BEARS, WOLVES, MOOSE, AND FOREST SUCCESSION, SOME MANAGEMENT CONSIDERATIONS ON THE KENAI PENINSULA, ALASKA

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ABSTRACT: We compared population dynamics for moose (*Alces alces*) and black bear (*Ursus americanus*) in an older (1947) and recent (1969) burn from 1978-1988. Moose densities in the 1947 burn were moderately high in early years of study (1.3 moose/km^2) but declined dramatically in later years (0.3 moose/km^2) as habitat quality declined. Moose densities in the 1969 burn were high (3.3 - 3.7 moose/km^2) in response to good habitat quality. Reproductive rates measured as percent of females with twins were 22 and 70% for the 1947 and 1969 burns. Estimates of neonatal moose calf survival using a Kaplan-Meier procedure were not different (P > 0.05) between the two areas (0.42 vs. 0.48). Predation accounted for 86% of all recorded mortalities; black bears accounted for 70% of all mortalities and 81% of all predation. Black bear density was similar in the two areas (205 vs. 258 bears/1000 km^2 in 1947 and 1969 burns). Reproductive success measured as age of first litter production and interval between weaning of yearlings was significantly (P < 0.05) better in the 1969 burn. Cub survival was significantly lower (P < 0.05) in the 1947 burn. Mean body size of bears in the 1969 burn was significantly greater (P < 0.05) than in the 1947 burn. Better performance of bears in the 1969 burn was attributed to a greater availability of moose calves per bear which represented a significant source of high quality food during spring when other available foods were of lower quality. It appeared the high density moose population on the Kenai Peninsula was regulated by habitat quality and quantity. Wolf (*Canis lupus*) density was high (11-20/1000 km^2) but not different between the two areas. Brown bears (*U. arctos*) numbers in the two study areas were low (23 - 28/1000 km^2) relative to black bears. Impacts of predation varied with changes in habitat carrying capacity and clearly defined management objectives determined when habitat enhancement or predator control was most appropriate.

Our understanding of the incidence of bear predation on neonatal moose calf mortality has improved in the past decade through use of mortality transmitters. Both black and brown bears have been identified as major predators of moose calves (Franzmann *et al.* 1980, Franzmann and Schwartz 1986, Ballard *et al.* 1981, Gasaway *et al.* 1983, Stewart *et al.* 1985, Boertje *et al.* 1988 and Larsen *et al.* 1989) and they may kill between 30-70 percent of the calves born each spring.

Although we now know bears can and do kill a large portion of the annual calf crop of moose, we must recognize bears may not represent the major factor controlling the dynamics of a given moose population. All wildlife populations responds to a number of factors which tend to reduce population size (i.e., predation, disease, habitat, and weather). Biologists recognize this process and manage populations based on defined objectives. When a manager is faced with a depleted population and an adequate habitat base, predator control may be a viable management option. The identification of bears as a major predator of moose has caused members of the public to assume that predator control is a necessary management practice for moose populations. For example, there were 23 proposals presented to the Alaska Board of Game in 1986 to liberalize brown bear seasons. Their justification was to enhance moose populations.

Studies of predators, including wolves, (Peterson *et al.* 1984), black bear (Schwartz and Franzmann in press) and moose calf mortality (Franzmann *et al.* 1980, Franzmann and Schwartz 1986) have been active on the

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Kenai Peninsula since the mid 1970's. Studies were conducted in two areas burned by wildfire at different times. During the time of our research the 1947 burn was past its peak relative to moose habitat quality and the population of moose was declining. Conversely, the 1969 burn was in a much earlier stage of vegetative regeneration and provided excellent moose habitat. The moose population in this area was increasing when we began our work. In this paper, we synthesized this information and discussed these findings relative to moose management on the Kenai Peninsula lowlands.

STUDY AREAS

Our study areas were located on the northern Kenai Peninsula lowlands in two forest stands burned by wildfire in 1947 and 1969. These 2 major wildfires produced large areas of early successional forests that provided excellent habitat capable of supporting high densities of moose.

The Kenai Peninsula lowlands supported a typical northern coniferous forest containing a mixture of white spruce (*Picea glauca*), black spruce (*P. mariana*), poplar (*Populus balsamifera*), aspen (*P. tremuloides*), and paper birch (*Betula papyrifera*). On dry upland sites the mature forest vegetation was white spruce, paper birch, aspen, or some combination of these species, whereas black spruce dominated poorly drained sites (Lutz 1956, Spencer and Hakala 1964). The deciduous tree species represent successional stages of revegetation after fire. The revegetation sequence following fire in the northern coniferous forest was related to fire intensity, preburn vegetation, composition and age, climate, time of burn, parent material, and weather (Lutz 1956, Viereck 1973, Rowe and Scotter 1973, Zasada *et al.* 1979).

Following fire, a lush herb layer was established; fireweed (*Epilobium angustifolium*) and bluejoint (*Calamagrostis canadensis*) were most common. Depending on the severity of the fire, shrubs (*Salix, Ledum, and Vaccinium*) reinvade from 6 to 25 years after a burn. As the overstory matured, many understory species were shaded out, leaving the more shade-tolerant plants like highbush cranberry (*Viburnum edule*) and scattered areas of rusty menziesia (*Menziesia ferruginea*) and Devil's club (*Oplopanax horridus*). Finally, when the white spruce forest matured, mosses and lichens were the dominant understory species (Oldemeyer and Regelin 1987). Moose began to use burned areas shortly after the fire was out, and Spencer and Hakala (1964) estimated that the productive life of a burn on the Kenai Peninsula was 20 years with a peak in production at 15 years. Biomass estimates of important moose browse (willow, paper birch, and aspen) were 37, 1399, 397, and 4.3 (kg/ha) measured at 3, 10, 30, and 90 years post burn, respectively (Oldemeyer and Regelin 1987: Tables 2 and 3).

The 1947 burn started in June as a result of road construction and burned for 6 weeks until extinguished by late summer rains (Spencer and Hakala 1964). According to Bangs *et al.* (1985) the 1947 burn (125,000 ha) occurred during average summer weather conditions. Because of topography, fuel loading, and changes in fire intensity over the duration of the burn, numerous unburned islands of mature timber were left. Bangs *et al.* (1985) estimated the amount of burned and unburned habitat within the entire burn perimeter and found significant differences in the habitat configuration between the boundary and center of the burn. The center had more burned forest (80%) and less remnant forest (11%) than the boundary areas (67% and 19%, respectively). A 2.5 km^2 sample in the center of the burn contained 624 individual stands ranging in size from 0.02 to 18.4 ha (LeResche *et al.* 1974). Remnant mature forest (i.e., 46% of the area, excluding water areas) composed 411 different stands. The 1947 burn supported a mosaic of vegetation types and was interspersed with lakes and ponds. The large number of stands and

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their irregular shapes created tremendous amounts of edge (112 km in the 2.5 km² area).

Light hunting pressure, a lack of wolves, and a succession of mild winters contributed to an increasing moose population that peaked in 1964. Seven years later a second population peak occurred. Subsequent habitat deterioration in the 1947 burn (Oldemeyer *et al.* 1977) combined with 3 severe winters (early 70's) resulted in more than a 50% decline in moose population by the mid 1970's. Concurrent with this decline, wolves, which had been extirpated from the Kenai Peninsula around 1913 reoccupied much of their former range (Peterson *et al.* 1984). Other contributing factors to the declining moose population were antlerless moose hunts from 1970-1974, road kills, and poaching.

The 1969 fire followed two of the hottest and driest summers on record. The fire was started in August and burned for 3 weeks (Bangs *et al.* 1985) consuming over 35,000 ha. The intensity of the 1969 burn resulted in only slight differences between habitat configurations within the center and boundary areas (Bangs *et al.* 1985). Approximately 72% of the area burned; 6-9% was unburned forest remnants, 9-17% was bogs or muskeg, and 5-9% was lakes and ponds.

METHODS

Most of the information contained in this review was previously published. Survival coefficients for moose calves in both the 1947 and 1969 burns were calculated with the Kaplin-Meyer procedure (Pollock *et al.* 1989). We compared survivor functions using an approximate Chi-square function with 1 degree of freedom (Pollock *et al.* 1989). Moose twinning rates in 1988 and 1989 were determined in the two burns using established procedures (Franzmann and Schwartz 1985).

RESULTS

Moose Population Dynamics

Harvest statistics (Alaska Department of Fish and Game [ADF&G], unpubl. data) of bull moose, suggested that the moose population in the 1947 burn peaked in 1964 (harvest = 573) and again in 1970 (harvest = 369); the density was estimated at 3.6 moose/km² in 1970-71 (Kenai National Wildlife Refuge, unpubl. data). The population declined to 1.3 moose/km² by the 1981-82. Oldemeyer *et al.* (1977) attributed the decline of moose in the 1970's to deteriorating habitat quality. A recent census (Gasaway *et al.* 1986) conducted in 1986-87 (ADF&G, unpubl. data) indicated a further declined to 0.3 moose/km². Moose numbers in the 1969 burn were estimated at 0.3 moose/km² in 1970-71, 3.3 moose/km² in 1981-82 (KNWR, unpubl. data) and 3.7 moose/km² in 1986-87 (ADF&G, unpubl. data).

Franzmann and Schwartz (1985) recommended using moose twinning rates to evaluate habitats. Moose populations in highly productive habitats contained a high percentage of cows with twin calves. A comparison of twinning rates between the 1947 and 1969 burns (Table 1) illustrated this concept clearly. In the 1947 burn only 22% of cows with calves had twins in years 1977 and 1978, and 31% had twins in 1989. This contrasted with the highly productive 1969 burn where 70%, 35% and 37% of cows with calves had twins in 1983, 1988, and 1989, respectively.

In the 1947 burn, of 69 cows observed between 24 May and 2 June 1989, 77% did not have a calf, while in the 1969 burn in 1988 and 1989, 38% and 40% did not have a calf (Table 1). In 1982-83, in the 1969 burn when habitat was highly productive, only 18% of all cows observed did not have calves. Unfortunately, comparable data were not available for the 1947 burn in 1977-78.

Twinning data reflected the general trend in the number of cows with twins, singletons, or with no calves relative to habitat quality. As habitat quality declined in the 1969 burn,

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Table 1. Adult moose twinning rates at peak of calving (20 May - 3 June) in two habitats on the Kenai Peninsula, Alaska.

Area and year	n calves with each cow	n cows observed	% cows with calves	% total cows observed
1947 burn				
1977-78[1]	None[2]			
	Single	38	78	
	Twin	11	22	
1989	None	53		77
	Single	11	69	16
	Twin	5	31	7
1969 burn				
1982-83[1]	None	23		18
	Single	31	30	25
	Twin	71	70	56
1988	None	23		38
	Single	24	65	40
	Twin	13	35	22
1989	None	31		40
	Single	29	63	38
	Twin	17	37	22
Unit 15 C[3]				
1989	None	10		31
	Single	13	59	41
	Twin	9	41	28

[1]Data were originally presented by Franzmann and Schwartz (1985).
[2]Single cows were not recorded during this survey.
[3]Data were collected in Unit 15C, near Homer, Alaska (Dave Holdermann, Pers. comm.)

the number of cows with calves producing twins declined from 70% to 35%, while the proportion of all moose with no calves increased from 18% to 40%. In the 1947 burn when habitat was poor, only 22% and 31% of the cows with calves had twins, in 1977-78 and 1989, respectively.

These data indicated that both twinning rate and the percent of cows without calves may be sensitive indicators of habitat quality. Early predation of neonates by black bears likely contributed to the proportion of cows observed without calves although surveys were timed to minimize this bias.

Moose calf mortality studies were conducted in the 1947 burn in 1977 and 1978 (Franzmann et al. 1980) and in the 1969 burn in 1982 and 1983 (Franzmann and Schwartz

1986). Black bears accounted for 34 and 35% of recorded mortalities in the 1947 and 1969 burn, respectively; total mortality was 57 and 51%. Brown bears and wolves accounted for 2-6% of total calf mortality.

Heisey and Fuller (1985) cautioned that simple percentages used in calculation of mortality rates contained inherent biases and consequently developed special techniques to estimate survival rates. More recently, Pollock et al. (1989) presented a method to use a staggered entry design to estimate survival of radio-tagged animals. This method has particular application to moose calf mortality studies where all individuals were not collared on the same day, and where censuring of radio-collared animals occurred.

We compared survival estimates generated in 1977 with those of 1978 from the 1947 burn. No significant difference ($x^2 = 0.085, 1$ df, $P = 0.771$) existed, so we combined these 2 years (Table 2). Similar comparisons between data from the 1969 burn collected in years 1982 and 1983 indicated no significant difference ($x^2 = 0.072, 1$ df, $P = 0.788$), so we combined these years (Table 2). Comparisons of study areas (1947 vs. 1969 burn) also revealed no significant difference ($x^2 = 0.380, 1$ df, $P = 0.538$) which suggested neonatal calf survival rates in the older 1947 burn were not different from the more productive 1969 burn. Combined data (Fig. 1) represented the mortality rates of neonatal moose calves for the Kenai Peninsula.

Moose hunting seasons on the Kenai Peninsula, in Unit 15A where we conducted our studies, traditionally opened on 1 September and extended until 20 September. Cow harvest occurred during the 60's and early 70's but was stopped in 1973 following a series of bad winters. Cow harvest by permit only was implemented in the 1969 burn in 1983 and ended in 1986. An average of 25 cows/year was harvested during this permit hunt. Bull moose hunting constituted the major human caused mortality in both burns. Bull harvest peaked in Unit 15A, in

Table 2. Comparison of survival distributions of radiotagged neonatal moose calves in the 1947 and 1969 burn areas on the Kenai Peninslua, Alaska.

Week	1947 Burn					1969 Burn				
	No. risk	No. deaths	No. censored	No. added	S (t)	No. risk	No. deaths	No. censored	No. added	S (t)
25 May-31 May	44	5	0	0	0.8864	73	12	0	0	0.8536
1 Jun-7 Jun	39	6	0	8	0.7500	61	9	0	2	0.7132
8 Jun-14 Jun	41	4	0	1	0.6768	54	7	1	0	0.6200
15 Jun-21 Jun	38	8	0	0	0.5343	46	5	0	0	0.5526
22 Jun-29 Jun	30	0	0	0	0.5343	41	2	1	0	0.5256
30 Jun-7 Jul	30	3	0	0	0.4809	38	0	0	0	0.5256
8 Jul-14 Jul	27	0	2	0	0.4809	38	3	0	0	0.5256
15 Jul-21 Jul	25	1	0	0	0.4617	35	0	1	0	0.4841
22 Jul-28 Jul	24	0	1	0	0.4617	34	0	0	0	0.4841
29 Jul-4 Aug	23	2	0	0	0.4215	34	0	0	0	0.4841
5 Aug-11 Aug	21	0	2	0	0.4215	34	0	0	0	0.4841

1964 at 573 (this corresponded to the peak in the population in the 1947 burn), declined steadily to a low of 101 in 1975, and then gradually increased to a peak of 351 in 1983 (this corresponded to the peak in the population of the 1969 burn). From 1983 to 1986, the harvest remained stable at 250-280 bulls/ season. The bull season was made more restrictive in 1987, and the harvest has declined to around 130 animals. Except for the heavy cow harvest in the early 70's, hunting probably did not greatly influenced the density or dynamics of the moose populations in either burn.
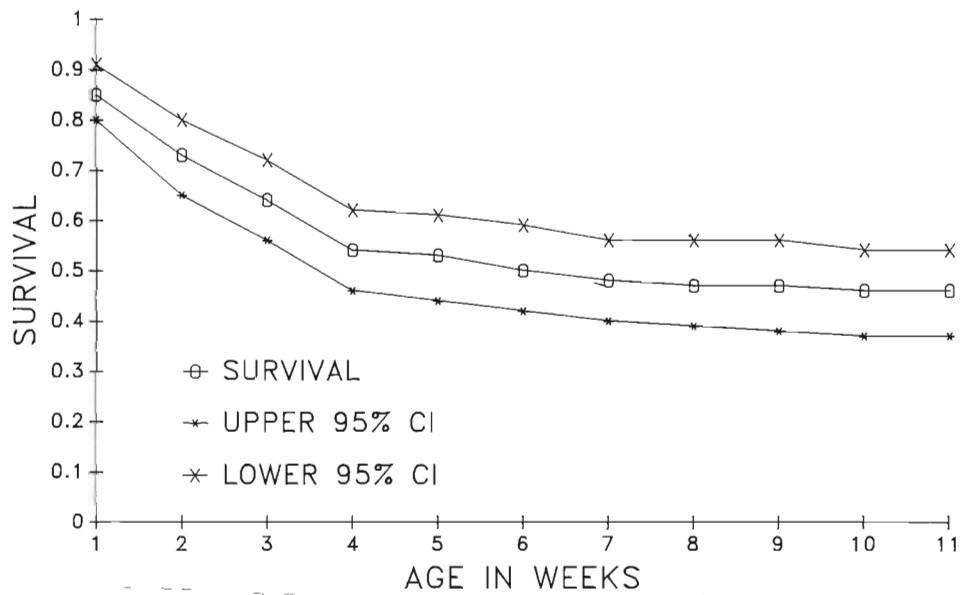

Fig. 1. The Kaplan-Meier survival function, modified for staggered entry animals, for neonatal moose calves tagged on the Kenai Peninsula, 1977-78, and 1982-83.

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Bears

Black bear demographics were monitored concurrent to the moose investigations (Schwartz and Franzmann, in press). Black bear densities in the two habitats were not different, with a mean of 205 and 258 bears/1000km² in the 1947 and 1969 burns, respectively. Sex ratio and age structure of the bear populations was similar, except the 1969 burn population contained more yearlings (Schwartz and Franzmann, in press). Reproductive success in the 1947 vs. the 1969 burn, measured as age of first litter production (5.8 vs. 4.6 yrs.) and interval between successful weaning of yearlings (2.4 vs. 2.0 yrs.) was significantly (P< 0.05) better for bears in the 1969 burn. Cub survival in the 1947 burn was significantly (P< 0.05) lower (0.74) than the 1969 burn (0.91). Body size of bears from the 1969 burn was greater (P< 0.05) than bears from the 1947 burn. Herbaceous food habits, movements, and home range sizes were similar between areas.

The only major difference detectable during these studies was the number of moose calves consumed per individual bear in the two burn subpopulations. Bears over 1 year of age in the 1947 burn ate 1.2 moose calves/season, while bears in the 1969 burn were estimated to eat 6.2 moose calves/season. The greater intake of high quality food was identified as the probable cause for the better reproductive performance and increased body size in bears from the 1969 burn (Schwartz and Franzmann, in press).

Brown bear numbers on the Kenai Peninsula have been estimated at approximately 200-250. Jacobs (1989) estimated that there were around 8800 km² of suitable range yielding an estimate of 23 - 28 brown bears/1000 km². Density did not differ between the two burns.

Wolves

Wolves were extirpated from the Kenai Peninsula about 1913, and reinvaded the Kenai Peninsula in the 1960's. Peterson *et al.* (1984) estimated wolf densities between 1977-82, at 11-20 wolves/1000km² in a study area which encompassed both the 1947 and 1969 burns. Densities of wolves within each burn were not estimated because packs did not live exclusively in either area, but wolf densities were probably similar (T. Spraker, pers. comm.). Recent estimates of wolf density in Unit 15A, which included both the 1947 and 1969 burns, ranged from 11-18 wolves/1000 km (ADF&G, unpubl. data).

Harvest by hunters and trappers was the primary cause of mortality in wolves on the Kenai Peninsula (Peterson *et al.* 1984). Harvest ranged from 15-42% of the fall population from 1976-81. Harvest in excess of 40% resulted in population declines, while harvest <35% resulted in increases (Peterson *et al.* 1984). Wolf harvest from 1982-85 ranged from 47%-63% of the estimated fall population (T. Spraker, pers. comm.). Density of wolves was likely limited by harvest from 1978-1985, but harvest has been below 18% since that time, and likely has not limited population size.

Moose were the single most important food source for wolves in winter and comprised a large portion (75% occurrence in scats) of their diet in summer (Peterson *et al.* 1984). During winter in the 1947 burn, 60% of the moose killed by wolves were calves, 33% adults >6, and 7% moose ages 1-6. In the 1969 burn, calf and adults >6 years old moose represented 32% and 40%, respectively, of the total moose killed, while moose aged 1-6 accounted for 28% (Peterson *et al.* 1984:Table 4).

DISCUSSION

Moose numbers have fluctuated with habitat quality and rates of predation. However, it was difficult to determine which agents (predation and/or habitat) influenced population change at any given time. It was our belief that predation and habitat quality operated in concert to control moose numbers. Mortality by either agent acted in a

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compensatory or noncompensatory fashion depending upon habitat quality, predator density, or winter weather (Gasaway *et al.* 1983, Crête 1987). For example, moose density in the 1947 burn increased following the burn in the absence of wolf predation; wolf density increased in the 70's concurrent with high rates of winter moose mortality (starvation).

Moose reproductive performance reflected range quality as demonstrated by the poor quality 1947 burn where only 7% of the cows produced twins, and 77% were observed without calves. In contrast was the high (70%) twinning rate and low (18%) proportion of cows observed without calves on the 1969 burn at its peak. Twinning rates remained relatively high (22-37%) in both habitats as forage quality declined.

Predation of neonates and adults occurred in both good quality and poor habitats. Survival rates of neonates in the 1947 and 1969 burns (Table 2, Fig. 1) were similar, with predation rate independent of moose density (Franzmann and Schwartz 1986). Predation by wolves was greater on calves in the 1947 burn than in the 1969 burn.

We propose that predators influence both the rate of change, and absolute densities of moose in various habitats on the Kenai Pen-insula, as in other areas in North America (Van Ballenberghe and Dart 1982, Gasaway *et al.* 1983, Messier and Crête 1985, Crete 1987). Following a burn on the Kenai Peninsula, the rate of increase of a moose population is likely retarded when predators are near carrying capacity. Similarly, the rate of decline following the peak in habitat quality, is faster and the absolute density of moose lower in habitats with significant predation (Fig. 2). In the absence of predation the opposite occurs. In Saskatchewan, removal of black bears from moose habitat promoted increased recruitment of calves into the fall population (Stewart *et al.* 1985). Recruitment of those calves into the population (i.e., as yearlings) depends on habitat quality and the relationship of moose density and vegetative carrying capacity. When moose populations are below carrying capacity and limited by predation, predator control can increase survival and recruitment (Gasaway *et al.* 1983). In Unit 15C on the Kenai Peninsula, where winter habitat is poor and the moose population is at carrying capacity. Here, predator numbers (both wolf and black bear) are low on the calving range and calf survival to fall is high. During severe winters virtually all calves starve, but even during average winters a moderate number of calves die of
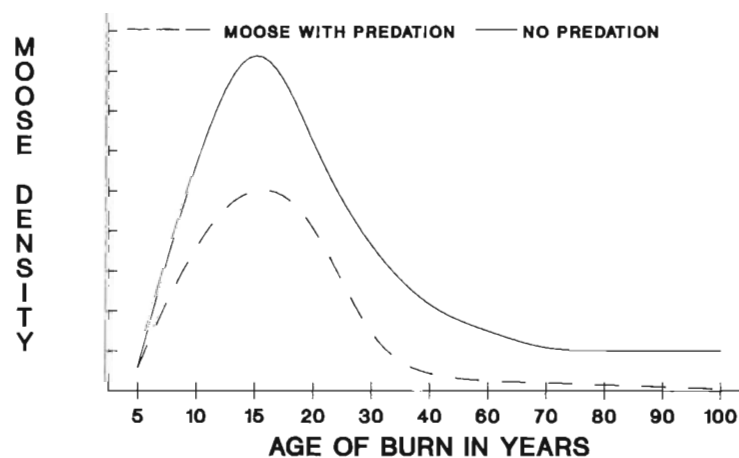

Fig. 2. Relationship of moose density and forest succession in the presence and absence of predators, following a burn on the Kenai Peninsula, Alaska.

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malnutrition (D. Holdermann, pers. comm.). This suggests that predator control in poor habitats will not result in large increases in recruitment of calves into the population as yearlings on the Kenai Peninsula.

Trends in moose population demographics on the Kenai Peninsula allow managers to assess past and potential actions. Management objectives dictate which action is most appropriate at any given time. If increasing moose numbers is a management objective, removal of predators in early seral forests, should result in greater intrinsic rates of increase than would occur if predators were present. Moose calves "spared" from bear or wolf predation, would likely survive the winter on quality habitat. In older seral stands habitat quality ultimately limits moose at lower densities. Predator reduction would raise moose densities only by a relatively small amount in these areas (Fig. 2). Thus, the first priority in raising moose density in older seral stands should be manipulating habitat.

If maintenance of moderate to high-density predator and moose populations is the primary objective on the Kenai lowlands, sustained habitat enhancement is the most appropriate management action while moose remain abundant. The 1969 burn sustantiated the value of high quality habitat. Moose increased to high densities in the 1969 burn when browse was excellent (late-70's to mid-80's). During the same period, predators were abundant, although wolf and black bear populations were at times limited by harvest (Peterson *et al.* 1984, Schwartz and Franzmann in press). The increase in moose numbers resulted from high moose reproductive rates (Franzmann and Schwartz 1985), low adult mortality (Bangs *et al.* 1989), and likely from initial shifts in home ranges of moose from the adjacent high density 1947 burn area (Peek 1974, Gasaway *et al.* 1989).

Theberge and Gauthier (1985) discussed the relationship of wolves and ungulates and developed a systematic set of questions that determine if wolves limit their ungulate prey. A similar approach would also be applicable to black bears on the Kenai Peninsula. Using their system, black bear and/or wolf control would be ruled out when the moose population was increasing, and only implemented on a declining population where (1) habitat was not limiting, (2) winter mortality was not a controlling variable, and (3) human harvest did not represent a significant proportion of the potential herd increase. Such an example was presented and discussed by Gasaway *et al.* (1983). In their area, moose populations had been depressed below vegetative carrying capacity by severe winters, heavy wolf predation, and overharvest by hunters. Wolf control resulted in significant increases in moose density.

Predation by bears on neonatal calves was the most important factor limiting rate of population growth on the Kenai. We believe that control of black bears would increase moose densities most rapidly and to greater levels if implemented in early seral stages of forest succession. Here, habitat quality is increasing, and reduced neonatal mortality would result in increased recruitment and rapid population growth.

Little was known about moose density on the Kenai Peninsula prior to the 1947 burn. Large wildfires in 1871 and 1910 created favorable habitat on the Kenai and moose density likely ranged from 0.2 to 0.6 moose/km² (Spencer and Hakala 1964). Moose therefore colonized the 1947 burn from a moderately low density population, but in the absence of wolves. Moose were abundant on the Kenai at the time of the 1969 burn as a result of the high quality habitat produced by the large 1947 fire and the absence of wolves until the early 1960's. Moose colonized the 1969 burn from a moderately dense population. Wolves were not abundant on the northern Kenai lowlands until the mid-70's and were likely limited by harvest until 1985.

Gasaway *et al.* (1983), VanBallenberghe (1987), and Messier and Crête (1985) con-

cluded that moose populations depressed to low densities infrequently escape control by predators. Once a moose population declines to low densities over a large area, habitat enhancement with fire may not be adequate to allow growth to high densities when both bears and wolves are near carrying capacity.

No large burns have occurred on the Kenai Peninsula since 1969. Habitat within the 1969 burn has deteriorated and the 1947 burn only supports a remnant moose population. Management to ensure a high density moose population and healthy managed predator populations dictates immediate habitat enhancement before the moose population declines to low densities in the 1969 burn. This is the last high density area on the Kenai Pensinsula.

ACKNOWLEDGEMENTS

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