).

Most if not all adult grizzlies studied killed calf moose, yet in both spring and summer a few grizzlies killed a majority of the calves (Fig. 3). All nine spring bears that were adequately sampled killed calves, yet four of these nine bears killed 21 (72%) of the 29 calves killed by these bears. We considered bears to be adequately sampled in spring if they were observed for twice the 7-day average interval between kills. In summer, no bears were sampled for twice the 23-day average interval between kills, yet 9 of 10 bears killed calves (Fig. 3).

We estimated each adult bear would kill at least 5.4 ± 0.8 (SE) moose calves annually if we assume the observed spring predation rate during the period May 22 through June 10, the summer predation rate during the period June 11 through August 10, and no predation thereafter (Table 2). We used the summer predation rate to extrapolate through the June 11-July 8 gap in the data because radio-collared calves died at a faster rate prior to June 10 than thereafter (Boertje et al.

1987). We also wanted to emphasize that all calf predation rates reported here are minimum rates.

Grizzly handling time for moose and caribou $\geq$1 year old

Adult grizzly bears consumed adult moose in 7-14 days. Accurate estimates of days required for grizzly bears to consume adult moose carcasses were obtained in four instances where single bears or family groups were observed on or immediately adjacent to carcasses (<100 m) during consecutive daily flights, and the bears completely consumed the carcasses before departing. These handling times were as follows: (1) an 11-year-old male grizzly spent 14 days on an adult bull during October, (2) an 11-year-old male spent 8 days on an adult cow during September, (3) an adult female and one 2-year-old spent 7 days on an adult cow during June, and (4) an adult female and two 2-year-olds spent 7 days on an adult bull during June.

Grizzly bears consumed caribou $\geq$1 year old in 2 to 3 days. An adult female bear completely consumed a 1.3-year-old caribou in 2 days, a female and two 2-year-olds consumed an adult female caribou in 3 days, and two lone grizzlies consumed a 2.3-year-old male caribou in 3 days (1 day by an adult female followed by 2 days by an adult male).

Food acquisition--predation versus scavenging

Collared grizzly bears killed about four times more animal biomass than they scavenged (Table 3). These data are available animal biomass at observed feeding sites, not necessarily biomass consumed by the collared bears.

Grizzlies scavenged more wolf kills than vice versa, probably largely because of greater relative grizzly densities (16 grizzly bears/1000 km^2 versus 5 wolves/1000 km^2 during spring 1986, Boertje et al. 1987). If either predator had an effect on the other's kill rate, then grizzlies elevated the wolf kill rate. However, wolf-killed moose contributed only about 200 kg (3%) of 6640 kg of adult moose available to collared grizzly bears (Table 3). Including other observations in the study area in late spring and summer, three of five adult moose killed by wolves were largely scavenged by grizzly bears. In contrast, only 1 of 12 adult moose killed by grizzly bears was largely scavenged by wolves.

Discussion

Biases

We discuss biases associated with estimating grizzly predation rates because identifying biases is vital to interpretation of existing data and for increasing comparability in future studies. However, biases discussed yield no quantitative basis for altering our results.

Biases associated with estimating grizzly predation rates on ungulates ≥1 year old

Several factors indicate we had a high probability of observing carcasses of moose and caribou >1 year old (Table 1) attended by collared grizzlies during the daily observation periods. First, we visually sighted non-denned bears on 99% of our attempts. Second, intervals between sighting of non-denned bears did not exceed 1 day. Third, all observed carcasses were sighted within 36 hrs of when bears made the kills (as evidenced by daily map locations of bears). Fourth, prior to necropsy of carcasses, bears were on or immediately adjacent to (<10 m), and protective of, all but one observed carcass. In this exception, the grizzly was approximately 50-100 m from the carcass; tracks in the snow indicated the grizzly had killed the moose.

Potential biases were inherent in estimating predation rates despite our high probability of observing kills of ungulates ≥1 year old. Two biases may have caused overestimation of predation rates. First, a collared bear could have displaced a non-collared bear from a kill and the kill attributed to a collared bear. This bias affects predation rates of large males more than small males and females. Ballard et al. (in press) appropriately attributed 0.5 kills to a collared bear if collared and uncollared bears were initially seen at the kill site. We had no similar cases. Second, disturbing bears from carcasses during our necropsy investigation could increase kill rates. This bias potentially overestimates male kill rates more than female rates because we chased males off kills more frequently than females.

Underestimation of the kill rate on ungulates ≥1 year old may have resulted from three sources. First, a radio-collared bear could have been displaced from a kill before we observed it; this bias affects predation rates by females most. Second, collared bears could possibly have killed and consumed yearling caribou between daily flights (<36 hrs), although this is unlikely since collared bears usually spent >36 hrs on July moose calves observed, which weigh about 20 kg less than yearling caribou. This bias affects rates by large males most because of their shorter handling time. Third, radio-collar malfunctions (one in our study) could have resulted from a moose's kick, and if the grizzly killed the moose, the predation rate would be underestimated. This bias affects predation rates by females most because they took longer to kill adult moose than males, as evidenced by sign around the kill site. To summarize our qualitative assessment, net bias tends to cause overestimation of predation rates by male grizzlies whereas net bias is unclear for predation rates by females.

The two previous predation studies of collared grizzlies based predation rates on number of observation days or visual sightings/kill or suspected kill ("kill"), which causes overestimation of predation rates; these biases void comparisons with our results. Predation rates based on observation days or visual sightings overestimate actual predation rates (Fuller and Keith 1980) on adult moose because the probability of observing a grizzly bear on an adult moose carcass is greater (up to 14 times greater in our study) than observing the bear the day on which the kill was made. For example, Ballard et al. (1981) reported an estimate of grizzly predation rates on adult moose as one adult moose "kill"/16 observation days ($\underline{n}$ = 28 "kills"). Ballard et al. (in press) reanalyzed data on "kill" rates of adult moose by excluding data from the first day of observation periods. They also summarized 2 additional years of data and reported that grizzly bears "kill" one adult moose/43.7 bear-days ($\underline{n}$ = 13.5 "kills") in spring. Their revised estimate remains potentially an overestimate because: (1) they did not confirm cause of death through necropsy; and (2) they observed collared bears revisiting carcasses (Spraker et al. 1981), therefore not all moose carcasses should have been counted as recent kills. In contrast, their revised estimate of the adult moose kill rate may be an underestimate because 20 additional unidentifiable "kills" were noted, some of which could have been adult moose.

To minimize biases in estimating grizzly predation rates on ungulates ≥1 year old, we recommend: (1) that bears are observed daily or at least once every 2 days, and (2) that carcasses be examined on the ground within 24 hrs of discovering the carcass. Because grizzly bears often quickly bury adult ungulate carcasses (Mysterud 1973), it is often impossible for an observer in an aircraft to determine the date of kill or degree of consumption.

Biases associated with documenting grizzly predation rates on moose calves

Observed predation rates on moose calves (Table 2) are minimum rates, although observed summer rates are more accurate than spring rates. Bears killed and consumed neonatal calves between our daily flights in one or two of nine instances of predation on single collared calves in 1984. Furthermore, Ballard et al. (in press) found that most calf carcasses (28 of 32) were attended by bears for <12 hours, based on two observation flights/day during late May and the first few days of June. Also, D. Larsen (pers. comm.) noted that grizzly bears attended neonatal calf carcasses for <4 hours in several instances in the Yukon. In contrast, larger summer calves were more reliably located; 10 of 12 single calves were attended by bears for two daily flights in our study area.

Predation by bears

Visual inspection of data suggests predation on adult and yearling moose is greatest in spring, lowest in summer, and intermediate in fall. Eide (1965), Haglund (1974), and Danilov (1983) confirm this seasonal pattern of predation on large ungulates by brown bears. Statistical detection of seasonal differences in predation rates on ungulates ≥ 1 year old in this study are confounded by small sample sizes, infrequent kills, and variability among bears, which contributed to large standard errors (Table 1).

Potential factors contributing to the higher spring predation rate include the relative scarcity of alternate food prior to the plant growing season and the vulnerability of adult female prey while giving birth and while defending neonatal young. Seven of eight adult moose killed during spring were cows and six of these were killed during the calving period, May 19 through June 10. Although only three of these seven cows were found with neonatal calves, all seven may have had calves. Observations in 1984 indicated that calves are sometimes killed 100 m or more from the cow when both are killed. We witnessed two instances of grizzly bears killing calves; both bears were 5-year-old females, and in each case the cow moose kicked the bear at least once. On one occasion the bear struck the adult moose on the shoulder before the moose departed. Similar encounters with more powerful adult male grizzlies would probably be fatal to adult female moose, as suggested by the fact that all six adult female moose killed during the calving period were killed by adult male grizzlies. Also, site examination revealed that male grizzlies killed adult moose almost instantly, compared with female grizzlies that often rode moose 100 m or more (as evidenced by moose hair) before killing a moose.

Our study is the first to report that male grizzlies kill significantly more ($P < 0.1$) adult moose than female grizzlies (Table 1). Combined biases probably overestimate male versus female grizzly predation rates on adult moose, yet we have no quantitative basis for altering results. No previous telemetry studies have investigated male versus female grizzly predation through necropsy of prey to distinguish predation from scavenging. However, tracking studies in Sweden revealed that adult male brown bears most frequently attacked adult moose (Haglund 1974).

Grizzly bear predation on moose calves occurs at a high rate during approximately the first 3 weeks of life and rapidly declines thereafter (Ballard et al. 1981, Boertje et al. 1987, Larsen et al. 1987). The latest a grizzly was observed with a calf was July 31 in our study, mid-July in southcentral Alaska (Spraker et al. 1981), and August 4 in the Yukon (Larsen et al. 1987). Grizzly predation rates may decline due to decreased vulnerability of calves (Ballard et al. 1980) and/or decreased interest in hunting calves.

Effects of grizzly predation on moose populations and management implications

Grizzly bears can have greater impacts on low than high-density moose populations because: (1) predation rates on calf moose by individual bears can be independent of calf density, and (2) bear density is not tightly linked to moose density. Density-independent predation rates on calves are exemplified by comparing our results with those from southcentral Alaska (Ballard et al., in press) for a comparable 20-day spring period. Collared bears killed 19-75% more calves in our study area despite about a 75% lower moose density and 60% fewer moose per bear (Miller and Ballard 1982; Ballard et al. 1987; Boertje et al. 1987; Miller et al. 1987). Grizzly bears also killed 52% of collared calves (n = 33) in our study area compared with 46% in southcentral Alaska (n = 165; Ballard et al. 1981; Ballard et al., in press).

Mechanisms by which grizzlies can kill at greater rates at low versus high prey densities are not understood. Bears may spend more time searching for moose calves, have a greater incentive to kill, and/or have a greater tradition of killing calves in some areas of low versus high prey densities. The southcentral Alaska study area afforded bears alternatives to consuming largely moose calves (Ballard et al. 1981), which may account for the lower predation rates on moose calves and corresponding lower impact on the moose population, despite a 50-75% greater grizzly bear density.

The second factor allowing grizzly bear predation to have a greater impact on low than high-density moose populations is the loose regulatory feedback between bears and moose. Densities of grizzly bears are not strongly linked to moose densities, in part, because of the omnivorous food habits of bears (Gasaway et al. 1983; Ballard and Larsen 1987). Therefore, bear density and total predation on prey populations can remain high as prey populations decline, causing the effect of predation to increase, i.e., antiregulatory control (Lidicker 1978; Gasaway et al. 1983). Reported grizzly bear densities in central Alaska (16-28 grizzly bears/1000 km^2; Miller and Ballard 1982; Boertje et al. 1987; Miller et al. 1987; Reynolds and Hechtel 1987) have a narrow range compared with moose densities in the same areas (175-720 moose/1000 km^2; this report; Ballard et al. 1987; S. DuBois and D. Haggstrom, Alaska Department of Fish and Game, unpublished data).

If moose decline to low densities, management may require reducing numbers of bears for moose survival to increase sufficiently for the moose population to grow. Foremost, managers should avoid allowing moose densities to decline to low levels (Gasaway et al. 1983, Van Ballenberghe 1985), particularly where grizzly numbers are difficult to reduce. In our study area, managers are faced with undesirably low numbers of moose and wolves due largely to sustained heavy grizzly predation. Attempts have been and are continuing to be made to reduce grizzly bear numbers through liberalized grizzly bear hunting seasons and increasing the number of potential bear hunters afield by increasing bull moose and caribou seasons. These actions have increased annual harvest rates of grizzlies in the study area to approximately 8% during 1982 through 1986, but we have inadequate data to assess the effect of this harvest on bear abundance and moose population dynamics (Boertje et al. 1987).

Lowering predation by grizzly bears can best be accomplished by simultaneously reducing numbers of males and females, even though males killed significantly more ($\underline{P} < 0.1$) moose ≥ 1 year old than individual females. Using mean estimates of predation, we calculated that an estimated eight adult male grizzlies present in our study area would kill 29 moose ≥ 1 year old, whereas 14 females WOC would kill only 10 moose ≥ 1 year old. Therefore, even though we estimated there were fewer male than female bears, males would have made most of the kills of moose ≥ 1 year old. Certainly, greater harvests of male grizzlies should be encouraged if managers desire to lower adult moose mortality rates. However, because male grizzlies are effective predators on grizzly cub(s) of the year (Reynolds and Hechtel 1984; R. Boertje, unpublished data), lowering only numbers of adult males may increase recruitment to the population (Young and Ruff 1982) and ultimately predation.

Predation versus scavenging

In respect to ungulate biomass available for consumption, grizzly bears were primarily predators, not scavengers, in this study where prey availability was low (11 moose/grizzly bear). Animal biomass available to collared bears from predation was about four times more abundant than from scavenging, even though bears were effective scavengers. Ballard et al. (1981, in press) assumed that grizzlies killed rather than scavenged most adult moose carcasses they observed from aircraft in spring, and, based on results presented here, we concur. However, scavenging may be more important where prey availability is relatively high. Grizzly bears had about 2.3 times more moose available per bear in Ballard et al.'s study areas, which suggests more carcasses would be available for scavenging, particularly during spring due to overwinter mortality.

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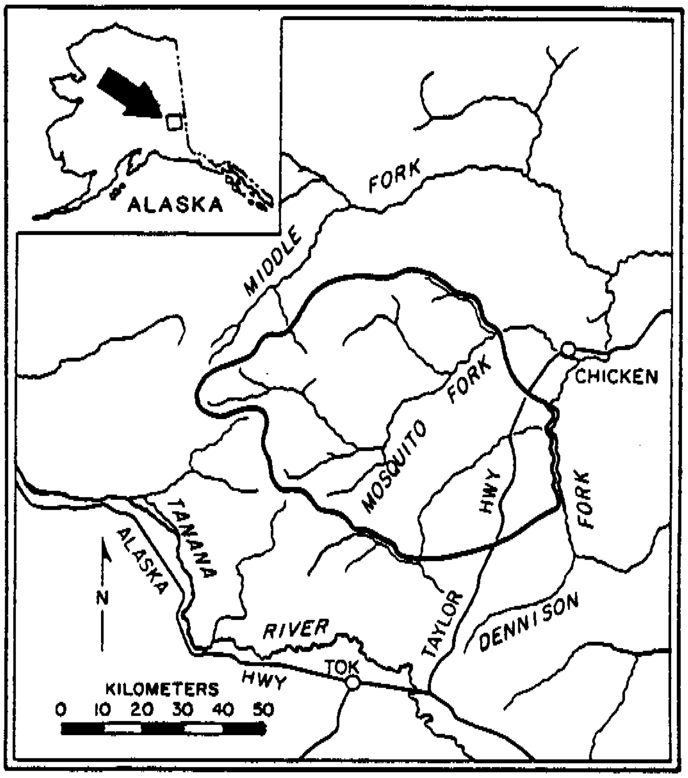

Fig. 1. Grizzly bear study area (4000 km^2) in eastcentral Alaska, 1985-86.

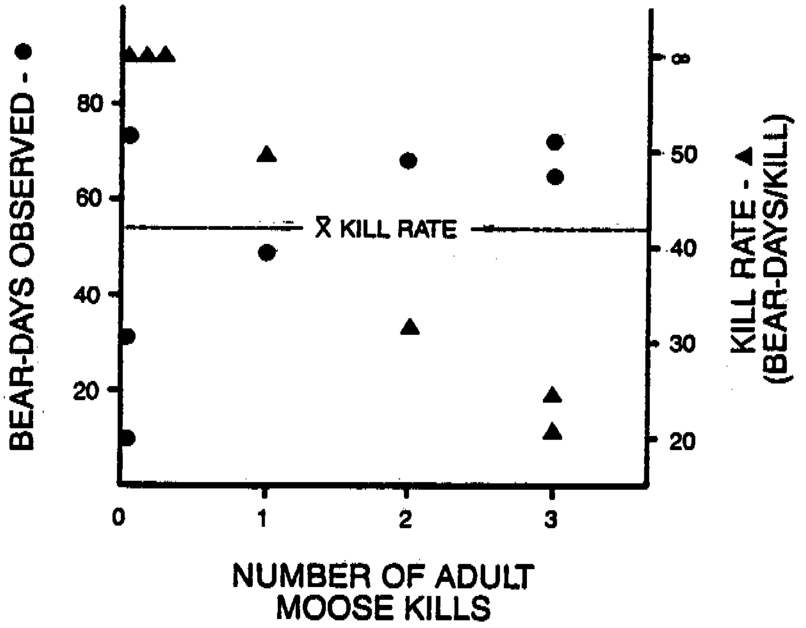

Fig. 2. Number of adult moose kills, number of bear-days observed (●), and kill rates (▲) of individual adult male grizzly bears radio-tracked during September 18, 1985-August 10, 1986, eastcentral Alaska. $\bar{x}$ kill rate is from Table 1.

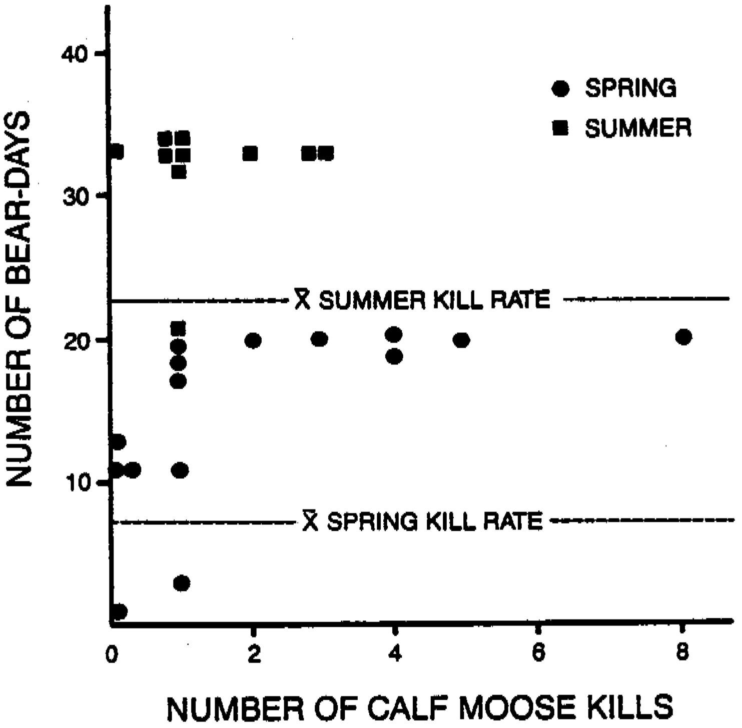

Fig. 3. Relationship between numbers of bear-days observed and calf moose kills of individual grizzly bears radio-tracked during spring (May 22-June 10) and summer (July 9-August 10) 1986, eastcentral Alaska. $\bar{x}$ kill rate is from Table 2.

Table 1. Numbers of radio-collared grizzly bears, bear-days, and adult moose and caribou kills observed on radio-tracking flights and used to extrapolate to annual grizzly bear predation rates, eastcentral Alaska, September 1985-August 1986.

Observation period	Spring 30 Apr- 10 Jun (42 days)	Summer 9 Jul- 10 Aug (33 days)	Fall 18 Sep- 18 Oct (31 days)	Total
Male bears ≥8 yrs old				
No. bears radio-tracked	6	4	4	7
No. bear-days	157	132	86	375
No. moose ≥1 yr old killed	6	1	2	9
No. caribou ≥1 yr old killed	0	0	0	0
No. bear-days/moose kill (SE)	26 (11)	132 (128)	43 (39)	42[a] (14)
Female bears ≥4 yrs old without cub(s) of the year				
No. bears radio-tracked	6	4	10	11
No. bear-days	204	120	237	561
No. moose ≥1 yr old killed	2	0	1	3
No. caribou ≥1 yr old killed	0	1	2	3
No. bear-days/moose kill (SE)	102 (59)	--	237 (231)	187[a] (76)
No. bear-days/caribou kill (SE)	--	120 (117)	118 (76)	187 (86)
No. bear-days/kill (SE)	102 (59)	120 (117)	79 (37)	94 (33)

[a] Mean total kill rates were significantly greater (*P* < 0.1, two-tailed Student's *t*-test) for males than females. No other means differed significantly (*P* > 0.1) when tested between sexes or among seasons or totals.

Table 2. Numbers of grizzly bears, bear-days, and moose calf kills observed on radio-tracking flights and used to extrapolate to minimum annual grizzly bear predation rates, eastcentral Alaska, 22 May-10 August 1986.

Observation period	Spring 22 May-10 Jun (20 days)	Summer 9 Jul-10 Aug (33 days)	Total
Male bears ≥9 yrs old			
No. bears radio-tracked	5	4	5
No. bear-days	74	132	206
Minimum no. moose calves killed	4	8	12
Minimum no. bear-days/kill (SE)	18 (7)	16 (5)	17 (4)
Female bears ≥5 yrs old without cub(s) of the year			
No. bears radio-tracked	6	4	6
No. bear-days	100	120	220
Minimum no. moose calves killed	20	5	25
Minimum no. bear-days/kill (SE)	5[a] (2)	24[a] (5)	9 (3)
Female bears with cub(s) of the year			
No. bears radio-tracked	4	2	4
No. bear-days	51	66	117
Minimum no. moose calves killed	7	1	8
Minimum no. bear-days/kill (SE)	7 (2)	66 (66)	14 (4)
Totals			
No. bears radio-tracked	15	10	15
No. bear-days	225	318	543
Minimum no. moose calves killed	31	14	45
Minimum no. bear-days/kill (SE)	7[b] (2)	23[b] (5)	12 (3)

[a] Spring and summer values differed ($P < 0.02$) for females without cubs.

[b] Total spring and summer values differed ($P < 0.02$) for all bears. No other means differed significantly ($P > 0.1$) when tested between seasons or among totals or classes of bears.

Table 3. Numbers and approximate weights of animals preyed upon and scavenged by collared grizzly bears, eastcentral Alaska, September 1985-August 1986. These data relate to available animal biomass at observed feeding sites, not necessarily biomass consumed by the collared bears.

	Predation						Scavenged					
	Spring		Summer		Fall		Spring		Summer		Fall	
Food item	n	Total kg	n	Total kg	n	Total kg	n	Total kg	n	Total kg	n	Total kg
Moose ≥1 year	8	3360	1	530	3	1450			0.5	200	2	1100
Moose calf	33	530	14	810			1	15				
Caribou ≥1 year			1	100	2	200	1	170			1	200
Caribou calf			1	35								
Caribou gut piles											2	60
Black bear	1	40			1	40						
Grizzly bear, adult female	1	100										
Grizzly bear cubs	4	40										
Total weight		4070		1475		1690		185		200		1360
Number bear-days		361		252		323		361		252		323
Animal biomass/ bear-day		11.3		5.9		5.2		0.5		0.8		4.2

Appendix B. Sex, age, cause of death, and percentage fat in long bone marrow of yearling and adult moose found dead in the experimental area and in the adjacent portion of Subunit 20D, Alaska, 1981-87.

Date of death	Investigated from ground (G) or air (A)	Sex	Age (yrs)	Cause of death	Percentage fat in marrow	Location
19 Feb 1981	G	M	12	Wolf	7	Mansfield Creek, 20D
20 Feb 1981	G	M	13[a]	Wolf	16	Fortymile River
Mar 1981	G	M	14	Wolf	35	Billy Creek, 20D
8 Mar 1981	G	F	12	Wolf	86	Mosquito Flats
10 Mar 1981	G	M	14	Wolf	93	Mosquito Flats
13 Mar 1981	G	F	17	Wolf	90	Mosquito Flats
16 Feb 1983	G	--	15	Wolf	87	Mosquito Flats
16 Feb 1983	G	F	17	Wolf	82	Mosquito Flats
10 Mar 1983	G	F	14	Wolf	85	Billy Creek, 20D
24 Mar 1983	G	F	11	Wolf	93	Billy Creek, 20D
Mar-Apr 1984	G	M	2	Drowned	--	Mosquito Flats
15 May 1984	G	M	6	Probably wolf or grizzly bear	89	West Fork
25 May 1984	G	F	10[a]	Wolves wounded/ grizzly bear killed	82	Mosquito Fork
21 May 1984	G	F	5	Grizzly bear	69	Mosquito Flats
28 May 1984	G	F	10[a]	Wolf	--	Mosquito Flats
16 Jun 1984	G	M	1	Wolf	28	Mosquito Flats
17 Jun 1984	G	F	14	Wolf	74	Mosquito Flats
Oct 1984	G	F	12	Probably grizzly bear	92	Ketchumstuk Creek
13 Mar 1985	A	--	Ad	Probably wolf	--	Ketchumstuk Creek
13 Mar 1985	A	--	Ad	Probably wolf	--	Ketchumstuk Creek
13 Mar 1985	A	--	Ad	Probably wolf	--	Sixtymile Butte
15 Mar 1985	A	--	--	Probably wolf	--	Mosquito Fork
29 Mar 1985	A	M	2-3[b]	Probably wolf	--	Joseph
2 May 1985	G	F	10[a]	Probably wolf or grizzly bear	--	Telegraph Creek
30 May 1985	A	--	Yrlg/ad	Probably grizzly bear	--	Ketchumstuk Creek
10 Jun 1985	G	F	13	Wolf	89	Mosquito Flats

Appendix B. Continued.

Date of death	Investigated from ground (G) or air (A)	Sex	Age (yrs)	Cause of death	Percentage fat in marrow	Location
10 Jun 1985	G	F	18	Probably grizzly bear	--	Mosquito Flats
18 Sep 1985	G	F	19	Grizzly bear	73	Mosquito Flats
1 Oct 1985	G	M	12	Fight with bull moose	--	Fish Creek
3 Oct 1985	G	M	9	Grizzly bear	94	Mosquito Flats
10 Oct 1985	G	M	11	Fight with bull moose	--	Dennison Fork
11 Oct 1985	G	M	13	Grizzly bear	76	Mosquito Flats
11 Oct 1985	G	F	13	Grizzly bear	50	Mosquito Flats
14 Jan 1986	G	--	Yrlg/ad	Probably wolf	67	Ketchumstuk Creek
17 Jan 1986	A	--	Ad	Wolf	--	West Fork
17 Jan 1986	A	--	--	Unknown, eaten by wolf	--	West Fork
22 Jan 1986	A	--	--	Wolf	--	Copper Creek
4 Mar 1986	G	F	10	Wolf	59	Gold Creek
16 Mar 1986	G	F	4	Wolf	78	Ketchumstuk Creek
9 May 1986	G	F	13	Grizzly bear	89	West Fork
9 May 1986	G	F	17	Wolf	10	Copper Creek
19 May 1986	G	F	9	Grizzly bear	72	Mosquito Flats
23 May 1986	G	F	17	Wolf	8	Cedar Creek
29 May 1986	G	F	3	Grizzly bear	69	West Fork
1 Jun 1986	G	M	10	Grizzly bear	63	Mosquito Fork
4 Jun 1986	G	F	14	Grizzly bear	22	Joseph Creek
5 Jun 1986	G	F	4	Grizzly bear	44	Little Whiteman Creek
9 Jun 1986	G	F	9	Grizzly bear	63	Telegraph Creek
10 Jun 1986	G	F	Ad	Grizzly bear	34	Ketchumstuk Creek
26 Jul 1986	G	M	17	Grizzly bear	91	Gold Creek
27 Jul 1986	G	F	15	Wolf	75	Mosquito Flats
8 Oct 1986	G	M	7	Grizzly bear	69	Mosquito Fork
9 Oct 1986	G	F	15	Shot	78	Mosquito Flats
1 Dec 1986	A	--	Yrlg/ad	Wolf	--	Cedar Creek
1 Dec 1986	G	F	15	Wolf	--	Mosquito Fork

Appendix B. Continued.

Date of death	Investigated from ground (G) or air (A)	Sex	Age (yrs)	Cause of death	Percentage fat in marrow	Location
1 Mar 1987	G	M	11	Wolf	44	Billy Creek
2 Mar 1987	A	M	Ad	Wolf	--	Middle Fork
3 Mar 1987	G	M	9	Wolf	65	Gold Creek
3 Mar 1987	G	F	11	Wolf	90	Middle Fork
14 Mar 1987	G	F	8	Wolf	90	Billy Creek
24 Sep 1987	G	M	Ad	Fighting, locked antlers	--	Ketchumstuk Creek
24 Sep 1987	G	M	Ad	Fighting, locked antlers	--	Ketchumstuk Creek

[a] Age estimated by wear.
[b] Age estimated by antler size.

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