MODELLED IMPACTS OF WOLF AND BEAR PREDATION ON MOOSE CALF SURVIVAL

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ABSTRACT: A deterministic moose population model was used to examine an alternative hypothesis of why moose calf survival did not increase following a 36% reduction in grizzly bear density. Modeling suggested that predation by an increasing wolf population could have accounted for the lack of improvement in moose calf survival. Modeling suggested, that at the observed predator-prey densities and rates of predation, manipulation of bear densities was unnecessary to allow the moose population to increase.

Identification of grizzly bears (*Ursus arctos*) as important predators of moose (*Alces*) has greatly complicated attempts to manage predator-prey systems (Ballard and Larsen 1987). Recently an attempt was made to increase moose calf survival in Game Management Unit (GMU) 13 of south-central Alaska by increasing the harvest of grizzly bears. Bear densities were reduced by approximately 36% during 1980 through 1987 by increased hunting, but moose calf survival apparently did not increase (Miller and Ballard 1992). Miller and Ballard (1992) suggested five possible explanations of why reduced bear densities may not have increased moose calf survival. Their explanations included: (1) predation from an increasing wolf (*Canis lupus*) population may have offset increases in moose calf survival caused by reduced bear predation, (2) bear predation may have been more compensatory at higher than lower moose densities, (3) remaining bears may have increased their predation rates on calves, (4) hunter-induced reductions in bear density may have different influences on predator-prey relationships than removal of all sex and age classes, such as a bear transplant program (*see* Ballard and Miller 1990), and (5) small to moderate increases in moose calf survival could be difficult to detect due to sampling variation in autumn moose sex-age composi-tion surveys. They stated that one or a combination of those factors could have contributed to their failure to detect an increase in moose calf survival. The purpose of this manuscript is to present available data and analyses supporting the hypothesis that increased wolf predation was the primary reason that reduced bear densities failed to increase moose calf survival.

STUDY AREA

The study was conducted in GMU 13, an area of 59,154 km², which is approximately centered on 61° N. and 147° E. GMU 13 is an important moose hunting area which lies between the population centers of Fairbanks and Anchorage and is bisected by four major highway systems (Ballard et al. 1991). Topography, vegetation, climate, etc. have been thoroughly described by Skoog (1968), Rausch (1967, 1969), Bishop and Rausch (1974), Ballard *et al.* (1981a,b; 1987; 1991), and Miller and Ballard (1992). Principal predators within GMU 13 include brown bears, wolves, and black bears (*Ursus americanus*) which during the mid-1970's occurred at spring densities of 10-28/1000 km², 1.8-3.6/1,000 km², and 0-90/1,000 km², respectively (Ballard 1992). Moose densities during the early 1980's averaged about 700/1,000 km² (Ballard *et al.* 1991) while caribou numbered

about 18,000 to 20,000 (Bergerud and Ballard 1988).

METHODS

Moose sex-age composition surveys have been conducted annually in 15 permanently established count areas in GMU 13 since 1955 (Fig. 1) (Ballard *et al.* 1991). Surveys have been conducted from fixed-wing aircraft (Piper Supercubs) at intensities averaging 0.4 min/km^2 (Ballard *et al.* 1991). Minimum ratios of calves per 100 adult (>2 years-of-age) cows were estimated by subtracting the numbers of yearling bulls (estimated from size and configuration of antlers) which are assumed to equal yearling cows, from the total number of cows counted. The method is a minimum estimate because sex ratios are probably skewed in favor of females due to differential mortality (Ballard *et al.* 1991). Also, not all yearling bulls can be identified from aircraft because an unknown number of yearlings have small spikes (unpubl. data).

Autumn moose composition count data may be biased but they provide useful data on trends in sex-age composition and an index of density (Gasaway *et al.* 1986, Ballard *et al.* 1991).

Moose densities in portions of GMU 13 (CA's 3, 6, and 7) were estimated in 1980 and 1983 by stratified random sampling techniques (Gasaway *et al.* 1986, Ballard *et al.* 1991). Trends in moose calf recruitment in relation to changes in bear and wolf densities were based upon autumn calf:adult cow ratios within moose count area (CA) 3 or estimates generated from population modeling. Modeling was based upon data collected in the Susitna River Study Area (SRSA) which was composed of CAs 3, 6, and 7 (Fig. 1; Ballard *et al.* 1991). Trends in moose calf:adult cow ratios were analyzed with Spearman's rank correlations (r_s) and Student's t-test (Conover 1971:260, Steel and Torrie 1960:409). Linear regressions were fit to calf:cow ratios for illustration purposes.
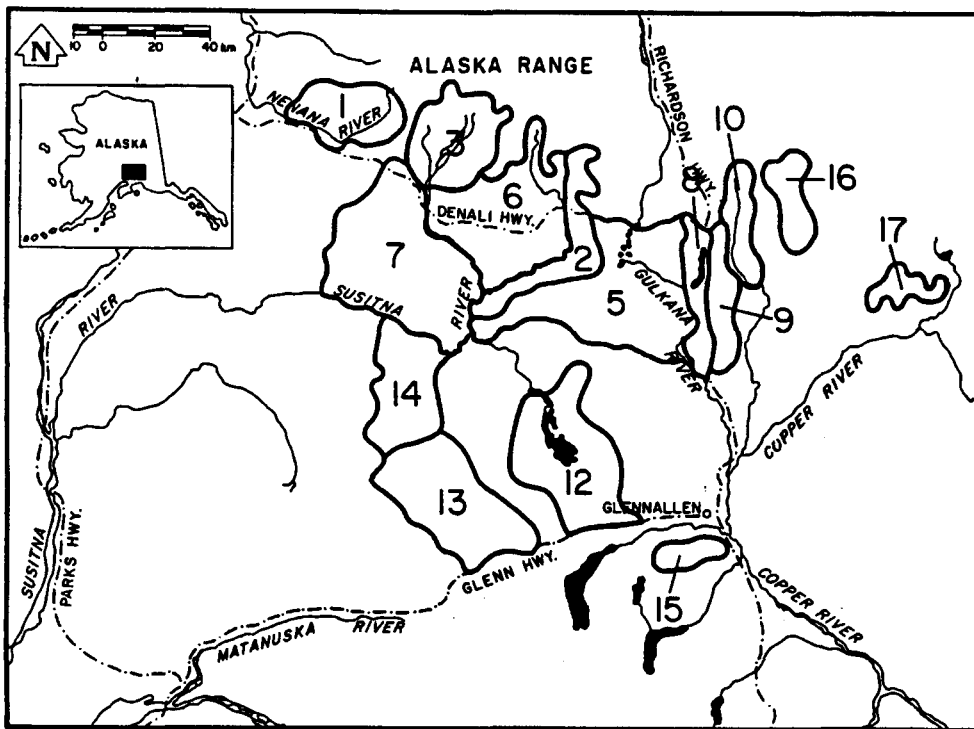

Fig. 1. Boundaries of 15 moose sex-age composition count areas that are surveyed annually within Game Management Unit 13.

Brown bear densities within SRSA were estimated using mark-recapture methods in 1979, 1985, and 1987 (Miller and Ballard 1982, 1992; Miller et al. 1987).

Wolf densities from 1975 through 1985 within SRSA were estimated from known numbers of wolves within radio-marked packs (Ballard et al. 1987, W. B. Ballard, unpubl. data). During 1986 through 1989, wolf densities were estimated from spring track counts conducted from fixed-wing aircraft after fresh snowfall within the SRSA (Ballard et al. 1987, Tobey 1989). After 1989 wolf densities were estimated by sampling with line-intercept transects (Becker 1991, Becker and Gardner 1991, and Ballard et al. 1992). However, because the latter estimates were not obtained in the SRSA and because they were derived by different methods they were not used in the modeling exercise. Autumn wolf densities after 1985 were estimated from spring estimates based upon correlations of autumn and spring estimates during 1975-85 (Ballard et al. 1987).

A deterministic moose population model was developed to examine the relationships of different levels of predation on the moose population (Ballard et al. 1984, 1986). Moose survival and mortality inputs to this model were derived from field studies of radio-collared moose (Ballard et al. 1991). Average adult moose productivity was 1.13 calves/adult cow (Ballard et al. 1991). Inputs on moose mortality due to wolf predation were based on estimated spring and autumn wolf densities. Wolf predation inputs were based on results of scat analyses that indicated 35% of the spring-early summer wolf diet was composed of calf moose (Ballard et al. 1987:Table 10). Based on an average calf weight of 39 kg and a wolf consumption rate of 7.1 kg/wolf/day, this translated to a late spring and summer annual wolf kill of 3.4 to 8.9% of the moose calves born. The latter estimates of mortality attributable to wolf predation were similar to those of radio-collared moose calves which averaged 2.5% (Ballard et al. 1991:19).

Although the wolf consumption rate of 7.1 kg/wolf/day that I used in the model was rather high relative to that reported in other studies (4.4 to 10.0 kg/wolf/day - Peterson 1977, Fuller and Keith 1980) it was based on intensive tracking of 5 wolf packs in or near the study area (Ballard et al. 1987). Also there were no differences in summer and winter consumption rates as reported in other studies (see Ballard et al. 1987:37).

The input bear population (Miller and Ballard 1982) was stable until 1979, at which time the population was reduced by 60% to reflect the impacts of the bear transplant experiment (Ballard and Miller 1990). During 1980-1989 the input bear population was reduced by 36% from 1978 levels to reflect increased bear hunting and any residual effects of the transplant experiment. Bear predation rates on moose calves for a 60 day period were estimated at 0.143 calves/adult bear/day (Ballard et al. 1990).

RESULTS AND DISCUSSION

Wolf predation is a significant source of moose mortality in GMU 13 (Ballard et al. 1984, 1986, 1987, 1991) and, consequently, wolf population trends are pertinent to a discussion of impacts of reduced bear populations on moose calf survival. History of the GMU 13 wolf population prior to 1975 was provided by Rausch (1967, 1969), Ballard et al. (1987), and Bergerud and Ballard (1988, 1989). Beginning in 1976, the wolf population within a 7,252 km^2 area which included CA 3 was subjected to an experimental control effort in addition to public hunting and trapping (Ballard et al. 1987). As a result of those efforts, spring wolf densities were reduced to about 1.7 wolves/1,000 km^2 by 1978 (Ballard et al. 1987). Following termination of wolf control activities in 1978, both spring ($T = 3.74$, $P = 0.007$) and autumn ($T = 2.81$, $P = 0.026$) wolf densities significantly increased

through 1986 (Fig. 2). After 1986 wolf densities declined in 1987 and remained relatively stable through 1989. During winter 1988-89, aircraft assisted shooting was banned and by spring 1990 wolf populations may have reached the highest level ever observed in GMU 13. Although spring wolf surveys were not conducted in CA 3 during 1989-90, surveys 60 kms to the south indicated a record high density from 10 to 23 wolves/1,000 km^2 (Becker and Gardner 1990). High wolf densities resulting from the regulation changes probably occurred throughout GMU 13. However, because the latter density estimates were not obtained within the SRSA they were not used in the model. For this analysis we only projected the effects of wolf predation for the period 1978 through 1989.

Moose Calf Survivorship Trends

If gradual reductions in bear numbers as a result of increasing bear harvests had im-

proved moose calf survival, autumn moose calf:cow ratios should have increased like those observed following a bear transplant experiment in 1979 (Ballard and Miller 1990, Miller and Ballard 1992). Increasing calf:cow ratios were not observed during 1980-1990 when bear numbers were reduced by 36% (Fig. 3; Miller and Ballard 1992). Calf:cow ratios in CA 3 were not significantly different from stable ($r_s = -0.25$, $P = 0.24$) suggesting that calf moose survival had not increased (Miller and Ballard 1992).

Predator-Prey Model Results

To examine the potential impacts of predation on the moose population, I modelled three scenarios using the deterministic moose population simulation model described by Ballard et al. (1984, 1986). First I modelled the moose calf/cow ratios using the actual observed numbers of bears (reduced by 36% during 1980-1990) and wolves (Fig. 2) in
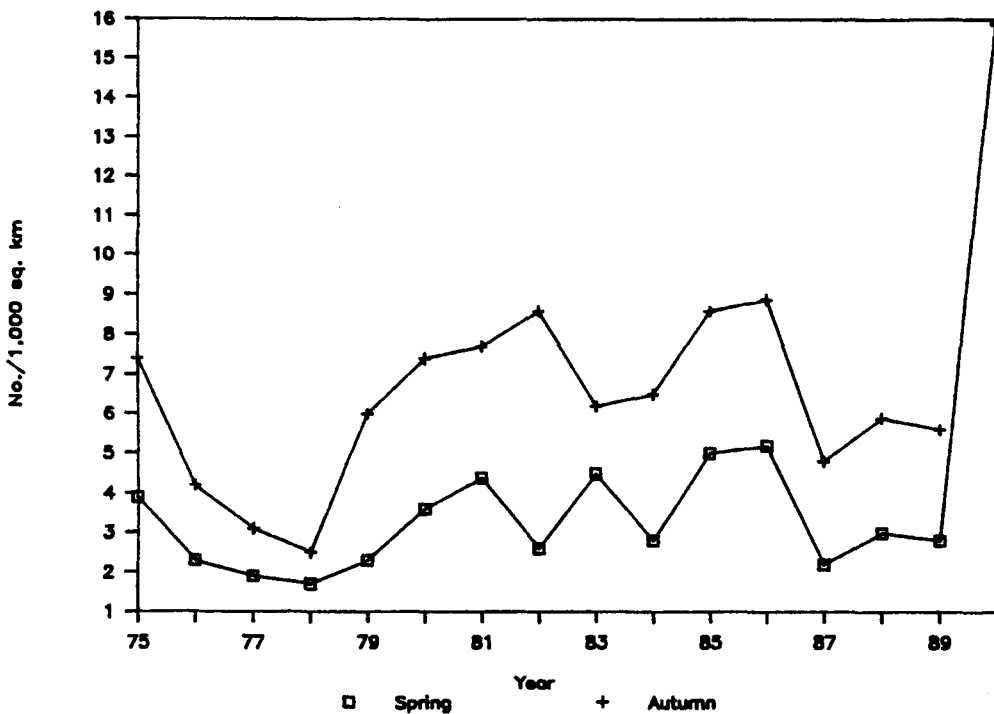

Fig. 2. Spring and autumn wolf densities within the Susitna River Study Area of south-central Alaska, 1975-1990. Density estimate for 1990 was based on an average of 3 estimates provided by Becker and Gardner (1990) which ranged from 10 to 23 wolves/1,000 km^2.

SRSA during 1975-1989. Then I modelled the effects of maintaining wolf numbers at 1978 levels (population low) while the bear population was reduced by 36% during 1980-1989. Lastly I modelled the impacts of keeping wolves constant at 1978 levels and not reducing bears from 1980-1989.

Increases in moose calf survival resulting from reductions in bear numbers during the 1980's could have been masked by increased predation by the growing wolf population (Fig. 4). Although calf/cow ratios appeared to increase during the 1980's, the slope was not significantly different from zero ($T = 1.7$, $P = 0.13$) which was similar to the actual data from CA 3 (Fig. 3). Modeling suggested that, had wolf numbers been maintained at low densities (1978 levels) while bear numbers were reduced, moose calf/cow ratios should have increased (Fig. 5, beta not equal to zero, $T = 4.9$, $P = 0.001$). If wolf numbers had been held at low numbers (1978 levels) and bears had not been reduced, moose/calf cow ratios

would have remained stable (Fig. 6, beta not different from zero, $T = -0.2$, $P = 0.84$).

Like all population models the simulations described herein assume that the model inputs were accurate and representative of the factors influencing moose in the SRSA. In fact, many of the parameters did not contain variance estimates and so some errors were likely. Observed moose calf/cow ratios were nearly always lower than those simulated in the model. In addition to the errors mentioned above calf/cow groups have the lowest sightability of any of the moose groupings and consequently actual calf/cow ratios are usually greater than those observed during aerial surveys.

Moose Population Trends

Moose in GMU 13 increased during the 1940's and 1950's. This increase was attributed to favorable range conditions, mild winters, low numbers of wolves and bears (caused by federal poisoning programs), and low hu-
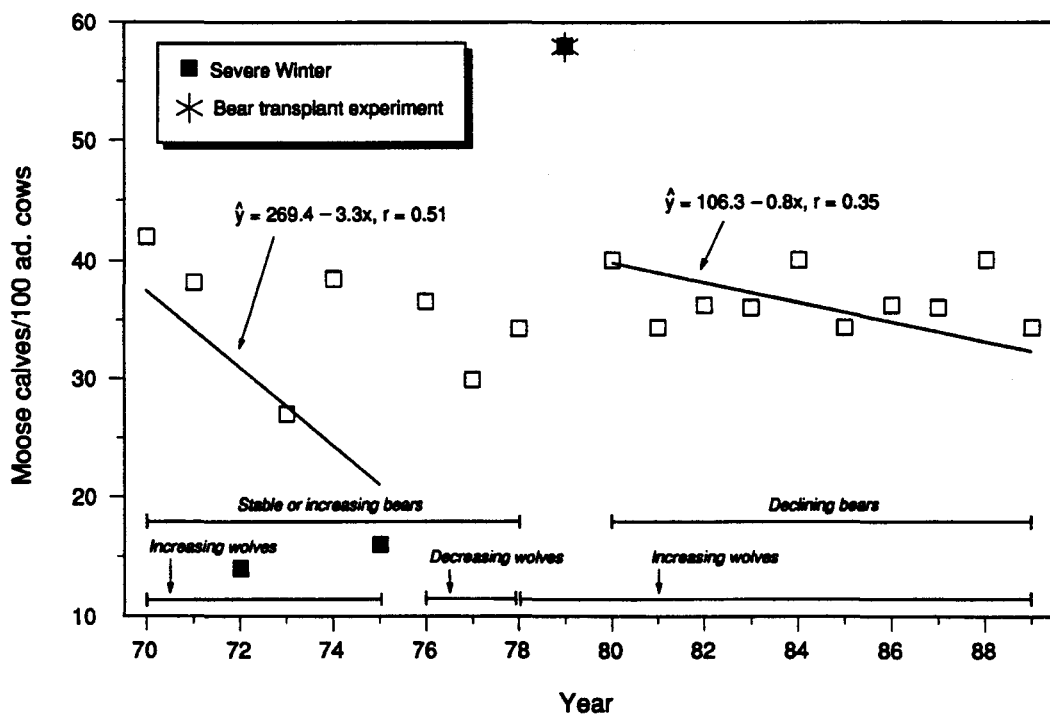

Fig. 3. Trends in autumn moose calf:cow (>2 years-of-age) ratios in moose Count Area 3 of south-central Alaska during 1970-1989 (modified from Miller and Ballard 1992).
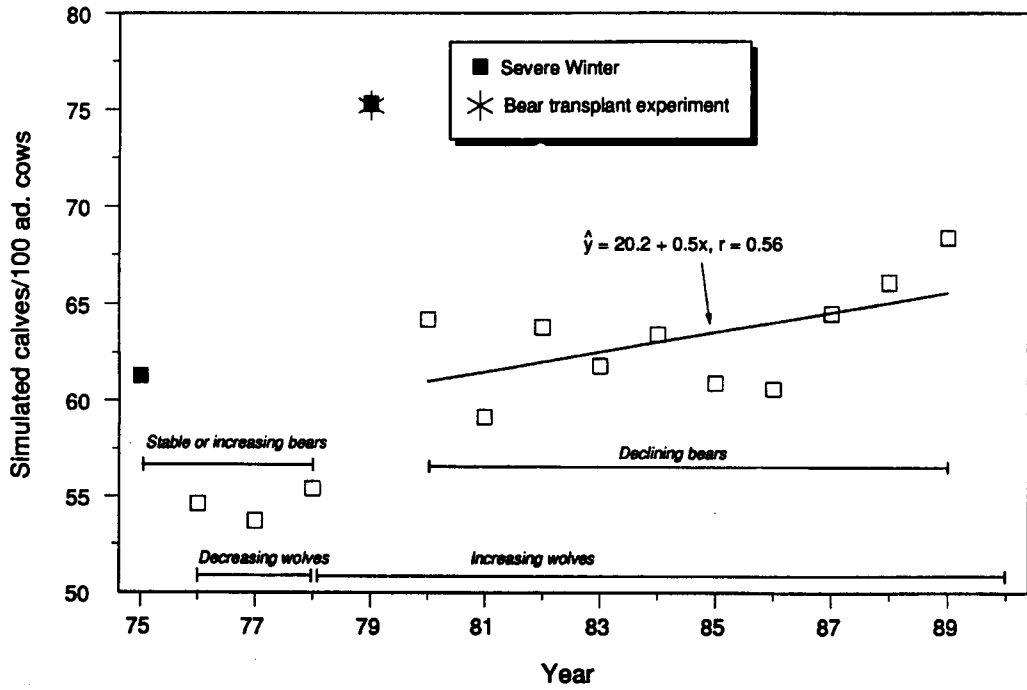
Fig. 4. Simulation results illustrating impact on moose calf:cow (>2 years age) ratios of observed changes in wolf and bear numbers within the Susitna River Study area during 1975 through 1989.
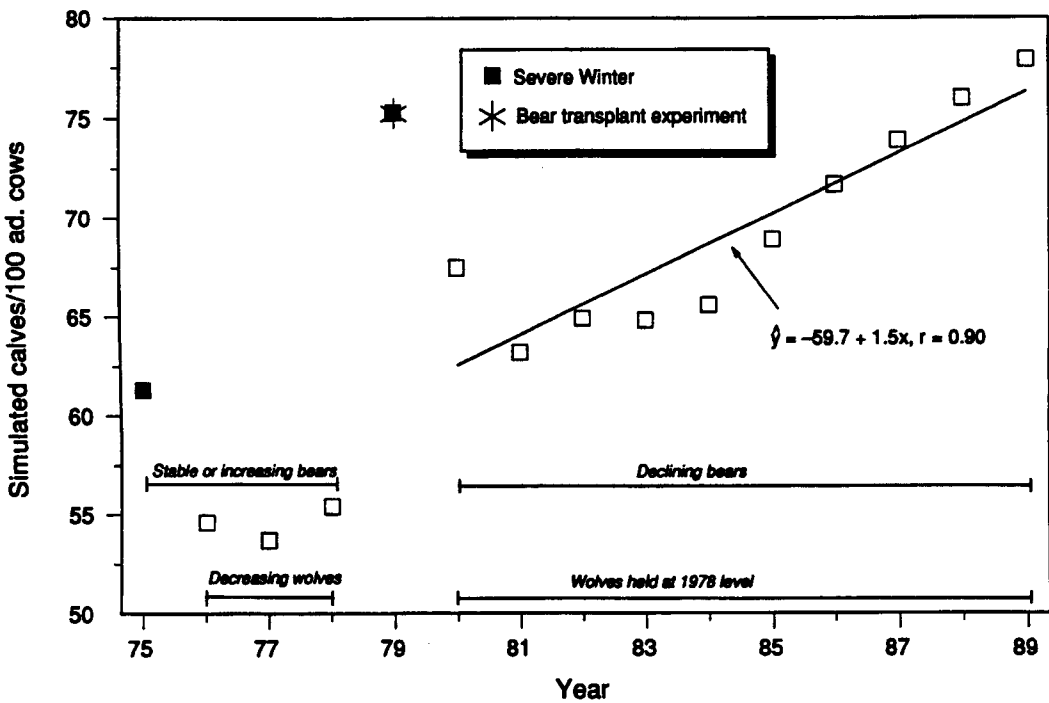

Fig. 5. Simulation results illustrating potential impacts on moose calf:cow ratios within the Susitna River Study Area of maintaining low wolf densities at 1978 levels (1.7/1,000 km²) while brown bears were reduced by 36% during 1980-1989.
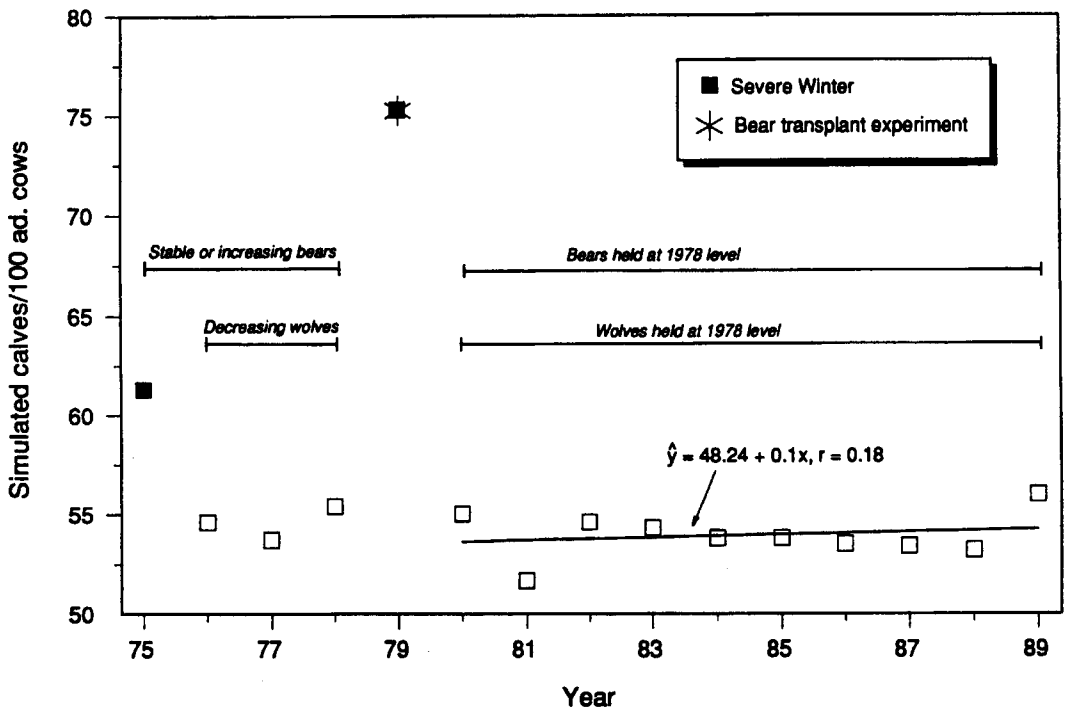
Fig. 6. Simulation results illustrating potential impacts on moose calf/cow ratios within the Susitna River Study Area of maintaining low wolf densities at 1978 levels (1.7/1,000 km²) while brown bear numbers remained stable at 1978 levels during 1980-1989.

man harvests (Bishop and Rausch 1974, Ballard *et al.* 1991). Based on numbers of moose observed per hour of survey, the population peaked about 1963. Subsequently, it declined following severe winters (in 1965-66, 1971-72, and 1974-75) and periods of high predation (Ballard *et al.* 1991). Record low numbers were reached in 1975 (Ballard *et al.* 1991). During 1976-1988, moose populations steadily increased although a severe winter in 1978-79 resulted in substantial moose mortality (Ballard *et al.* 1991). The increase in the moose population was attributed to a combination of relatively mild winters, reduced numbers of wolves and bears, and reduced human harvests (Ballard *et al.* 1991). Winter 1988-89 may have been more severe in localized areas than average winters and appeared to have caused some decline in moose numbers. Winter 1989-90 was severe (winter severity index [Ballard *et al.* 1991] = 28.5), and wolf densities were relatively high.

Significant losses of calf and adult moose occurred (R. Tobey and C. Gardner, ADFG, Glennallen, Ak., pers. commun.).

Moose population increases during the 1980's were also indicated by quadrant-sampling techniques (Gasaway *et al.* 1986) and population modeling (Ballard *et al.* 1984, 1986, 1991). During autumns 1980 through 1983, census data indicated that moose densities increased by factors of 1.02 to 1.23 while population modeling indicated annual rates of increase of 1.03 to 1.06 during 1976 through 1984. Miller and Ballard (1992) calculated a compounded annual growth rate of 7.2% for CA 3 during 1980-83.

The moose population began to recover from historic low numbers in 1975 (Ballard *et al.* 1991). The recovery was well underway before bear populations were reduced by 36% from liberalized bear hunting initiated in 1980. In the area where the 1979 bear transplant experiment occurred (CA 3), calf survivorship

had not improved (Miller and Ballard 1992).

Population modeling using parameters measured in the area during 1975-1986 demonstrated that the observed numerical increases in the wolf population were sufficient to mask any improvements in moose calf survival as a result of the bear reduction. However, the other four potential explanations provided by Miller and Ballard (1992) of why reduced bear densities failed to improve moose calf survival can not be entirely dismissed and could have contributed to our failure to detect an increase in the moose calf survivorship.

Miller and Ballard (1992) speculated that perhaps bear predation had become more compensatory at higher than lower moose densities. During the period 1977 through 1984 when moose calf mortality studies were conducted (Ballard et al. 1991) moose densities increased from about 486/1,000 km^2 in 1975 to 848/1,000 km^2 in 1983 (Ballard et al. 1991, Miller and Ballard 1992). During that period, neonatal mortality attributable to bear predation ranged from 38% in 1979 to 52% in 1984 (Ballard et al. 1991). Following the bear transplant experiment in 1979 moose mortality was reduced and survival of that cohort was high for at least 2 years. Based on other studies in Alaska (Schwartz and Franzmann 1991) we would expect that if mortality due to predation were compensatory such mortality would occur during winter. Consequently for this analysis calf survival should be high through autumn following reductions in predator numbers. At this point all available evidence suggests that calf mortality from predation through autumn is additive and not compensatory.

Miller and Ballard (1992) also suggested that following bear reductions, the remaining bears may have increased their predation rates. Following the bear transplant experiment in 1979 two of the remaining bears appeared to have greater predation rates (Ballard and Miller 1990). Therefore it was possible that increased predation rates by the remaining bears

could have lowered moose calf survival.

When bears were transplanted from the study area in 1979 all sex, age, and family classes were removed (Ballard and Miller 1990). Ballard et al. (1990) reported that although there were no apparent differences in predation rates on calf moose by sex, age or family class of bear, there were large differences between individual bears. However, Boertje et al. (1988) did find significant differences in predation rates by sex and age class in east-central Alaska. Reductions in bear density caused by the bear transplant involved all classes of bears while those caused by hunting would result in reductions of large males and females. Few females with young would have been removed since those groups are protected by regulation. Consequently, it is possible that because of differences in predation rates among individual bears, reductions in bear density caused by hunting (large males and females removed) may have had a different effect on the moose population than when all groups were removed as during the bear transplant experiment.

Lastly, Miller and Ballard (1992) suggested that sampling variation in autumn moose sex-age surveys could have contributed to failure to detect small to moderate increases in moose calf survival as a result of reduced bear density. Prior to the bear removal experiments calf:cow ratios in CA 3 were highly variable among years (Fig. 3). The tendency of this area to exhibit large variation in autumn calf:cow ratios could have contributed to our failure to detect increases in calf survival following the 36% bear reduction caused by hunting. Also, it should be remembered that the reduction did not occur in 1 year but over 7 years.

If the wolf predation hypothesis is correct, it suggests that biologists must manage wolf populations if high moose calf survivorship is desired. The fact that the moose population was increasing in spite of relatively heavy predation by grizzly bears

(see Ballard et al. 1981a, 1984, 1991), prior to initiation of the bear reduction program, suggests that it may not be necessary to manage grizzly bears to favor moose under similar conditions. During the early phases of the moose population recovery, moose densities ranged from 486 to 741/1,000 km^2 (Ballard et al. 1991, Miller and Ballard 1992), wolf densities from 1.8 to 3.6/1,000 km^2 (Ballard et al. 1987), and grizzly bear densities from 24 to 28/1,000 km^2 (Miller and Ballard 1992, Miller et al. 1987). Reduced bear densities may have altered the rate of moose population increase but the moose population was increasing anyway (Ballard 1992). At lower moose densities (i.e., 150/1,000 km^2) such as in east-central Alaska (Gasaway et al. 1992) manipulation of both wolves and bears may be necessary to permit the moose population to recover. However, to achieve significant improvements in moose calf survival bear densities may have to be reduced by >50% while maintaining wolf densities at low levels (Ballard 1992).

ACKNOWLEDGEMENTS

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