A Further Analysis of the Nelchina Caribou and Wolf Data
Author(s): L. L. Eberhardt and K. W. Pitcher
Source: *Wildlife Society Bulletin*, Vol. 20, No. 4 (Winter, 1992), pp. 385-395
Published by: Allen Press
Stable URL: http://www.jstor.org/stable/3783056
Accessed: 16/09/2009 14:33

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/action/showPublisher?publisherCode=acg.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.

Allen Press is collaborating with JSTOR to digitize, preserve and extend access to *Wildlife Society Bulletin.*

http://www.jstor.org

Wildl. Soc. Bull. 20:385–395, 1992

A FURTHER ANALYSIS OF THE NELCHINA CARIBOU AND WOLF DATA

L. L. EBERHARDT, *Pacific Northwest Laboratory, Battelle Memorial Institute, P.O. Box 999, Richland, WA 99352*

K. W. PITCHER, *Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99502*

The Nelchina caribou (*Rangifer tarandus*) herd in south-central Alaska expanded from a population of roughly 5,000 animals in 1948 to >70,000 in 1962 and then dropped to <10,000 by 1972 (Van Ballenberghe 1985). Although the herd has continued to expand since this low in the early 1970's, management of wolf (*Canis lupus*) populations in this area remains controversial today (Van Ballenberghe 1985). The history of the herd is controversial because of differing interpretations of the available records. High hunter harvests presumably contributed to the decline of this caribou population (Doerr 1979, Van Ballenberghe 1985, Bergerud and Ballard 1988). Bergerud and Ballard (1988, 1989) believed that wolf predation was of major importance in causing the decline, but Van Ballenberghe (1985) felt that severe winter weather was a key factor and that wolf predation played only a minor role in the decline. Doerr (1979) believed that low calf recruitment during the decline was related to poor range quality.

The controversy about the role of wolves in the decline of the Nelchina caribou herd has been discussed in detail by Van Ballenberghe (1985, 1989) and Bergerud and Ballard (1988, 1989). We used simple models to more clearly define conditions during the decline, to make these findings available for management of the herd, and to examine the prospects for future tests of hypotheses about population regulation as suggested by Eberhardt (1988).

DATA AND METHODS

Caribou Abundance

We used caribou population estimates and harvest data (assembled by K. W. Pitcher, Susitna Hydroelectric Project, Big Game Studies, Vol. IV: Caribou, Alas. Dep. Fish and Game [ADFG] Final Rep., Anchorage, 1987) in our analyses. Wolves had little impact on the initial growth of the caribou herd in the 1950's (Rausch 1969). Population size was estimated to be about 40,000 in 1955–1956 (Van Ballenberghe 1985). Siniff and Skoog (1964) estimated a posthunting population of about 71,000 in 1962, and a prehunting estimate of 61,000 is available for 1967 (Van Ballenberghe 1985). A series of estimates also was available for 1972–1984 (K. W. Pitcher, Susitna Hydroelectric Project, Big Game Studies, Vol. IV: Caribou, ADFG Final Rep., Anchorage, 1987).

Mandible Lengths

Samples of mandibles from hunter-killed caribou were measured during 1964–1968 when the herd was at a high level (>70,000 and declining) and again in 1989 and 1990 when the herd was at a moderate level (~30,000 and increasing). Complete mandibles of each sex were measured from the base of the first incisor to the posterior end of the ramus in each year of collection as an index to skeletal growth (Suttie and Mitchell 1983). Age classes were assigned to each animal based on tooth replacement and wear (Skoog 1968). Mean mandible lengths by sex and age class were compared among time periods using Wilcoxon rank-sum tests.

Wolf Numbers

Estimates of wolf numbers in the 1950's and 1960's are few and based on limited information. Van Ballenberghe (1981, 1985) reviewed and revised the earlier estimates. Bergerud and Ballard (1988) used an initial population of 12 wolves in 1953 and projected it forward on the basis of an average rate of growth (λ = 1.29) of 7 other wolf populations reported by Keith (1983). Ballard et al. (1987:22) provided ranges for the earlier population estimates, obtained detailed spring and fall estimates from 1975–1982, and reported estimates of wolves harvested from 1971–1982.

The data of Ballard et al. (1987:22–23, 28) were used with the "projection" method described below to estimate the trend in wolf populations from 1954–1982. Wolf harvest data from 1966–1970 (ADFG files, Anchorage, unpubl. data) are of somewhat uncertain validity as compared to data beginning in 1971, when all wolves that were killed had to be individually "sealed" (i.e., recorded by a representative of ADFG). Because our method projected populations backward in time, uncertainty about the earlier information has no effect on the estimates from 1971 onward. We extrapolated the population data obtained by Ballard et al. (1987) backward in time, using a constant value of λ and recorded removals of wolves (assumed 0 prior to 1966).

The Projection Models

Two simple models were suggested by Eberhardt (1987) as a means to project population trends from records of population size and removal:

$$N_t = N_{t-1}\lambda - K_t \tag{1}$$

$$N_t = (N_{t-1} - K_t)\lambda . \tag{2}$$

In both models, N_t denotes population size at time t, and K_t represents removals, whereas λ is the "finite population multiplier." The choice of model depends on timing of major removals with respect to recruitment into the population. For the 1971–1989 caribou data, we used the second model fitted by nonlinear least-squares. The resulting fit then was used to project backward in time to yield a caribou population estimate for 1971.

Both spring and fall population estimates were available for wolves, so population projections were made by both models. To combine the 2 sets of data, joint fitting by least-squares was used to estimate λ.

Caribou Model Based on Age Structure Data

We constructed a model for estimating caribou population trends by using age structure data. Bergerud and Ballard (1988) and Van Ballenberghe (1989) examined the proportion of 2.5-year-old caribou in harvest samples of animals $\geq$2.5 years old. We used essentially the same data, but the age structure of older animals was explicitly considered in the model. Because 0.5- and 1.5-year age classes were not harvested in proportion to their abundance in the population, our model is based on animals $\geq$2.5 years old. Thus, the main source of information for the model is data on adult caribou, with subadults estimated from various ratios (described below).

Because growth of the population was rapid in the 1950's, we assumed high initial adult survival rates. The initial age structure of the population was based on an assumed λ of 1.2 and mortality of 2%/year. Pitcher (K. W. Pitcher, Susitna Hydroelectric Project, Big Game Studies, Vol. IV: Caribou, ADFG Final Rep., Anchorage, 1987) estimated about a 9% annual mortality of females from nonhunting causes and believed that about 14 out of 17 such deaths were caused by wolves, giving a mortality rate of about 2% attributed to factors other than wolves and hunting. Recruitment to the population was based on the observed ratio of 2.5 year olds to all older individuals in the samples of harvested animals. Subsequent survival rates were calculated as survival through the hunting season (s_1) and from wolf predation (s_2):

$$s_1 = 1 - \frac{\text{hunting kill}}{N} \tag{3}$$

$$s_2 = 1 - \frac{a(\text{number of wolves})}{s_1 N}, \tag{4}$$

where a represents the annual number of adult caribou killed/wolf, as estimated in fitting the model, and N denotes population size at the time survival rates were estimated. We assumed that the survival rates should be applied sequentially, so that s_1 represented survival through the hunting season and s_2 through the winter and spring when killing by wolves was most prevalent. Some winter hunting would occur at the same time as wolf kills, so the 2 rates are not wholly independent.

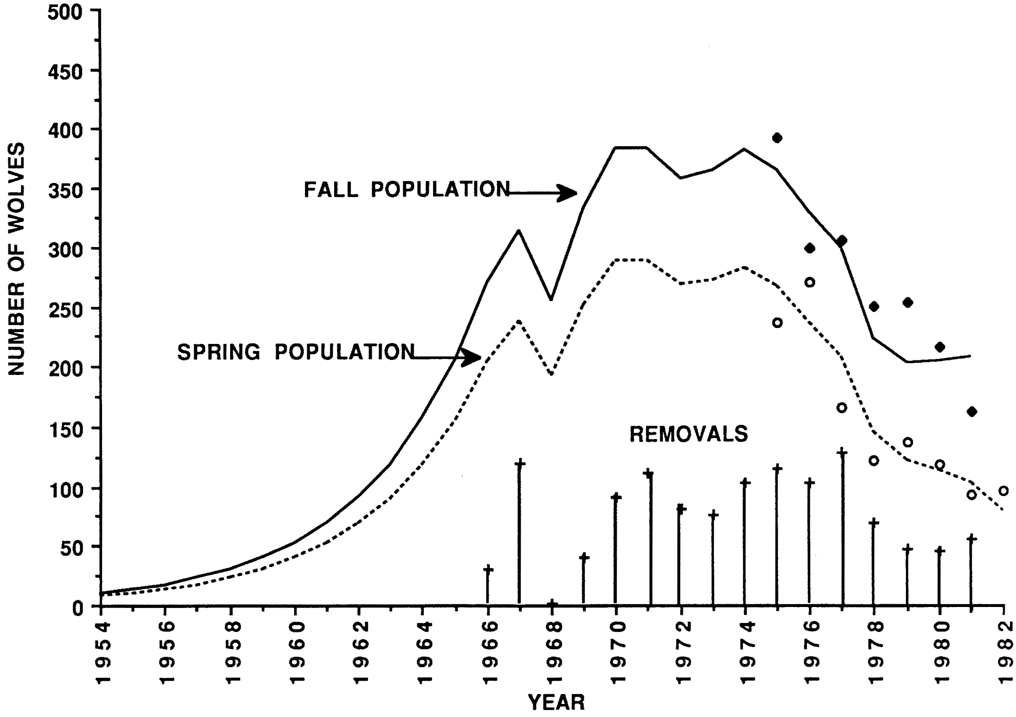
We used the average of spring and fall estimates (Fig. 1) to represent wolf populations in computing caribou survival in equation 4 of the model. The initial caribou survival rate of 0.98 was retained to account for losses not caused by wolves or hunting, so the overall survival is the product $s_1 s_2(0.98)$.

Age composition of the harvests was estimated from the overall harvests (K. W. Pitcher, Susitna Hydroelectric Project, Big Game Studies, Vol. IV: Caribou, ADFG Final Rep., Anchorage, 1987) by using the age and sex ratio of the kill recorded at checking stations (ADFG files, Anchorage, unpubl. data) to segregate the total estimated kill into age and sex cohorts (Table 1).

The pattern of recruitment, calculated as a ratio of 2.5 year olds to all older caribou, was then used to project an initial population forward to estimate adult ($\geq$2.5-year-old) female caribou numbers from 1954–1972. Because the available population estimates are for total caribou numbers, it was necessary to estimate proportions of subadults and sex composition. Bergerud and Ballard (1988) reported the percentage of calves and yearlings observed in aerial "composition" surveys. Comparable data were available for 1954–1962 and

⟶

Fig. 1. Backward projections (upper panel) of spring (open circles) and fall (solid squares) wolf populations (Nelchina area, Alaska) as estimated by Ballard et al. (1987). The projections were obtained by the method of Eberhardt (1987), which uses population size and annual removals (annual removals shown as crosses). The lower panel shows wolf population estimates for the period prior to the 1975–1982 study of Ballard et al. (1987). Open squares denote estimates characterized by Ballard et al. (1987) as based on "miscellaneous observations." Solid circles denote estimates from fall censuses, and solid squares denote those for spring surveys.


NUMBER OF WOLVES
500
450
400
350
300
250
200
150
100
50
0
FALL POPULATION
SPRING POPULATION
REMOVALS
1954
1956
1958
1960
1962
1964
1966
1968
1970
1972
1974
1976
1978
1980
1982
YEAR

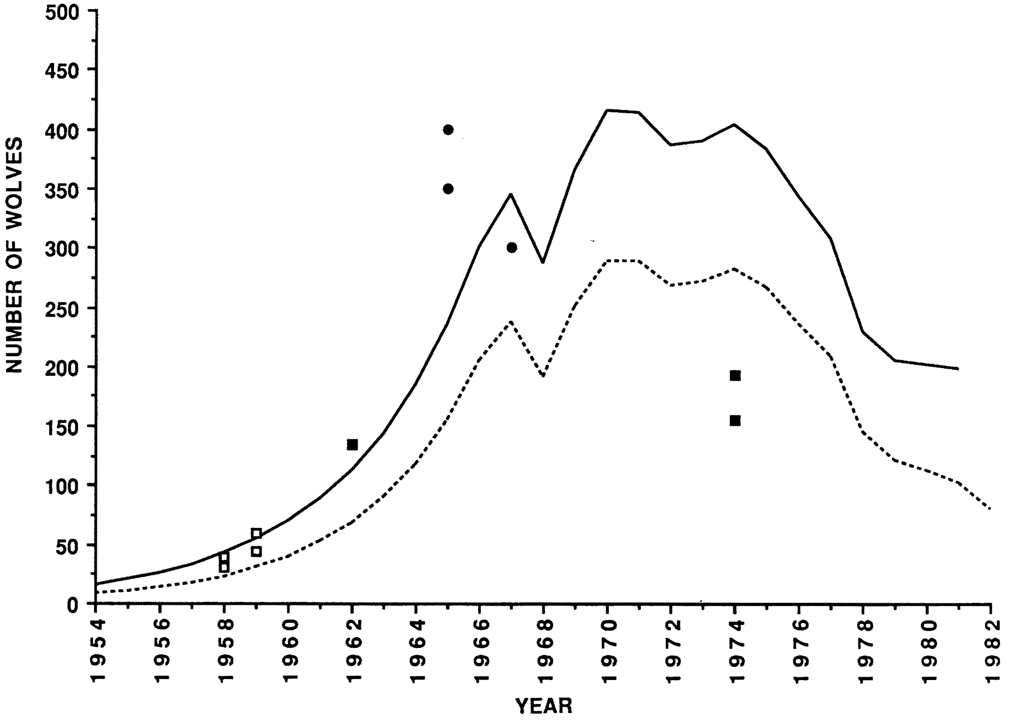

NUMBER OF WOLVES
500
450
400
350
300
250
200
150
100
50
0
1954
1956
1958
1960
1962
1964
1966
1968
1970
1972
1974
1976
1978
1980
1982
YEAR

Table 1. Estimated composition of harvests from the Nelchina caribou herd, Alaska.

		Age composition from checking stations					
Year	Total harvest	Juvenile females	Adult females	Juvenile males	Adult males	Total aged	Estimated adult females harvested
1954	2,000	31	153	73	344	601	509
1955	4,000	9	33	24	121	187	706
1956	3,500	27	127	63	208	425	1,046
1957	2,500	11	58	17	152	238	609
1958	3,500	4	41	6	43	94	1,527
1959	4,000	26	46	52	107	231	797
1960	5,500	44	120	79	156	399	1,654
1961	8,000	53	140	63	147	403	2,779
1962	3,500	66	110	88	288	552	697
1963	6,300	45	176	57	326	604	1,836
1964	8,000	74	144	88	266	572	2,014
1965	7,100	16	108	19	182	325	2,359
1966	5,500	12	62	20	149	243	1,403
1967	4,000	2	27	6	12	47	2,298
1968	6,000	21	92	37	100	250	2,208
1969	7,800	31	175	38	195	439	3,109
1970	7,247	13	170	25	178	386	3,192
1971	10,131	69	467	82	267	885	5,346

averaged 21.3% calves (the percent of total caribou seen in Oct–Nov surveys) and 21.3% yearlings (the percent ≥ 1 year old in Mar–Apr surveys). Consequently, we assumed the initial population to include 21.3% calves, 16.8% yearlings [$0.213(1 - 0.213) = 0.168$], and 61.9% adults ≥ 2.5 years old.

The initial population was assumed to be 40,000 caribou in 1955, as estimated from the aerial survey reported by Watson and Scott (1956). The initial proportion of females was assumed to be 60%, as reported by Skoog (1968:641). The autumn 1971 population was estimated to be 18,700 caribou by the backward projection of the 1972–1989 population estimates available from aerial counts (K. W. Pitcher, Susitna Hydroelectric Project, Big Game Studies, Vol. IV: Caribou, ADFG Final Rep., Anchorage, 1987, and ADFG, Anchorage, unpubl. data). Sex ratio (63.6% females) in the 1971 population was calculated from the harvest data (Table 1) because the harvest in 1971 removed approximately 50% of the herd. Consequently, we assumed that females were taken in proportion to their actual abundance in that year. The same fractions of immatures (calves and yearlings as given above) were assumed for that year, resulting in an estimate of 7,360 adult females and 4,220 adult males in 1971.

The overall population trajectory from the model could then be compared with the available population estimates. We assumed that the fraction of immatures (21.3% calves and 16.8% yearlings) in the herd was the same as calculated above, except for the years 1964–1967, when it was reduced to conform to the substantial reduction in those age classes reported below.

The model made proportional adjustments to each year's population. Recruitment consisted of adding a proportion of the overall adult population as 2.5-year-old recruits, and survival rates (eqs. 3 and 4) were applied to estimate the number of older animals surviving from the previous year.

RESULTS

Trends in the Wolf Population

We estimated $\lambda = 1.28$ for the fall population when fitted to equation 2 by nonlinear least-squares. The spring data gave an estimate of $\lambda = 1.35$. Combining the 2 sets yielded $\lambda = 1.31$. The population trajectories of the separate fits follow that of the combined fit very closely, but the fall population had ~20–30 more wolves at the peak population levels than the combined estimate (Fig. 1).

The major discrepancies between the original estimates prior to 1975 and our backward projection occurred in 1965 and 1974 (Fig. 1). Van Ballenberghe (1981, 1985) indicated that the 1965 estimate was based on a larger area than that studied by Ballard et al. (1987) and proposed that the 1965 population estimate should be revised to a range of 170–206 so that the upper limit of his estimate coincides with our projected value (Fig. 1). Both the original

Table 2. Age structure data for female caribou observed at checking stations, Nelchina herd, Alaska.

Year	Age classes[a] 0.5	1.5	2.5	3.5	Prime[b]	Mature[b]	Old[b]	Total
1954	6	25	23	30	90	10	0	184
1955	1	8	4	6	19	4	0	42
1956	**4**[c]	23	26	39	42	14	6	154
1957	**4**	**7**	11	14	22	9	2	69
1958	2	**2**	**7**	6	12	12	4	45
1959	8	18	**3**	5	26	11	1	72
1960	20	24	22		64	30	4	164
1961	34	19	28		77	28	7	193
1962	19	47	26		58	18	8	176
1963	30	15	34		111	24	7	221
1964	**30**	44	25		88	25	6	218
1965	**8**	**8**	17		33	56	2	124
1966	**4**	**8**	**1**		40	15	6	74
1967	2	**0**	**1**		17	6	3	29
1968	9	12	**4**		17	59	12	113
1969	10	21	45	20	60	39	11	206
1970	2	11	30	35	31	45	29	183
1971	42	27	74	75	133	95	90	536
Total	235	319	381	230	940	500	198	2,803

[a] Age classes are those used at checking stations.

[b] See text for definition of these classes.

[c] Bold-faced type indicates years when recruitment seemed to be reduced.

1974 estimates and Van Ballenberghe's revision were substantially less than the trend we estimated from the data of Ballard et al. (1987).

Trends in the Caribou Population

The relatively low numbers of calves and yearlings in the age structure data from the harvests (Tables 2 and 3) indicate that these age classes usually were not taken in proportion to their abundance in the population. Sharp reductions in recruitment occurred in 1964–1966 and possibly during 1956 and 1957. The reductions in 1964–1966 are further confirmed by inspection of detailed age structures available in 1969–1971, when age was determined by tooth sectioning and counts of growth annuli (ages for earlier years were estimated from tooth wear and replacement patterns). The reductions in recruitment also are evident in the recruitment rates (Fig. 2).

Chi-square values for individual age groups from the model compared to the observed age data (Tables 2 and 3) suggest some discrepancies from the model but do not seem to indicate any persistent pattern. In particular, the first (1954) age sample does not seem consistent with the remaining data. Also, it is possible that discrepancies in 1969 and 1970 were associated with the sharp decline of recruitment in the year classes of 1964–1966 (Table 2). Determination of age (excepting the 1969–1971 data) by tooth wear and replacement patterns very likely resulted in most of the discrepancies between calculated and observed ages. Some age classes were combined in field aging and labelled "prime," "mature," and "old" (Tables 2 and 3). In 1960–1962, these included ages 3.5–7.5, 8.5–12.5, and >13.5 years, respectively. Age categories were changed for 1961–1968 to 3.5–5.5, 6.5–9.5, and >10.5 years, respectively.

The overall population trajectory (Fig. 3) confirms a generally held opinion that the 1967 census estimate was too high. Calculated male survival rates were lower than those for females (Fig. 4). Hunting survival rates were generally lower than those from wolf predation

Table 3. Age structure data for male caribou observed at checking stations, Nelchina herd, Alaska.

Year	Age classes[a]							Total
	0.5	1.5	2.5	3.5	Prime[b]	Mature[b]	Old[b]	
1954	8	65	66	74	173	31	0	417
1955	2	22	27	31	45	14	4	145
1956	**17**[c]	46	53	44	53	51	7	271
1957	**4**	**13**	36	40	48	25	3	169
1958	2	**4**	**14**	12	11	4	2	49
1959	15	37	**34**	**11**	45	11	6	159
1960	36	43	31		96	25	4	235
1961	24	39	55		71	19	2	210
1962	24	64	42		176	55	15	376
1963	26	31	60		238	23	5	383
1964	**23**	65	53		78	126	9	354
1965	**6**	**13**	18		48	109	7	201
1966	**3**	**17**	**8**		98	35	8	169
1967	4	**2**	**2**		9	1	0	18
1968	12	25	**7**		75	13	5	137
1969	15	23	44	**25**	93	30	3	233
1970	9	16	41	49	58	23	7	203
1971	50	32	60	106	72	20	9	349
Total	280	557	651	392	1,487	615	96	4,078

[a] Age classes are those used at checking stations.
[b] See text for definition of these classes.
[c] Bold-faced type indicates years when recruitment seemed to be reduced.

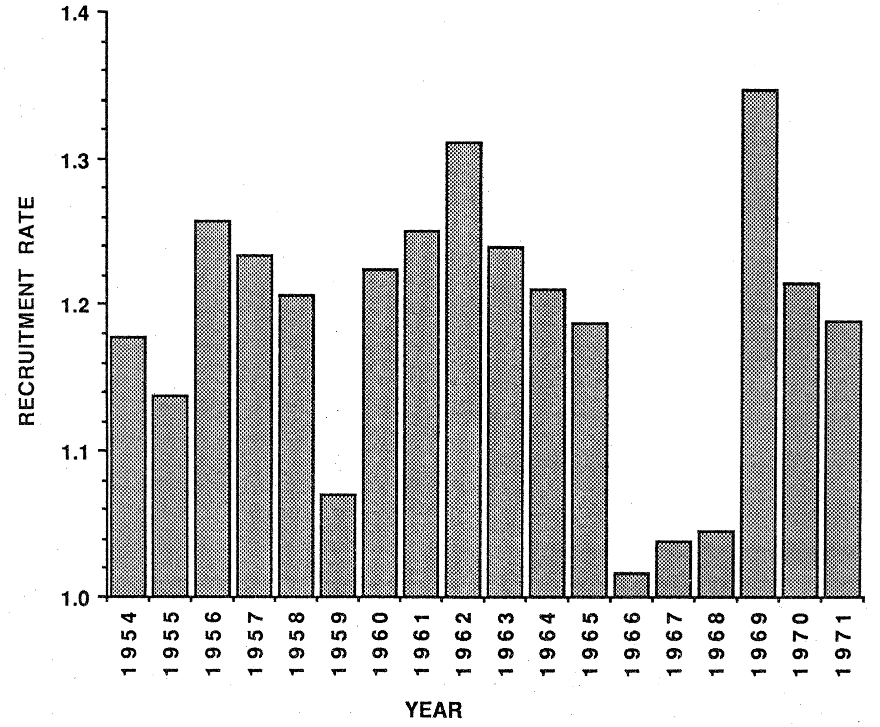


Fig. 2. Recruitment rate for female caribou calculated as the ratio of 2.5 year olds to all older caribou observed at checking stations.

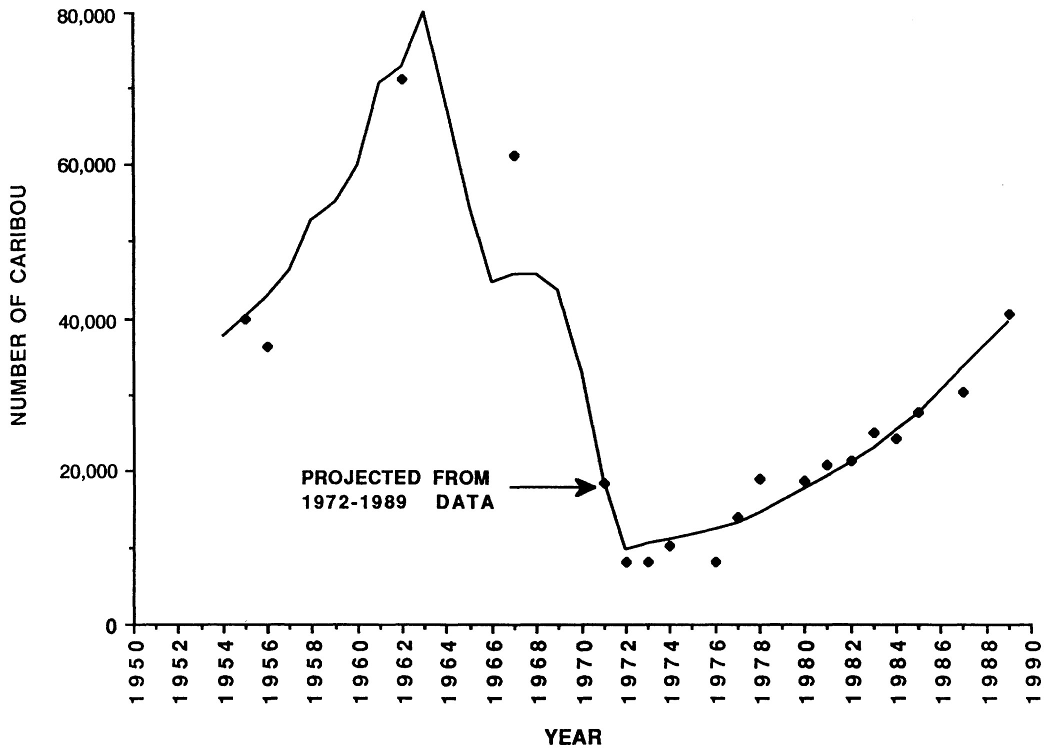


Fig. 3. Trend of the Nelchina caribou herd from the age structure model. The proportion of calves was arbitrarily assumed to be 5% in 1964, whereas calves and yearlings were assumed to be 5% in 1965 and 1966 and yearlings 5% in 1967 as suggested by a sharp reduction in recruitment rates in 1964–1966 year classes. Plotted points represent direct population estimates, except the point for 1971, which was estimated from the subsequent censuses (see text for details).

(Fig. 5), in part because wolf numbers did not reach high levels until the 1970's (Fig. 1).

Mandibles were shorter during the mid-1960's than in 1989–1990 (Fig. 6). Mean mandible length during the mid-1960's for mature females ($\geq$4 years old) was 275 mm compared to 287 mm in 1989–1990. For mature males ($\geq$5 years old), mean mandible length was 297 and 321 mm, respectively. Mandible lengths differed between time periods and sexes ($P < 0.001$).

DISCUSSION

Both hunters and wolves influenced caribou survival, but the key factor in the ultimate decline seemed to be the sharp reduction in recruitment in 1964–1967. No field observations were available on the role of wolves in the drop in recruitment in those years.

We believe that the improvements provided by our analysis have largely to do with refinements in interpolation and extrapolation of existing data points. For wolves, we used a backward projection based on the extensive set of census data from 1975 onward collected by Ballard et al. (1987). One weakness lies in uncertainty as to the accuracy of the 1966–1970 wolf harvest data and especially in the large number reported killed in 1967–1968. The backward projection also rests on the assumption of a relatively constant rate of increase (λ). Because it seems quite certain that there was only a small population of wolves (possibly

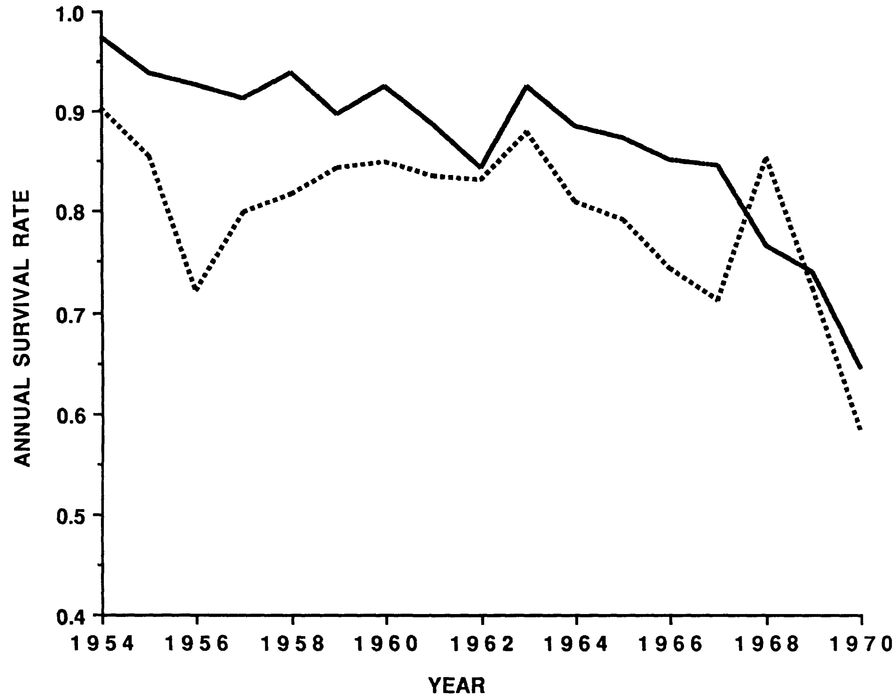


Fig. 4. Estimated female (solid line) and male (broken line) caribou survival rates, based on age structure samples used in a population model (see text for details).

<20 individuals) in the Nelchina area in the early 1950's, and that the wolf population was unhunted and had a very large prey base, λ for wolves might have been higher and diminished as the wolf population became larger. However, the rate that we estimated from the data of Ballard et al. (1987) (about 1.3) seems to be in agreement with values obtained by Keith (1983) for 7 wolf populations. Our estimated trend line seems to agree with the earlier estimates (Fig. 1).

Annual caribou population estimates in previous studies were largely based on 3 census values (1956, 1962, and 1972) by linear interpolation between pairs of census values. The 1967 estimate (61,000) was reduced sharply to fit into the trend of this sequence. Van Ballenberghe (1989) gave 7 such sequences of points. Other assumptions about constancy of λ between census points can be made (Eberhardt 1987) and thus include the 1967 census value in a reconstruction of population trend. The advantage of our approach is that estimates of each year's recruitment and kill rates were used, so that the intracensus estimates are based on actual data for those years. Our process nonetheless involves some interpolation because we selected wolf predation rates that brought the projected population down to the 1971 caribou population estimate obtained by back-projecting the 1972–1984 censuses. We also suspect that the 2.5-year-old females may have been killed slightly less readily by hunters than were older females.

In most discussions, emphasis has been placed on the roles of predation, winter weather, and hunter harvest in the decline of the Nelchina caribou herd with little consideration given to food limitation. Only Doerr (1979) speculated that decreased recruitment of calves was related to range quality. Mandible measurements indicated that growth was reduced during the mid-1960's when caribou density was high. This implies that food resources may have

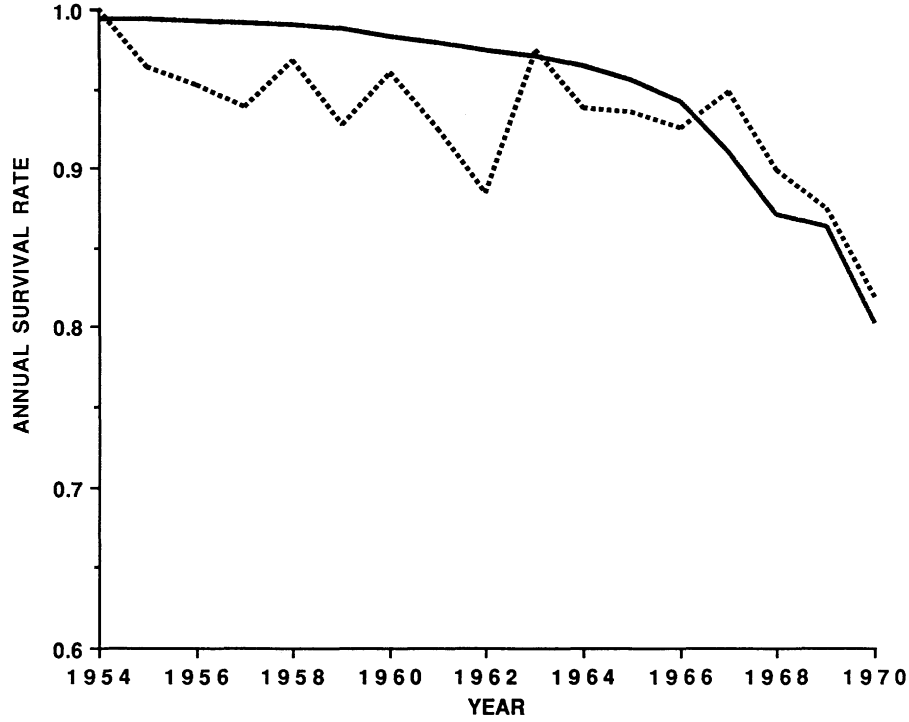


Fig. 5. Annual survival of female caribou associated with hunting (broken line) and wolf predation (solid line), based on age structure samples used in a population model (see text for details).

been suboptimal. Pegau and Hemming (R. E. Pegau and J. E. Hemming, Caribou Rep., ADFG, Juneau, 1972) found that range conditions in 1970, particularly the lichen component, had deteriorated substantially from earlier surveys. Hence, food limitation could have played a role in the initial decline of the Nelchina caribou herd. We believe that prudent management requires that the herd be maintained below the peak level of the 1960's. Such management is feasible through hunting alone. The role of wolves in caribou population dynamics needs to be determined by socioeconomic considerations. Monitoring caribou growth and physical condition should be an integral part of the management program.

MANAGEMENT IMPLICATIONS

The lack of frequent and reliable censuses of the Nelchina herd hindered detection of the decline that occurred between 1964 and 1972 (Fig. 3). The annual or biennial censuses conducted since 1972 should be sufficient to prevent such an oversight from occurring in the future. In retrospect, the initiation of the decline in caribou numbers was clearly foreshadowed by a sharp drop in recruitment. The relative contributions to low recruitment of wolf predation, winter severity, and resource limitation are not known. In the future, annual measures of recruitment will be essential to provide protection against a similar decline. Sampling with direct counts of the proportion of calves in the herd has an advantage as a measure of recruitment over using the proportion of 2.5-year-old animals in the hunter harvest because it provides an immediate indicator of calf recruitment. However, it gives no protection against unusual winter losses. Hence, it is apparent that collection of age samples from hunter harvests also is necessary.

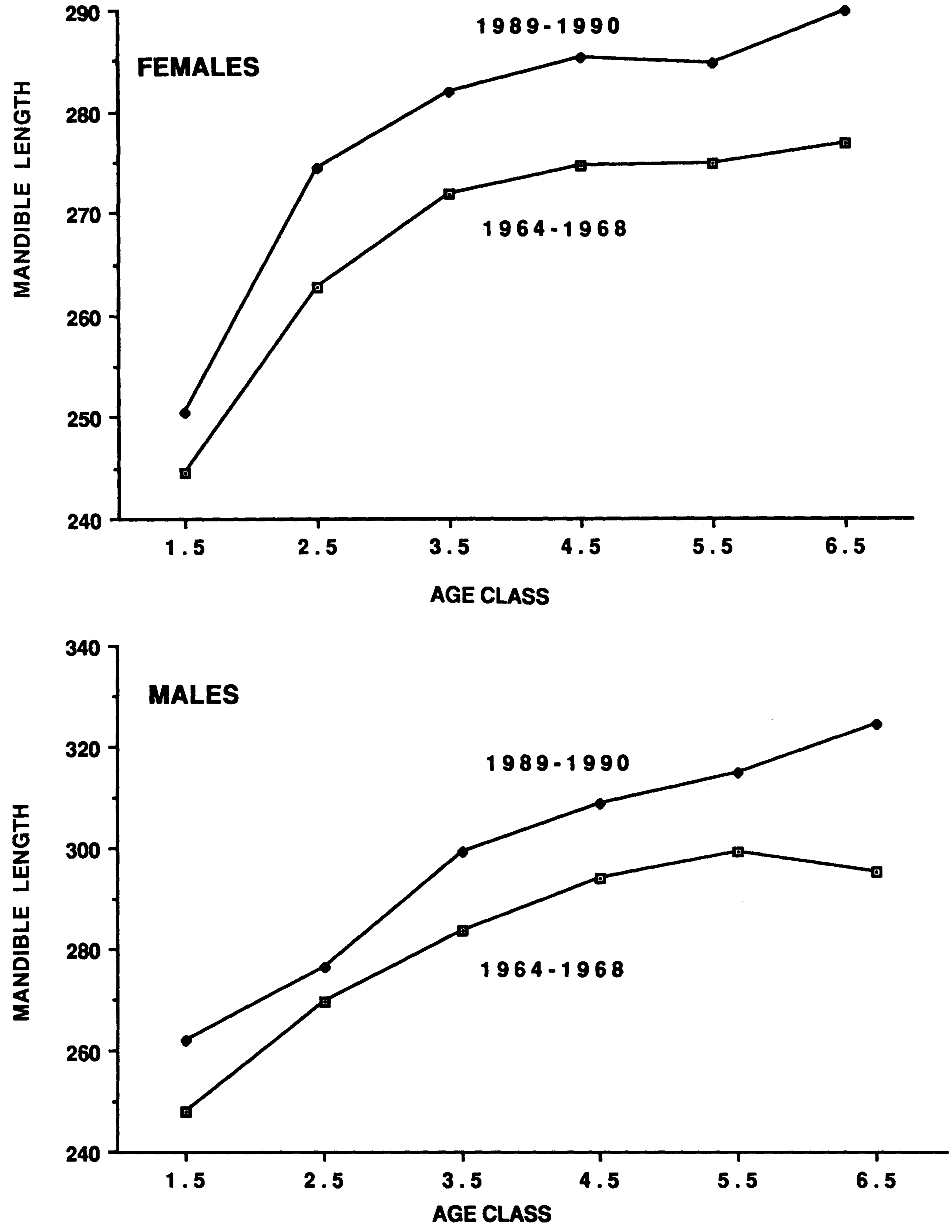


Fig. 6. Mandible lengths for male and female caribou for 2 time periods.

With increasing wolf populations and increasing caribou density, monitoring adult survivorship will be important. If a major reduction in recruitment or adult survivorship occurs, a curtailment of hunter harvests will be needed. The continued high harvests in the late 1960's and early 1970's (Table 1) exacerbated the effects of the low recruitments from 1964–1966.

We doubt that harvest levels during most of the 1960's, even with poor recruitment, were high enough to drive the caribou population to an unacceptably low level, as indicated by the estimated survival rates (Fig. 4). Curtailment of harvests of female caribou starting in 1968 would likely have maintained the herd at 30,000–40,000, a level that has taken 20 years to again obtain.

If a particular management policy for the herd is adopted and consistently enforced, its success or failure may constitute a valuable "test" of important hypotheses about population interactions, including such aspects as the role of wolves in population regulation. Acceptance of the outcomes will depend on how carefully the competing hypotheses are defined in advance and how accurately and precisely populations are monitored. Even so, a single trial on 1 herd, no matter how well designed and executed, cannot be expected to settle the role of predation in caribou population dynamics.

SUMMARY

Simple models were used to examine wolf and caribou population data in the Nelchina Basin of south-central Alaska. Use of a projection method made it possible to back-calculate previous wolf abundance from a sequence of recent population estimates, and an age structured model permitted interpolation between the few historical census points available for caribou. Adult survival rates calculated from the caribou data indicate that, although the sharp reduction in recruitment in 1964–1966 undoubtedly reduced population size substantially, curtailment of female harvests in 1968 would likely have precluded the "crash" of 1970–1971.

LITERATURE CITED

BALLARD, W. B., J. S. WHITMAN, AND C. L. GARDNER. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildl. Monogr. 98. 54pp.

BERGERUD, A. T., AND W. B. BALLARD. 1988. Wolf predation on caribou: the Nelchina herd case history, a different interpretation. J. Wildl. Manage. 52:344–357.

———, AND ———. 1989. Wolf predation on the Nelchina caribou herd: a reply. J. Wildl. Manage. 53:251–259.

DOERR, J. 1979. Population analysis and modeling of the western Arctic caribou herd with comparisons to other Alaskan *Rangifer* populations. M.S. Thesis, Univ. Alaska, Fairbanks. 340pp.

EBERHARDT, L. L. 1987. Population projections from simple models. J. Appl. Ecol. 24:103–118.

———. 1988. Testing hypotheses about populations. J. Wildl. Manage. 52:50–56.

KEITH, L. B. 1983. Population dynamics of wolves. Pages 66–77 *in* L. N. Carbyn, ed. Wolves in Canada and Alaska. Can. Wildl. Serv. Rep. Ser. 45.

RAUSCH, R. A. 1969. A summary of wolf studies in south-central Alaska, 1957–1968. Trans. North Am. Wildl. and Nat. Resour. Conf. 34:117–131.

SINIFF, D. B., AND R. O. SKOOG. 1964. Aerial censusing of caribou using stratified random sampling. J. Wildl. Manage. 28:391–401.

SKOOG, R. O. 1968. Ecology of caribou (*Rangifer tarandus granti*) in Alaska. Ph.D. Thesis, Univ. California, Berkeley. 699pp.

SUTTIE, J. M., AND B. MITCHELL. 1983. Jaw length and hind foot length as measures of skeletal development of red deer (*Cervus elaphus*). J. Zool. London 200:431–434.

VAN BALLENBERGHE, V. 1981. Population dynamics of wolves in the Nelchina Basin, southcentral Alaska. Pages 1,246–1,258 *in* J. A. Chapman and D. Pursley, eds. Proc. worldwide furbearer conference. R. R. Donelly and Sons, Co., Falls Church, Va.

———. 1985. Wolf predation on caribou: the Nelchina herd case history. J. Wildl. Manage. 49:711–720.

———. 1989. Wolf predation on the Nelchina caribou herd: a comment. J. Wildl. Manage. 53:243–250.

WATSON, G. W., AND R. F. SCOTT. 1956. Aerial censusing of the Nelchina caribou herd. Trans. North Am. Wildl. and Nat. Resour. Conf. 21:499–510.

Received 17 May 1991.
Accepted 11 April 1992.
Associate Editor: Swihart.