

MODELING A SOUTH-CENTRAL ALASKAN MOOSE POPULATION

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Abstract: A moose (Alces alces) population model was developed which utilizes parameters routinely measured by wildlife managers in Alaska. Information on the distribution, abundance, sex, and age characteristics of moose populations have been collected annually for harvest management since the early 1950's. Since 1975, research on the population status and dynamics of moose and three of its important predators, brown bear (Ursus arctos), black bear (Ursus americanus) and gray wolf (Canis lupus) has been in progress. Much of the research focused on quantifying predator-prey relationships and identifying potential impacts of hydroelectric development on moose and other wildlife. The availability of such information presented a unique opportunity to examine the structure and dynamics of the moose population occupying the upper and middle Susitna River Basin of south-central Alaska. The model, required information, and several examples of predicted future fluctuations are presented.

The feasibility of using the Susitna River as a source of hydroelectric power for south-central Alaska has been the subject of several studies since 1948 (Taylor and Ballard 1979). Proposals have ranged from two to twelve dam systems, but recently the two dam system was considered the most feasible. Preliminary wildlife studies were initiated in 1975 and intensive studies of moose were initiated in 1980 (Ballard et al. 1982b).

As part of the process for evaluating the potential impacts of the Susitna project on wildlife, population models for several species including moose, were developed and used for predicting the results of various development scenarios (R. Everitt et al. unpub. data). The moose population model was extremely general and contained a number of assumptions which did not appear applicable to moose in the Susitna area. Consequently, we developed a moose population model which was tailored to fit the project area and the types of data collected during this and other studies within Game Management Unit 13 (GMU 13) (Taylor and Ballard 1979; Ballard and Taylor 1980; Ballard et al. 1980, 1981ab, 1982ab, 1983; Miller and Ballard 1982ab). The purpose of this report is to describe how the model works, explain the basis for the important variables, and present a few predictions to illustrate the benefits and shortcomings of the approach.

STUDY AREA

Moose were studied in the upper and middle Susitna River Basin of southcentral Alaska where two impoundments have been proposed

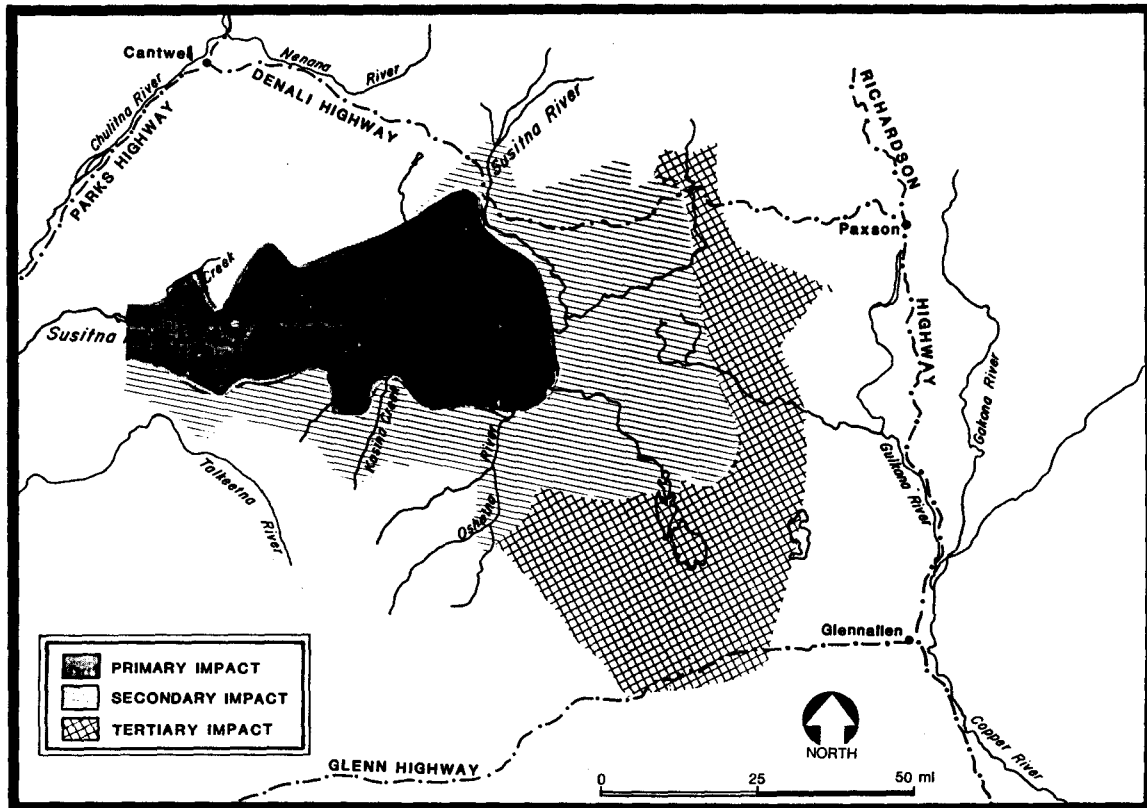


Figure 1. Boundaries of primary, secondary and tertiary zones of impact for the Susitna Hydroelectric Project based upon movements of radio-collared moose from 1976-1982 in Game Management Unit 13 of southcentral Alaska.

(Taylor and Ballard 1979; Ballard et al. 1982b). Our study area (Fig. 1) included the suspected year-round ranges of moose subpopulations that may regularly encounter the two proposed impoundments. Moose sex-age composition counts, winter distribution surveys and preliminary moose movements studies (Ballard and Taylor 1980; Ballard and Gardner 1980; Ballard et al. 1982ab) were used to delineate the area. Vegetation, topography and general climate of the area have been previously described by Skoog (1968), Bishop and Rausch (1974), Ballard and Taylor (1980) and Ballard et al. (1983, 1985).

DESCRIPTION OF MOOSE POPULATION MODEL AND ITS VARIABLES

Components of the model have been divided into a series of events which occur through the annual cycle of a moose population. These events are arranged in such a manner that each natality and mortality component can be changed to meet any set of assumptions (Fig. 2). Population estimates are calculated for each year at calving, and subsequent mortalities act on the population and cause it to decline until parturition occurs again the following year. Descriptions and background of inputs into the various events follow:

Initial Population Size

The starting population size for this simulation was estimated from the following formula:

$$X = \frac{(A) (B)}{C}$$

C

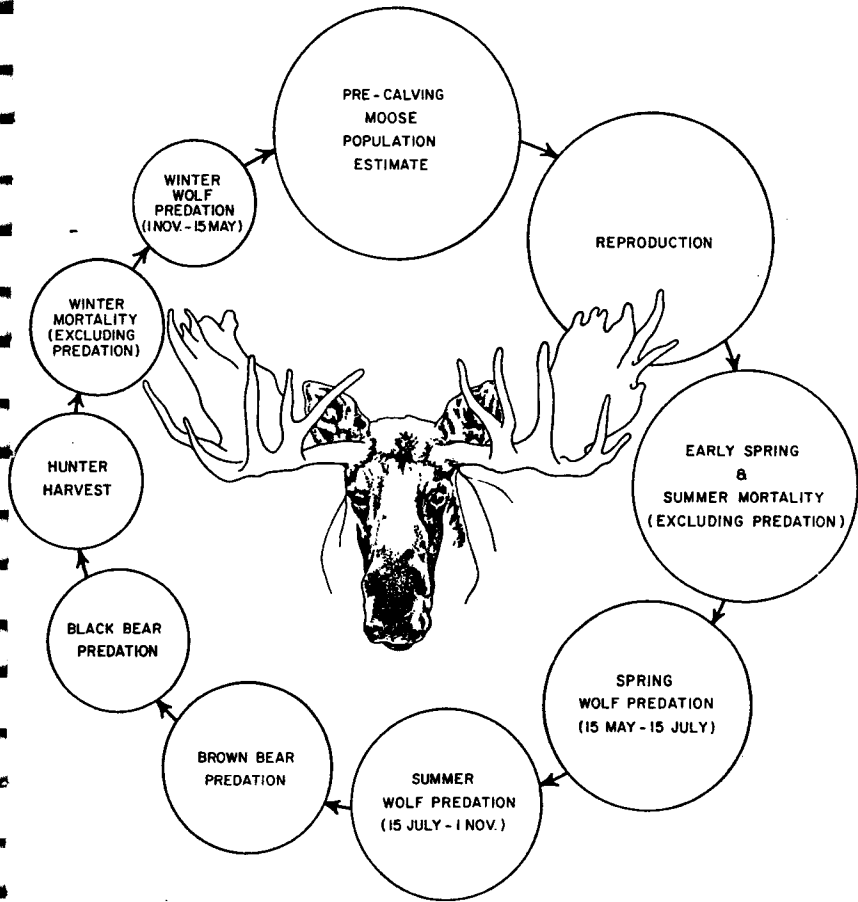


Figure 2.

Timing and sequence of natality and mortality factors used in moose population models for GMU-13 and Susitna River Study Area of southcentral Alaska, 1976-82.

Where

A = the number of moose observed per hour during the 1975 autumn composition counts,

B = 1980 moose population estimate, and

C = number of moose observed per hour during 1980 autumn composition counts.

Autumn composition counts in south-central Alaska are typified by low search intensity transects conducted from fixed-wing aircraft designed primarily to gather sex and age composition information, not total population size (see Gasaway et al. 1981 for descriptions of types of surveys). In this specific case, we began the model in 1975 when the GMU-13 moose population declined to low levels and intense moose and predator population studies were initiated. Moose population estimates derived from censuses conducted in 1980 and 1983 were used as a check for the population size generated by the model.

We assumed that for the model to be valid, the fall 1980 and 1983 population estimates derived from the model should fall within the 90% confidence intervals of both census estimates. A number of other methods can also be used for estimating not only initial population size but many of the other variables to be described in subsequent sections of this paper. Our specific estimates are offered as one method of determining model inputs.

Event 1-Reproduction and Sex and Age Structure

The sex ratio at birth was assumed to be 50:50 while the sex ratio of yearlings and adults was determined by the previous year's

estimate of reproduction and mortality. In the case of the starting population (year 1), the sex ratio was determined by the fall moose composition count and was calculated to correspond with population size at calving. All initial age classifications were directly extrapolated from the count data except for percent calves in the herd and percent yearlings. Percent calves in the herd was adjusted upward by 5% because lone cow-calf groups are less likely to be observed during low intensity surveys compared with other types of aggregations (Gasaway et al. 1981 and Ballard et al. 1982a).

Preliminary simulation runs suggested that our estimates of yearlings based on antler identifications during composition counts were low because this age group became extinct after just a few years. Estimates of the number of yearling bulls in the herd were originally based on the number of males with spike, forked, and small palmated antlers observed during composition counts added to the reported human harvest that year. Total (males and females) number of yearlings in the herd was then estimated by doubling the estimated number of yearling males. We subjectively assumed yearling sex ratios were equal. During capture efforts, we observed that some yearling males only had knobs (2-5 cm) for antlers. It was likely that these individuals were classified as adult cows during the surveys. To allow the initial model moose population to advance into subsequent years, our estimates of numbers of yearlings in 1975 had to be adjusted upward. This resulted in doubling our initial estimate of the number of yearlings in the herd based on composition counts.

Pregnancy rates of cow moose were determined from rectal palpation of adults captured in 1976, 1977 and 1980 (Ballard and Taylor 1980 and Ballard et al. 1982ab). Although some minor variations in rates were noted in subsequent samples, we assumed that 88% of sexually mature cows (> 2 years of age) were pregnant each year.

Estimates of moose productivity were determined during calf collaring programs conducted from 1977 through 1979 (Ballard et al. 1980, 1981a). Based on an 88% pregnancy rate and an observed average twinning rate of 35% (19-52%, 1977-79), productivity was estimated at 1.19 calves per adult cow. We had few data on productivity of 2-year-olds (2 of 5 pregnant) so we relied on an estimate of 0.29 calves per cow provided by Blood (1974). For our model we assumed that productivity remained constant each year. We realize that this was probably not the case and that it can vary based on the severity of the preceding winter or a host of other factors (Ballard et al. 1980). However, we had no way of providing an accurate annual estimate.

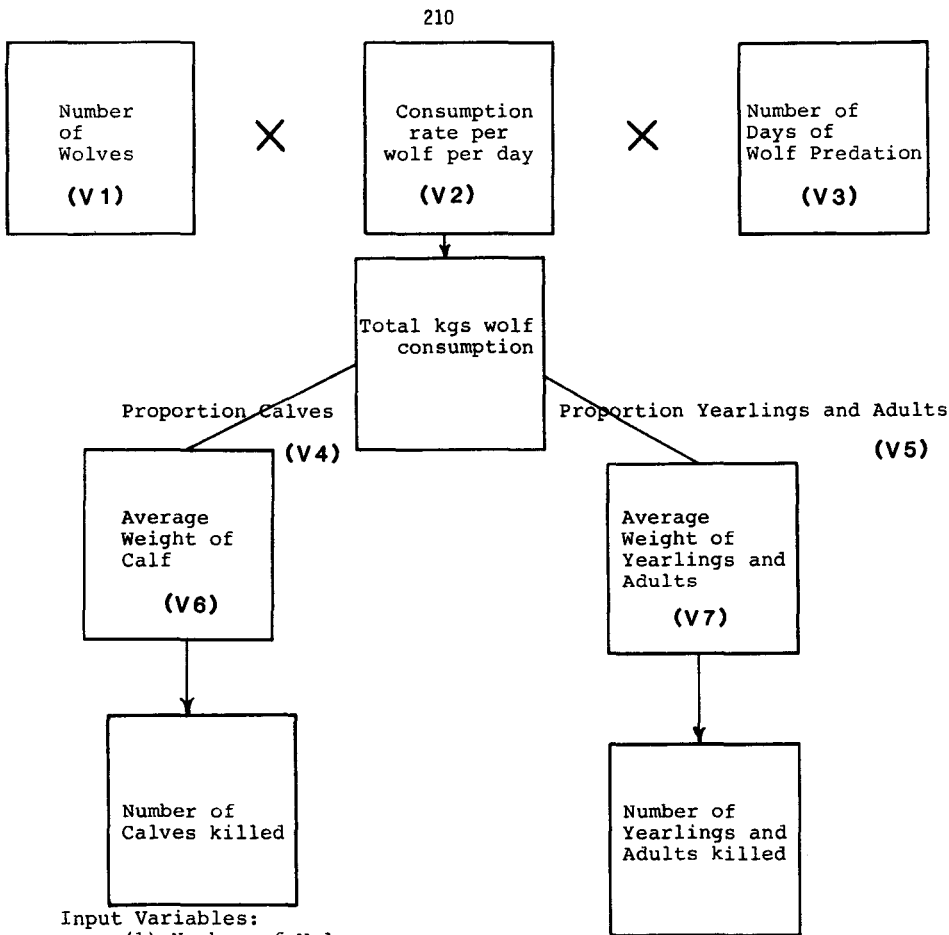
Event 2-Spring and Early Summer Mortality (except predation)

Following birth, both calf and adult mortality estimates were subtracted from the population. Immediately after birth, 6% of the calves were assumed to die from natural factors other than predation (Ballard et al. 1981a). These deaths included stillbirths, drownings, cows stepping on their calves, pneumonia, and other accidents. We assumed no losses among adults or yearlings during this time period.

Events 3, 4, and 9-Wolf Predation

Estimates of annual moose mortality due to wolf predation were divided into 3 time periods to correspond with changes in the wolf population and its diet. Variations in pup production, human harvests, natural mortality, and changes in diet are all factors which can influence the magnitude of wolf predation on moose. The time periods were: #1) 15 May-15 July (Event 3); #2) 16 July-31 October (Event 4); and #3) 1 November-14 May (Event 9) (Fig. 3). Period #1 encompassed the wolf denning period. Because pups are small and dependent on the alpha female for nourishment, they were excluded from moose consumption estimates during this time period. Period #2 encompassed the post-denning period and represents the highest level of the wolf population (adults plus pups prior to hunting and trapping season) during the year. For this time period we assumed that pups had similar food requirements as adults. Period #3 encompassed both the wolf populations highest (before hunting and trapping mortality) and lowest (after hunting and trapping mortality) numbers during the year. Consequently, we used the mid-point between the two population estimates to provide an average number of wolves during winter. Estimates of wolf population numbers were from Ballard et al. (1981b, 1982b, 1983 and unpub. data).

Estimates of percent biomass of moose consumed by wolves for Period 1 were based entirely on scat analyses according to methods described by Floyd et al. (1978). The analyses indicated that 91% of the biomass of prey consumed by wolves from 15 May-15 July was composed of ungulates (calf - 35%, adult - 47%).



Input Variables:

- (1) Number of Wolves
- (2) Consumption Rate of Wolves
- (3) Number of Days of Wolf Predation
- (4) Proportion of Wolf Kill Consisting of Calves
- (5) Proportion of Wolf Kill Consisting of Yearlings and Adults
- (6) Average Weight of Calves
- (7) Average Weight of Yearlings and Adults

Fig. 3. Schematic diagram of inputs and outputs of Events 3, 4 and 9 (wolf predation) for the moose population model.

Estimates of percent biomass of calf and adult moose consumed by wolves during Periods 2 (16 July-31 October) and 3 (1 November-14 May) were determined from kills observed while monitoring radio-marked wolf packs. The estimates for the study were divided into 2 time periods to correspond with the increased importance of caribou as wolf prey from 1979-1981. From 1975-1978 we estimated that from 16 July-31 October (Period 2) calf and adult moose composed 12% and 78%, respectively, of the prey biomass, while from 1 November-14 May (Period 3) calf and adult moose composed 18% and 73%, respectively, of the biomass. During Period 2 from 1979-1981, percent biomass of adult moose declined to 73%, while the percent of calf moose remained constant. Percent biomass declined to 17% and 68% calf and adult moose, respectively, during Period 3 from 1979-1981.

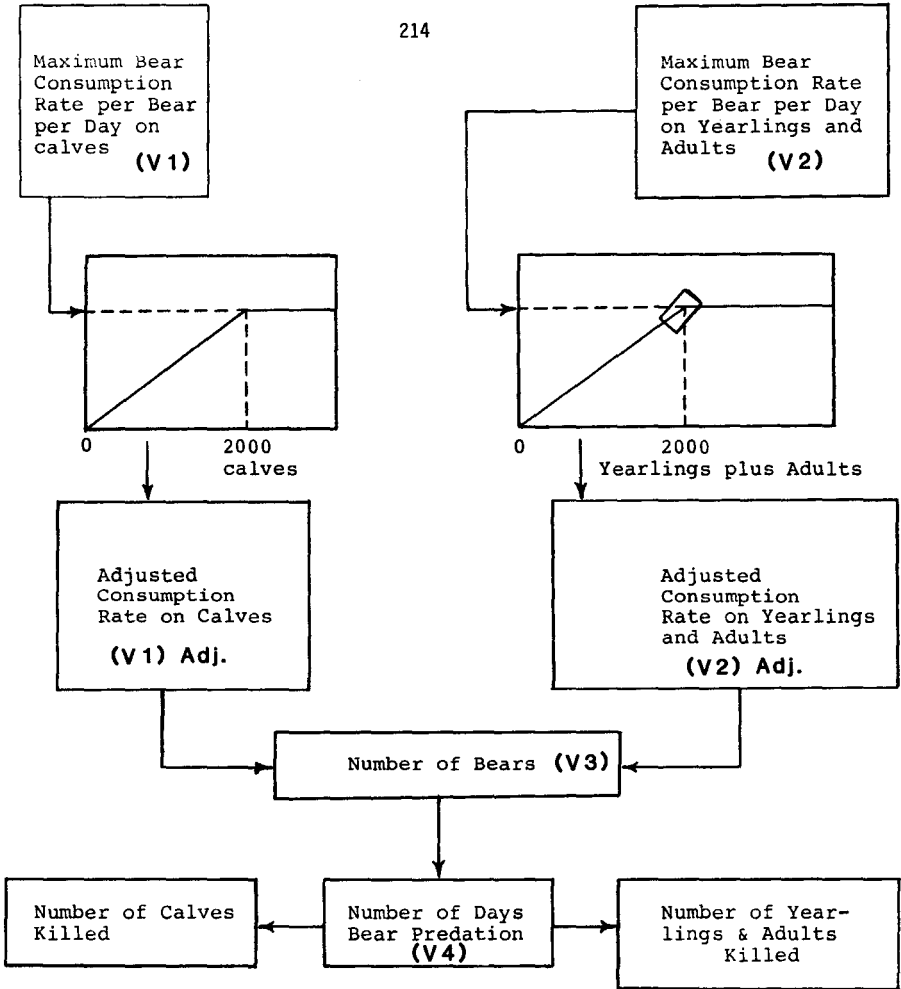
The estimated biomass of calf and adult moose killed by wolves during each time period per year was extrapolated from wolf population estimates for each period multiplied by the numbers of days in each period multiplied by the estimates of daily consumption rates. It was assumed that wolves consumed 7.1 kgs of prey/wolf/day during all 3 time periods (Ballard et al. unpub. data). Estimates of percent biomass by prey species were then multiplied to derive estimated biomass. For each time period, the number of moose killed was estimated by dividing the average weight of each age class for each period derived from literature and field studies into the estimated biomass.

Predation rates by brown bear on adult and calf moose were derived from observations of kills while monitoring 23 adult radio-collared bears (Ballard et al. 1981). Most observations were made between 15 May-15 July, the period of greatest brown bear predation on moose (Ballard et al. 1981). Estimates of adult moose mortality due to brown bear predation were calculated by assuming that we observed all adult moose killed by the 23 radioed bears between 15 May to 15 July, and after this time no adult moose were killed. Observed rates of calf moose killed were 1 calf/9.4 observation days/adult bear. These kill rates were extrapolated to the adult bear population estimates for the Susitna Study Area (Miller and Ballard 1982ab; Miller et al 1986). We estimated the bear population in the area where moose populations were modeled to be 117 adult bears. No data were available concerning annual fluctuations in bear numbers. For these simulations, we assumed a stable population except during 1979 when bear numbers were reduced in part of the area during an experimental bear transplant program (Ballard et al. 1982a; Miller and Ballard 1982ab).

Preliminary simulation runs indicated that kill rates on calf moose were too high because the moose population quickly became extinct due to bear predation alone. It seemed likely that estimates of bear kill rates on calf moose would be underestimated even from daily relocation flights because many bears remained on calf kills less than 24 hours and, in some cases, less than a half-hour (Ballard and Miller unpub. data). Subsequent studies of predation rates also suggest that our initial estimates of bear predation may have been too high (Ballard et al. in prep.). Therefore, we modified the

estimates of calf kill rates by assuming that the magnitude of bear predation was dependent on the density of moose calves. We calculated that bears preyed on about 50% of the estimated number of calves produced during 1977 and 1978 within the upper Susitna River Study Area. Based on an estimated 2000 calves produced, we estimated that bears preyed on calves at a rate of 0.14 calves/day/adult bear. Adult moose were estimated to have been preyed on at a rate of 0.02 adults/day/adult bear. In both cases it was assumed predation occurred over a 60-day period. Although we did not know if there was a relationship between calf moose density and rate of kill by brown bears, we assumed that there was a relationship. When less than 2,000 calves were produced, we subjectively assumed a linear relationship existed between calves killed by bears and calves produced (Fig. 4). At higher levels of calf production we assumed predation rates remained constant. During 1979 we reduced brown bear predation on calf moose by transplanting 47 bears from a portion of the area for a 2-month period in late spring and summer 1979. This reduction in bear numbers greatly increased moose calf survival that year (Ballard et al. 1980, 1982a, and unpub. data). To model this improvement in calf survival for 1979 we quantified the percent increase in calf survival due to the program, and then proportionately reduced individual bear predation rates from 0.14 to 0.10 calves/bear/day.

Preliminary simulation runs also suggested that our estimates of bear predation on adult moose were too high because the moose population quickly became extinct. Our original estimate of predation rates resulted in more than 20% adult moose mortality.



Input Variables:

- (1) Maximum Consumption Rate on Calves
- (2) Maximum Consumption Rate on Yearlings and Adults
- (3) Number of Bears
- (4) Number of Days of Bear Consumption

Fig. 4. Schematic diagram of inputs and outputs of Events 5 and 6 (brown bear and black bear predation) for the moose population model.

Predation rates on adult moose were modified similarly to those for calf moose in that we subjectively assumed there was a relationship between rates of predation and moose density. When the study area moose population exceeded 2,000 adults we assumed predation rates remained constant at 0.02 adult moose/day/adult bear. At lower numbers, a linear relationship between daily predation rates and moose numbers was assumed (Fig. 4). Under these assumptions adult moose mortality was still high with bears being responsible for 7% adult moose mortality.

Event 6-Black Bear Predation

We estimated that 111 black bears were in the study area (S.D. Miller unpub. data). Data on predation rates on moose by black bears are scarce. Our original estimates based on a small sample of radio-collared bears were 0.021 and 0.012 moose/day/bear on calf and adult moose, respectively. Our initial estimates of either the numbers of bear or their predation rates were too high because the moose population quickly declined. Because data from other areas in North America indicate that black bears can be a significant source of neonatal ungulate mortality (Ballard and Larsen 1986), we subjectively lowered black bear predation rates to 0.003 and 0.000 moose/day/bear for calf and adult moose, respectively. Kill estimates were entered into the model in the same fashion as that described for brown bear (Fig. 4).

Event 7-Hunter Harvest

Annual hunting mortality, which during this study affected bulls only, was determined for each year of the study from mandatory harvest reports. Harvest reports from successful and unsuccessful moose hunters are a regulatory requirement in GMU-13. However, enforcement is very difficult and compliance is less than 100%. To encourage moose hunters to report results of their hunt, reminder letters are sent to all those who obtained a harvest ticket but did not report hunt results. Because no reminder letters were sent in 1980, the harvest for that year was determined by comparing the number of returned reports with returns in prior years, and extrapolating the additional harvest.

Antler measurements on harvest reports since 1978 provided a basis for a rough estimate of the number of yearlings killed, although some measurements were undoubtedly false. Antler measurements <76 cm were considered to be yearlings or younger. Beginning in 1980, only bulls with antler spreads of ≥ 91 cm or at least 3 brow tines could be legally harvested. For the 1978 and 1979 hunting seasons, 55% of the measured moose had antler measurements <91 cm. Therefore, we assumed that half of the human harvest each year was composed of yearling bulls.

We subjectively estimated crippling loss and unreported harvest at 15% of the estimated harvest. When future moose populations are predicted with the model, we arbitrarily assume human harvests will equal 33% of the yearling and adult bulls present at the beginning of the 20 day hunting season. The latter harvest approximates the number of bulls currently killed.

Event 8-Winter Mortality (excluding predation)

Estimates of winter mortality were subtracted from the estimated number of moose present each November following the hunting season. The magnitude of winter mortality, usually by starvation, was initially estimated from radio-collared moose as described by Hayne (1978) and Gasaway et al. (1983). Winter mortality data for these moose population simulations were derived for calf moose for the period 1977-1981, for yearling moose from 1979-1982, and for adult moose from 1976-1982. Winter mortality was calculated as follows (from Gasaway et al. 1983):

$$\text{Percent mortality} = \frac{a}{b}$$

where

a = number of winter mortalities of radio-collared moose, and

b = estimated number of collared animal months.

b was estimated as: (C) (D)

$$b = \frac{\text{---}}{c}$$

where: C = mean # months radio-collars transmitting
(excluding dead moose),

D = total # radio-collared moose (including
dead moose), and
 e = time interval for annual mortality.

Based on relative survival rates of radio-collared moose we classified winters as moderate, severe and very severe. Most of the estimates of winter mortality by sex and age class for moderate and severe winters were based on radio-collared moose during 1976 through 1982 from equations described above. However, estimates of mortality during very severe winters were based on our best guess since we had no literature or previous experience with winter severity equal or exceeding the 1971-72 level. Based on historical snowfall data, severe winters have occurred on 3 occasions during the past 22 years and very severe winters once. For simulation runs a table of random numbers was used to predict the occurrence of winter conditions over consecutive 22 year periods.

During mild winters calves suffered mortality rates of about 6.0% (winters 1975-76 through 1977-78 and 1979-80 through 1983-84)(Table 1). Winter 1978-79 was considered relatively severe (Eide and Ballard 1982) with high rates of calf mortality during late winter. These higher rates of winter mortality were used for simulation runs when relatively severe winters had occurred or were predicted. During the one severe winter that moose mortality was measured, only calf moose died. No estimates of yearling mortality during such conditions were available so we used rates obtained during moderate winters; 2.4% and 6.0% for yearling females and males, respectively (Table 1).

Table 1. Estimates of winter mortality by sex and age class determined for radio-collared moose in GMU-13 of southcentral Alaska, 1977-1982.

Winter Severity	Age	Sex	
		Males	Females
Moderate	Calves	0.060	0.060
	Yearlings	0.060	0.024
	Adults	0.072	0.036
Severe	Calves	0.571	0.144
	Yearlings	0.100	0.024
	Adults	0.144	0.036
Very Severe ¹	Calves	0.900	0.250
	Yearlings	0.350	0.087
	Adults	0.200	0.072

¹Rates of mortality during very severe winter were subjectively estimated.

Annual winter mortality rates for adult cows varied from 0 to 5.6% during 1976 through 1982 (Table 1). The overall winter mortality rate was estimated to be 3.6% and this was used for each year of the simulation unless otherwise stated. Apparently the winter of 1978-79 was severe enough to cause significant mortality in calves but not for adults.

Because male ungulates typically have higher rates of natural mortality than females (Wallmo 1981), we assumed that during mild winters adult bull moose suffered rates of winter mortality (7.2%)

twice that of adult cows (3.6%) (Table 1). During relatively severe winters we also assumed adult bull mortality was twice as great as during winters of moderate severity, and that adult cow mortality remained about the same. Yearling bull mortality during severe winters was subjectively estimated at 10%. Estimates of adult and yearling mortality during very severe winters are poorly documented and deserve study effort. Estimates of winter mortality were subtracted from the posthunt moose population similar to methods described for early spring and summer mortality.

PREDICTION OF SUSITNA RIVER MOOSE POPULATION TRENDS

Prior to the early 1950's, few data were available concerning the abundance and distribution of moose. However, they were apparently not abundant at the turn of the century but the population increased and peaked about 1960 (Bishop and Rausch 1974). Moose were thought to have increased during this latter period in response to reduced predator populations, favorable range conditions (created by frequent wildfire), mild winters, and low human harvest pressure.

After 1960 the moose population began to decline. Severe winters in 1961-62, 1965-66, and 1971-72 resulted in high moose mortality. A federal predator control program from 1948 to 1953 reduced numbers of wolves and probably bears to low levels. After 1960 severe winters apparently caused the moose population to decline. During this period predator populations were increasing and fire prevention policies by federal and state agencies halted wild fires that had created favorable range conditions in the past. Therefore, range quality might have been declining as well (Bishop and Rausch

1974; McIlroy 1974). Human harvests also increased during the 1960's. The combined effects of all of these factors probably caused the moose population to decline, even during mild winters. Calf recruitment reached a record low by 1975.

The moose population increased after 1975 in response to reduced numbers of predators and generally mild winters. Wolf numbers were reduced during a State wolf control program in portions of the Susitna hydroelectric study area during 1976 through 1978. Brown bear numbers were also temporarily reduced in part of the area by an experimental transplant in 1979. After State wolf control ceased in 1978, wolf numbers were controlled by public hunting and trapping. Human harvests of moose, which had always been limited to bull only hunting in the study area, were further restricted in 1980 when only bulls with antler spreads ≥ 36 inches or 3 brow tines on one side were allowed protecting calves and most 1 and 2 year old bulls. During 1983 only bulls with spike or forked antlers (mostly small yearlings) could be legally harvested. After 1983 the 36-inch regulation was in effect. Winters were generally mild or moderate with the exception of 1978-79, and starvation rates were relatively low. The combined effect of all of these factors was that the moose population increased between 1975 and 1985.

The total numbers of moose present each fall in the Susitna hydroelectric moose study area under preproject conditions as predicted from modeling for the period from 1975 through 2022 are illustrated in Figure 5. Year 12 is equivalent to 1986 and for all subsequent runs we assumed the project became operational (post-construction) during year 12 and that the life of the project

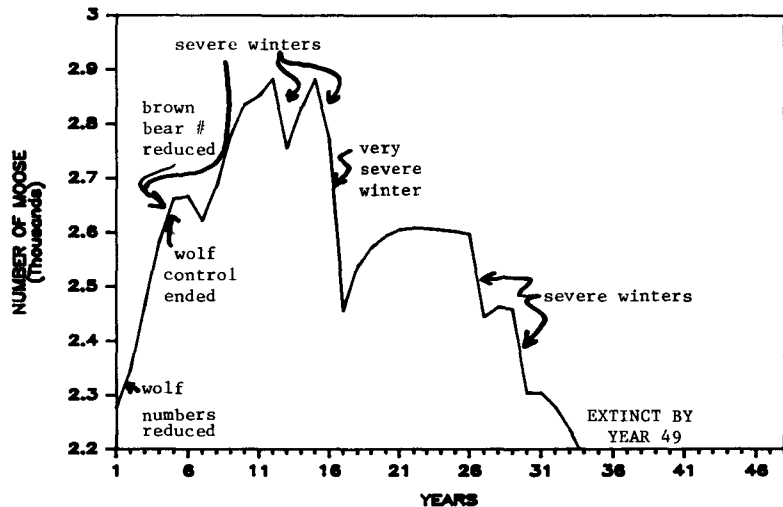


Fig. 5. Past and predicted moose population numbers in the Susitna River Study Area as determined from population modeling. See text for assumptions and input variables.

was 55 years. From year 1 (1975) through year 11 (1985) the model was adjusted to fit existing population data all of which indicates an increasing population trend. All inputs were based on current studies and most were made on the basis of annual surveys and estimates. However, following year 11 several major assumptions were made to allow prediction of moose population trends beyond the existing data base. These assumptions are briefly listed to insure that readers understand the basis for the model's predictions.

Major assumptions for the model's predictions are as follows:

1. Productivity was held constant each year.
2. Early spring and summer calf mortality from accidents was held constant.
3. Wolf numbers from 1975 through 1985 for each event were estimated from surveys and radio-collared packs. After year 11 wolf numbers were held constant in subsequent years at year 1 levels (1975-prior to wolf control).
4. Numbers of adult brown bears were held constant at 117 except during 1979 when brown bear numbers were reduced by transplant.
5. Black bear numbers were held constant at 111.
6. Reported hunter harvests were used from year 1 through year 11. After year 11 we assumed hunters killed 33% of the adult bulls and 33% of the yearling bulls present in the population just prior to the hunting season.
7. Estimates of numbers of moose starving to death each year were estimated by a combination of available data and subjective evaluation (Table 1).

Without the proposed project the model predicts that the moose population would decline to extinction by year 49 (Fig. 5). The predicted sequence of severe winters in addition to losses from predation produce a scenario where mortality exceeds natality at the lower moose densities. A different random selection of severe winters probably would have produced a different projection. However, this scenario illustrates that, although the moose population has grown over the past decade, changes in winter severity can cause the population to decline even if we assume predation and other mortality factors remain stable. Existing information concerning predation by bears and wolves suggests that once the decline has occurred, predation alone may prevent population recovery (Gasaway et al. 1983; Ballard and Larsen 1986). There does not appear to be any fast acting feedback mechanism between moose and predator populations, particularly for bears which are not dependent on predation for survival (op. cit.). By year 30, after 2 relatively severe winters, moose densities are too low to allow the moose population to escape projected levels of predation and other natural mortality. Moose densities at year 30 are nearly identical to those at year 1 (1975) when the moose population actually reached a record low level. If the moose population actually declined as projected by modeling, the most likely management action is that a predator control program would be proposed to reverse the decline.

Instead of allowing the moose population to decline in year 30 (Fig. 5), we assumed the Department would initiate a predator removal program to increase moose recruitment and halt the population decline as depicted in Figure 6. Because bears have a much lower rate of

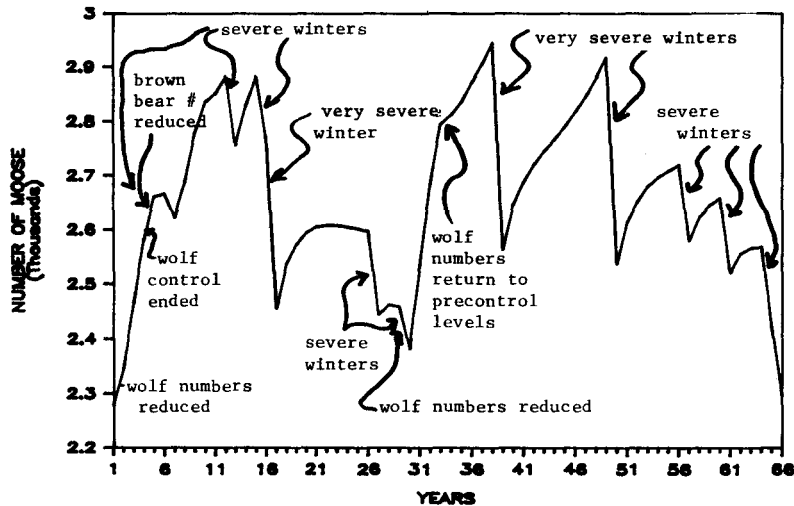


Fig. 6. Past and predicted moose population numbers in the Susitna River Study Area as determined from population modeling. See text for assumptions and input variables.

reproduction than wolves, we also assumed that wolf numbers rather than bear numbers would be controlled. We assumed that in year 30 a predator reduction program would reduce wolf numbers to the same densities which existed in years 2 through 4. Thereafter, we assumed that wolf numbers once again returned to precontrol densities. This reduction was sufficient to allow the moose population to grow (Fig. 6). It allowed moose numbers to increase to high enough densities so that the population was able to rebound from severe winters in future years. However, by year 66 moose densities were once again sufficiently low that some management action would likely be necessary if the moose population was to again recover from severe winters. We used the moose population run illustrated in figure 6 as our baseline population for examining various levels of impact due to the project.

PREDICTION OF PROJECT IMPACTS BASED UPON POPULATION MODELING

Several impact scenarios provide a general idea of what might happen to the moose population as a result of hydroelectric development. The purpose of these runs is not to quantify losses but to indicate the general trend the moose population might take if one or all of the predicted changes were to occur. A detailed account of the potential impacts of hydroelectric development on moose was provided by Ballard and Whitman (1987). The model does not consider interaction among potential impacts nor does it consider compensatory effects. All of the runs predict that the area's moose population will become extinct during the life of the project. This is because we have made no attempt to alter any factors which remain constant during the simulations. For example, except during years 30 through

32 (Fig. 6) when we forecast wolf control, we kept numbers of predators constant. When the moose population begins to decline in response to the project, initiation of predator control may avert a drastic decline or at least slow the rate of decline. However, for any management action to succeed it assumes that critical habitats remain unchanged. Loss of critical habitat through inundation and avoidance may negate that assumption. That all of the runs suggest that the population will decline indicates the project is likely to have serious implications for the management and uses of moose in the future. The exact magnitude of the losses can not be accurately predicted.

Scenario # 1

Annual productivity of adult cow moose was predicted to be reduced as a result of the project by 5% from an average of 1.19 calves per cow to 1.13 calves per cow. The model suggests that following a severe and a very severe winter, the reduced level of productivity is not sufficient to allow the moose population to recover during intervening years of mild winters (Fig. 7). The population theoretically becomes extinct by year 38.

Scenario # 2

Adult moose are expected to be in poorer physical condition following winter as a result of the project. This will result in less viable calves being produced. Calves will suffer higher rates of stillbirth and accidental mortality than under preproject conditions. We speculated that if the project were completed, calf mortality would

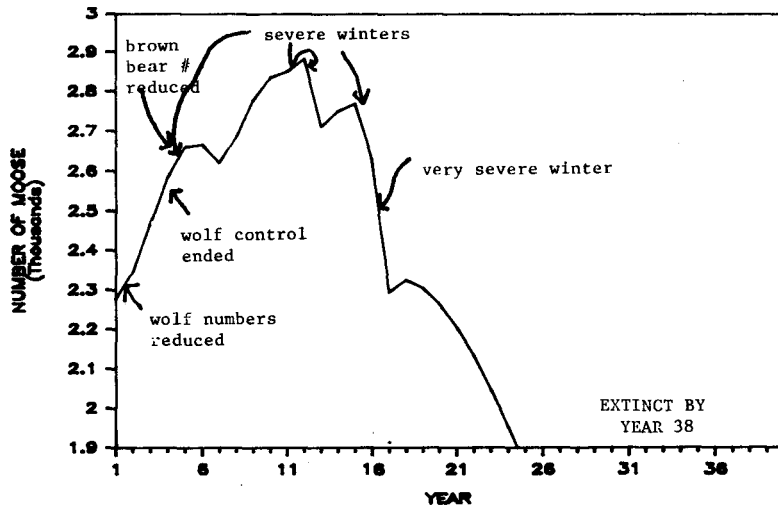


Fig. 7. Past and predicted moose population numbers in the Susitna River Study Area as determined from population modeling. Productivity rates decreased by 5% in year 12 from 1.19 calves/adult cow to 1.13 calves/adult cow and for yearling females from 0.29 to 0.25 calves/yearling cow. See text for additional assumptions and input variables.

increase from 6.0 to 6.7%. This increase in calf mortality, although relatively small, causes a significant difference in how the moose population responds to severe winter conditions (Fig. 8). Following the very severe winter in year 16 the population rebounds slightly but continues to decline until wolf control is theoretically initiated in year 30. The population increases while wolves are reduced but again declines once predator populations rebound. The population becomes extinct by year 47.

Scenario # 3

Predators will be concentrated on smaller areas as a result of inundation. Surplus killing (Kruuk 1972) of moose is expected to increase. Both bears and wolves are expected to take advantage of the increased vulnerability of moose. To reflect these changes in predator-prey relationships as a result of the project, we assumed that both wolf numbers and kill rates would increase by 10%. These changes were programmed to occur during years 12 through 16. Afterwards we assumed wolf numbers and kill rates returned to preproject levels. Increases in predation would be sufficient to cause the moose population to decrease further and not rebound during years of mild winters and wolf control in years 30 through 32 (Fig. 9). Relatively small changes in numbers of predators or their rates of predation can be expected to cause the moose population to remain stable or to decline, particularly following severe winters. The prey population may not increase for decades without major changes in predator-prey ratios. Modeling suggests the moose population would become extinct by year 37.

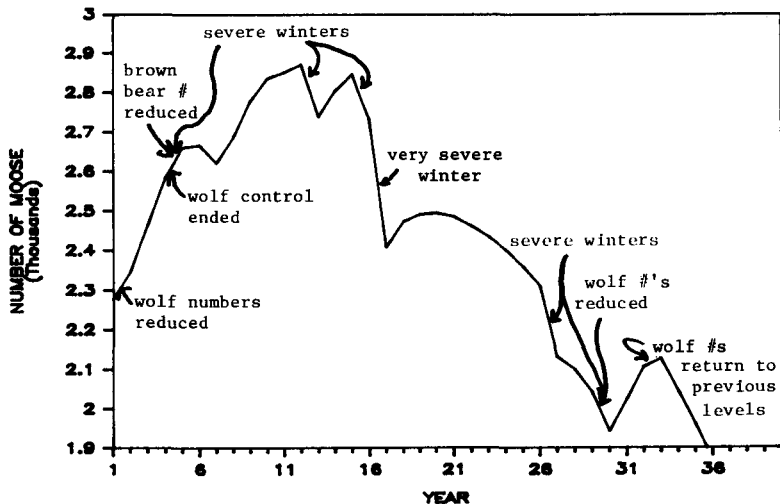


Fig. 8. Past and predicted moose population numbers in the Susitna River Study Area as determined from population modeling. During year 12 early spring-summer mortality was assumed to increase by 10% from 6.0 to 6.6%. See text for additional assumptions and input variables.

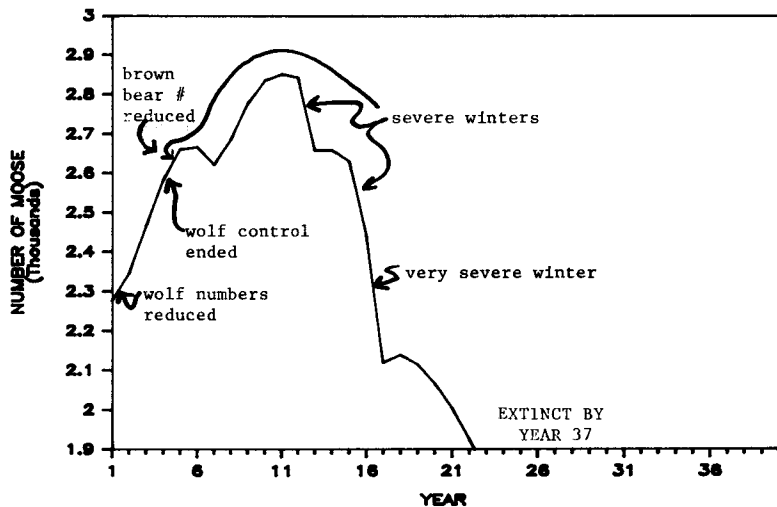


Fig. 9. Past and predicted moose population numbers in the Susitna River Study Area as determined from population modeling. During year 12 wolf numbers and consumption rates increased by 10% through year 16. See text for additional assumptions and input variables.

Scenario # 4

Brown bears will also lose habitat and will likely take advantage of increased prey concentrations and increased vulnerability due to the project. Brown bears were assumed to increase their rates of predation on calf moose from 0.14 to 0.154 calves/bear/day and on adult moose from 0.02 to 0.021 adult moose/bear/day. The moose population decreased (Fig. 10) similarly to that forecast for the increased wolf predation scenario (Fig. 9). Predation apparently was great enough to cause the population to continue to decline in spite of intervening years of mild winters and reduced wolf densities from years 30 through 32. Theoretically the moose population would be extinct by year 37.

Scenario # 5

Construction and operation of both impoundments is expected to flood most of the black bear dens which occur in the area (Miller 1985). Loss of den sites and habitat, and other factors will ultimately result in the death of most black bears which live in the area. Prior to the project, black bears were responsible for only 13% of the total mortality of neonatal moose calves (Ballard et al. 1985). In other areas, however, they have been a significant source of calf mortality (Schlegel 1976; Franzmann et al. 1980; Ballard and Larsen 1986). We assumed that for a few years black bears would be sufficiently stressed so as to increase their predation rates on calf moose. Two different levels of black bear population response were simulated: 1) predation on moose calves would increase by 50% from 0.003 to 0.0045 calves/bear/day and 2) that black bears would become

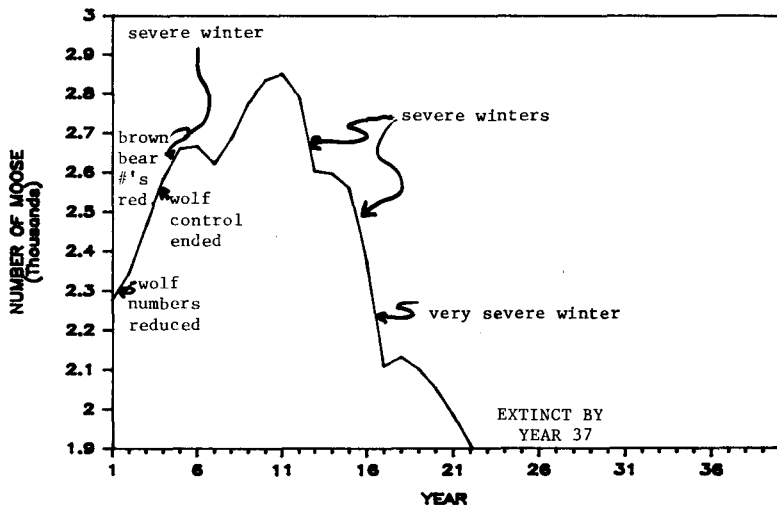


Fig. 10. Past and predicted moose population numbers in the Susitna River Study Area as determined from population modeling. From year 12 through 16 brown bear predation rates on calves increased by 10% from 0.14 to 0.154 calves/bear/day and on adult moose from 0.02 to 0.021 adults/bear/day. See text for additional assumptions and input variables.

efficient predators of moose calves and increase their rates of kill so that they have predation rates half as great as that of brown bears (from 0.003 to 0.07 calves/bear/day). In both cases we assumed that black bears would increase their rates of predation for 3 years and then rapidly decline and become extinct by the 4th year. Increasing black bear predation rates to half those of brown bears causes the moose population to decline quickly and the population would theoretically become extinct by year 27 (Fig. 11). By increasing the rate of black bear predation on calves by only 50%, the moose population would closely mimic that of the preproject simulation through year 33, after which the moose population declined (Fig. 11). By year 51 the population theoretically would be extinct. This latter simulation was different from other simulations involving predators in that the moose population was able to rebound and continue to exist under the standard assumptions. However, even this simulation became subject to the predator pit problem; predation causes the prey population to decline further and at the very least prevents it from recovering.

Scenario # 6

We speculated that losses of habitat would result in a 10% increase in starvation mortality during both mild and severe winters. Figure 12 depicts a 10% increase in winter mortality rates beginning with year 12 (simulated year of operation of project). Following the first series of severe winters, mortality would be great enough to cause the population to continue to decline even if we assume no changes in levels of predation or other forms of natural mortality

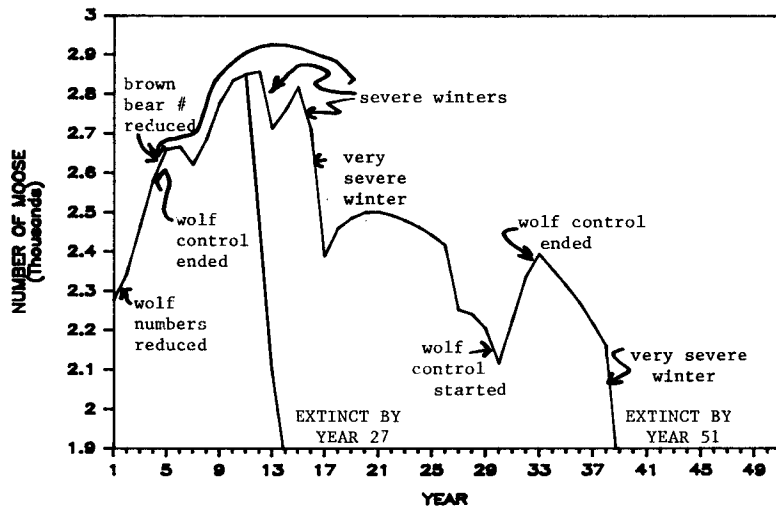


Fig. 11. Past and predicted moose population numbers in the Susitna River Study Area as determined from population modeling. During years 12 through 14 black bear predation rates increased to 0.07 calves/bear/day (moose pop. becomes extinct by year 27) or 0.0045 calves/bear/day. See text for other assumptions and input variables.

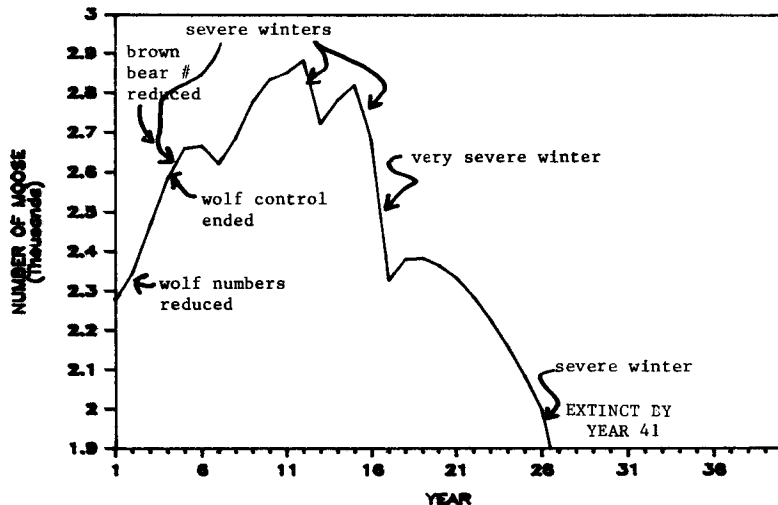


Fig. 12. Past and predicted moose population numbers in the Susitna River Study Area as determined from population modeling. During year 12 assumes winter mortality rates increased by 10%. See text for additional assumptions and input variables.

(Fig. 12). Under the above conditions the moose population would become extinct by year 41.

SUMMARY OF PROJECT IMPACTS AND DISCUSSION OF THE MODEL

All moose population scenarios suggest that losses to the moose population from a potential hydroelectric development project could be great. This finding is consistent with the hypotheses of biologists in other areas of North America where riparian habitats important to moose have been inundated or altered (K. Childs pers. comm.; F. Harper pers. comm.). Actual losses can not be predicted and will not be known until pre- and post-impoundment data can be compared. Because of the extent of the preproject moose studies this project could offer one of the best opportunities for actually determining the impacts of hydroelectric development on moose. However, this can only be accomplished by comparing preproject populations with those occurring after development.

Our population model has been useful as an additional tool for attempting to assess potential impacts of hydroelectric development and understanding the dynamics of the moose herd. The model contains several limitations which affect its usefulness as a predictive tool, but it allows us to examine a range of possibilities quickly. Other advantages are that it is relatively simple and easy to use and it incorporates many of the types of parameters routinely measured by wildlife managers. It has been most useful in attempting to understand historical population fluctuations and for generating additional hypotheses.

Perhaps the greatest limitation of the model for predictive purposes is that many of the parameters are fixed and do not functionally respond to other values. For example, predation would not cause a moose herd to become extinct because ultimately the predator population would respond to the greatly reduced prey density and either become greatly reduced themselves or switch to alternate prey. However, the model has the capacity to become considerably more complex if investigators wish to estimate these functional responses.

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