PROCEEDINGS OF THE

# SECOND INTERNATIONAL REINDEER/CARIBOU SYMPOSIUM

## 17. – 21. SEPTEMBER 1979

## RØROS, NORWAY

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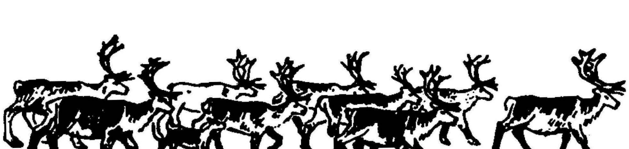
DIREKTORATET FOR VILT OG FERSKVANNSFISK
TRONDHEIM 1979



Reimers, E., Gaare, E. and Skjenneberg, S. (eds.) 1980.
Proc. 2nd Int. Reindeer/Caribou Symp., Røros, Norway,
1979. Direktoratet for vilt og ferskvannsfisk, Trondheim.

# POPULATION DYNAMICS OF ALASKA'S WESTERN ARCTIC CARIBOU HERD

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## ABSTRACT

Since the late 1940's when large caribou herds were first censused systematically, Alaska's Western Arctic Herd attained the largest size of any caribou herd in North America. Some investigators, without census data, estimated that the herd numbered over 300000 in the 1960's. Based on an aerial photo census, the herd was estimated to number at least 242000 in 1970. By July 1976 the population had declined to a minimum of 75000, the lowest in over 4 decades. Heavy harvest by rural "subsistence" hunters (including waste), and substantial predation by wolves were the primary causes of caribou mortality during the post-1970 decline. Reduced yearling recruitment, although unsubstantiated, may have contributed. Reduced harvest, reduced predation, and a probable increase in yearling recruitment allowed the herd to increase to about 113000 by July 1979. Computer simulation indicates that known or estimated harvest levels, predation rates, and herd productivity data can account for the observed population changes without any emigration, immigration, or catastrophic die-off.

## 1. INTRODUCTION

Concern for conservation and management of caribou (*Rangifer tarandus granti*, Banfield) in Alaska has increased steadily during the 1970's. This is because of rapidly increasing exploration and development in the North coincident with heightened environmental awareness and recent major declines in some Alaska caribou herds (Klein and White 1978). Major herds that declined include the Delta, Fortymile, McKinley, Nelchina, and Western Arctic (WAH). Between 1970 and 1977 the Alaskan caribou population declined between 42% and 55% (Davis 1978a).

Because the WAH was the largest herd in North America and its decline was numerically most dramatic, the population dynamics and management of the herd have been a focus of public and scientific attention since the decline was documented in 1975 (Davis and Valkenburg 1978).

Several studies addressing many facets of the ecology of the WAH were initiated in 1975 and 1976, but results are just beginning to be published. Results of several of these studies are reported in these proceedings. Doerr (1979) analyzed the population data available for 1961 through 1976 with an emphasis on modeling and his proceedings paper is based on the findings. Our paper is primarily descriptive and emphasizes the period of 1976 through 1979.

## 2. STUDY AREA

The range of the WAH encompasses the northwest quarter of Alaska, approximately 362600 km$^2$ (cf. Fig. 3, in Davis 1980). The physical environment has previously been described in detail (Spetzman 1959, Lent 1966, Skoog 1968, Hemming 1971).

The range of the herd extends from 65°N to 71°N and from 148°W to 166°30'W. Vegetation varies from boreal forest in the south to wet coastal tundra in the north. The area is bisected into north and south sections by the western part of the Brooks Range.

## 3. METHODS

### 3.1. Population size and dynamics

Many of our pre-1975 data were obtained from the literature and the unpublished reports and files of the Alaska Department of Fish and Game (ADF&G). Herd size estimates since 1975 were obtained from calving ground count-extrapolation censuses and aerial photo-direct count-extrapolation censuses which are described in Davis and Valkenburg (1978). We used a refined aerial photo-direct count-extrapolation procedure in 1978 (Davis et al. 1979).

We used iterative arithmetic models and computer simulations to analyze population dynamics of the herd. Initial computer simulations were made by Doerr (ADF&G files); these simulations were refined using the ONEPOP program through the courtesy of Dr. J. Gross (ADF&G files). Final modeling was done using an improved ONEPOP program; during analysis we referred to modeling in Doerr (1979).

### 3.2. Harvest by humans

Caribou harvest was recorded in 1975–1976 by local data collectors in some villages, and in other villages through periodic visits by ADF&G biologists who made personal observations, interviewed residents, and obtained additional information from village councils and public officials (Davis and Valkenburg 1978).

Commercial use of caribou, allowed until 1976, was estimated by interviewing the major buyers. Crippling loss and waste of caribou were evaluated by personal observation, aerial and ground surveys, interviews, pilot reports, complaints from villagers, and public meetings. Also, observations regarding harvest and waste were contributed by other investigators conducting field work on the WAH (Shea 1978, Doerr 1979, D. Klein pers. comm.).

A permit system was initiated in 1976 and has been in effect since. During 1976–1977, village harvests were determined with the assistance of village residents employed to collect mandatory harvest reports. Since 1976–1977, harvest has been determined from mandatory harvest reports required under provisions of the permit hunts (Davis and Valkenburg 1978).

### 3.3. Composition and productivity

We sampled the sex and age composition and productivity of the herd several times annually by conducting classification counts from the ground, from helicopters, and from fixed-wing aircraft. The latter was used only when survey objectives were to obtain neonate calf/adult ratios or calf percent of sample (Davis and Valkenburg 1978). In addition, the age structure of the WAH was examined by Doerr (1979) and ADF&G from a sample of 522 jaws from 1959–1961 and 736 jaws from 1975–1976. Ages of calves and yearlings from the 1959–1961 collection and calves from the 1975–1976 sample were determined by eruption and wear methods(Skoog 1968, Miller 1972). Ages of older animals were determined by counting cementum annuli with a technique described by Davis (1978b) which is similar to one used by Miller (1974).

### 3.4. Predation and natural mortality

Data on wolf densities were obtained from intensive field studies in relatively small areas (Stephenson 1975) and from aerial surveys designed to estimate density over large regions (Stephenson and James in press, unpubl. ADF&G data). Using several indices, we inferred upward or downward trends; for instance, during aerial surveys of caribou we recorded frequencies of wolf sightings, wolf tracks, and dead caribou which had apparently been killed or eaten by predators (ADF&G unpubl.). We also interviewed persons with knowledge of local areas and wolf harvest trends.

Natural mortality rates were primarily extracted or extrapolated from the literature.

## 4. RESULTS

### 4.1. Population size

Credible population estimates for the WAH prior to the 1950's are not available. However, information about the relative abundance of caribou in northwest Alaska from the early 1800's is available (Lent 1966, Skoog 1968). Caribou were generally abundant in the mid-1800's but were locally scarce by the late 1800's. They had declined to low levels by the early 1900's.

An increase in caribou numbers in the area was noted in the early 1920's (Bailey and Hendee 1926, Murie 1935). The caribou population in northwestern Alaska continued to grow through the late 1920's, perhaps augmented by shifts of animals from the east and by a general movement from the south (Skoog 1968). In the mid-1930's caribou were being sighted along the Bering Sea coast north of the Seward Peninsula, and reindeer herders began to have serious problems with reindeer joining migrating bands of caribou (Rood 1942).

Scott et al. (1950) reported the first attempt to census caribou in arctic Alaska using aircraft. They concluded that northwestern Alaska supported 119000 caribou in 4 populations. Subsequent studies identified only 1 population (Hemming 1971). Skoog (1968) recognized the biases and inaccuracies in the estimates made by Scott et al., and utilized more recent knowledge (Watson and Scott 1956) to revise the earlier statewide estimate of 160450 upward to 325000. Assuming a proportional adjustment, the WAH would have numbered 238000 in 1950.

Lent (1966) conducted the first intensive study of the WAH between 1959 and 1962. Using a method similar to the aerial photo-direct count-extrapolation (APDCE) technique developed in the late 1960's (Hemming and Glenn 1969, Hemming 1972), Lent estimated that the minimum precalving population in 1961 was 130000 animals. He calculated the July post-calving population to be 156000 animals but thought that the population actually numbered between 175000 and 200000 because he had probably missed some calving segments of the herd.

In 1964 Skoog (1968: 250) estimated the population to be 300000 animals based on the magnitude of the village harvests. It was not until 1970 that another census was conducted. Hemming (1972) counted a total of 179843 caribou from photographs of the 1970 post-calving aggregations, and visually counted an additional 10380 in areas not photographed. He estimated the total population in 1970 to be 242000 animals and calculated that there were 97394 cows older than yearlings.

In 1975 Davis and Valkenburg (1978) made herd estimates ranging from 67000 to 121000 and concluded that 102704 was the best estimate. In 1976, when the herd reached its recent lowest level, Davis and Valkenburg (1978) reported a minimum estimate of 65000, but indicated that the population was likely larger. For 1977 they calculated estimates of 77000 to 82000.

Davis et al. (1979) generated 1978 estimates of 90000 to 122000 and concluded that ca. 102000 was the best estimate for the WAH exclusive of 4000 in the recently recognized Teshekpuk herd (Davis 1978b, Davis 1980). Extrapolation from a calving ground census in 1979 (ADF&G unpubl.) produced a 1979 herd estimate of 113000+. The population changes from 1970 to 1979 are depicted in Fig. 1.

#### 4.2. Harvest

Annual estimates of harvest from the WAH since 1962 were summarized in Davis and Valkenburg (1978). Few harvest data prior to 1962 are available. From 1963 through June 1976 there was no closed season and no bag limit for hunting caribou north of the Yukon River. During this period humans annually harvested 20000 to 30000 ($\overline{x}$ = 25000) caribou from the WAH. An estimated minimum of 95% of these caribou were taken by rural residents, mostly Native Alaskan "subsistence" hunters. This included only the retrieved harvest and not necessarily the substantial loss to wounding and waste (Davis and Valkenburg 1978, Doerr 1979).

Findings from 1975 resulted in major harvest restrictions in regulatory year 1976–1977 (i.e. July 1, 1976 through June 30, 1977) when hunting was limited to 3000 permits issued for taking bulls only. Of these 2334 (77.8%) were issued. A harvest estimate of 1687 was extrapolated from permit returns. Adding known and suspected harvests, we estimated that harvest for the year was between 2700 and 3500. A high percentage of these were bulls.

In 1977–1978 a 3000 bull harvest quota was in effect. Permits were available to all applicants, but only 2883 were issued. A liberal extrapolation from hunter report summaries indicates a harvest of 1932; however, we believe that the actual harvest was larger (perhaps 4000). Also, a substantial but unknown portion consisted of illegal females. During the 1978–1979 season a harvest quota of 5000 bulls was in effect and permits were again issued to all applicants. During this split season hunt, 2196 permits were issued in the fall and 2490 in the spring. Combined reported harvest was 1151. However, field reports (ADF&G files) indicate a larger harvest. We estimate that actual harvest was at least double that reported and again included a substantial but unknown proportion of illegal females.

#### 4.3. Herd composition and productivity

Doerr (1979) discussed the age structure of the herd as determined from jaw collections obtained from the hunter kill. Changes in herd composition and productivity as determined by periodic field surveys are given in Tab. 1, Fig. 2. Although fall composition data can be quite variable and are not necessarily representative of true herd composition (Davis et al. 1979, Doerr 1979), the data in Tab. 1 suggest a net decline in the adult bull/cow ratio since 1970. The mean bull/cow ratio for 1968 and 1970 (no 1969 data) was 63 bulls: 100 cows compared to the 1975 through 1978 mean of 45 bulls: 100 cows. Available calf natality and survival data suggest a substantial improvement in post-1975 survival rates of calves from birth to post calving (3–4 weeks of life) and fall (16–18 weeks) compared to pre-1976 values.

The composition data presented in Tab. 1 likely are not an accurate estimate of yearling recruitment to the herd (i.e. survival of calves to 12 months of age). (We acknowledge that actual recruitment must be calculated as breeding stock replacement.) These data were obtained from October counts when yearlings are extremely difficult to classify accurately. Bergerud has proposed an adjustment to fall yearling ratios (1.4 x observed) to compensate for underestimates. Our observations confirm the likelihood that fall composition counts underestimate yearlings. Consequently, we estimated yearling recruitment rates by conducting over-

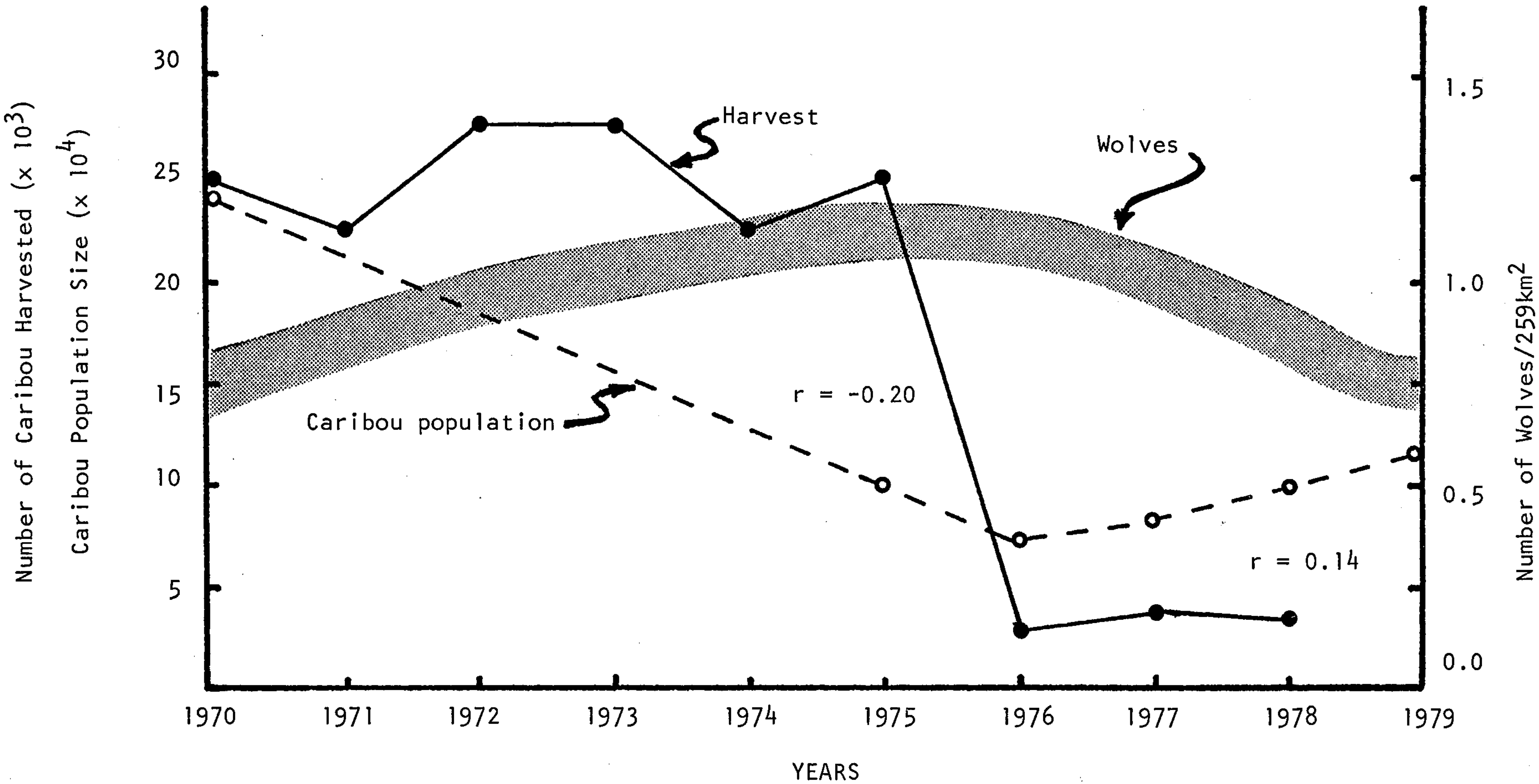


Fig. 1. Trends in the caribou population size, number of caribou harvested by humans, and relative wolf abundance in the range of the Western Arctic Caribou Herd, 1970-1979.

Tab. 1. Fall herd composition data from the Western Arctic Herd, 1961-1978.

| | Total Bulls per 100 cows | Yearlings per 100 cows | Calves per 100 cows | Yearling % in sample | Calf % in sample | Cow % in sample | Bull % in sample | Sample size |
|---|---|---|---|---|---|---|---|---|
| 10/18/52 | | | | | 26.0 | | | 320 |
| 10/18/52 | | | | | | | 10.0 | 614 |
| 10/16-19/53 | | | | | 24.0 | | | 164 |
| 9/20-24/54 | | | | | 28.0 | | 19.0[1] | 393 |
| 10/18-21/61 | 55.0 | 8.2 | 37.3 | 4.2 | 18.6 | 49.8 | 27.4 | 1006 |
| 10/26-28/68 | 62.0 | 23.0 | 34.0 | 10.6 | 15.6 | 45.6 | 28.3 | 2217 |
| Oct 1970 | 64.0 | 20.0 | 44.0 | 8.7 | 19.2 | 43.8 | 28.0 | 6222 |
| 10/18-19/75 | 31.0 | 13.0 | 48.0 | 7.0 | 25.0 | 52.0 | 16.0 | 2231 |
| 10/16-18/76 | 58.0 | 26.0 | 48.0 | 11.3 | 20.6 | 43.1 | 25.0 | 7140 |
| 10/19-21/77 | 43.2 | 28.5 | 41.7 | 13.4 | 19.5 | 46.9 | 20.3 | 6881 |
| 10/14-20/78 | 47.6 | 20.6 | 47.7 | - | - | - | - | - |

[1] Bulls older than yearlings.

winter calf survival surveys in April of 1977, 1978 and 1979.

We also attempted to ascertain the chronology of calf mortality through aerial composition counts. Initial calf production in the core calving area of the WAH was 76.9 calves:100 cows in 1976. Calf production in peripheral areas was lower, about 60 calves:100 cows. The weighted mean was 73. There was a 26.3% reduction in the ratio from peak of calving in mid-June to early July due, in part, to an influx of non-parturient cows and groups of cows with lower calf ratios from peripheral areas. However, some loss of calves was observed, primarily to grizzly bears (*Ursus arctos horribilis,* Ord). Because the calf/cow ratio was unchanged from July to October, we concluded that calf mortality between early July and late October was proportional to the mortality rate of cows. We estimated that this rate was less than 1.5% by pro-rating a 5% to 6% annual mortality rate (Kelsall 1968, Skoog 1968, Bergerud 1971). We believe that this rate was low, in part because of very low wolf density (Stephenson and James in press) on the arctic coastal plain where the herd summered.

Subsequent calf survival from late October 1976 to mid-April 1977 was 94.1%, based on comparison of calf/cow ratios and assuming 1) that no mortality of cows occurred during this period, and 2) that one-half of the yearlings classified in October 1976 were females. In October 1976 we observed 54 calves:100 cows and in April, after adjusting for the 2-year-old cows (i.e. long yearlings, 23 months old) not distinguishable from adult cows, we calculated a ratio of 51.5 calves:100 cows. It should be mentioned that April calf/cow ratios were obtained only from a sample of the herd that wintered south of the Brooks Range. However, in a sample of 1195 caribou that wintered north of the Brooks Range, 22% were calves. Therefore, we concluded that over-winter calf survival for the entire herd approached 94%.

However, we emphasize that calf survival calculated from changes in ratios are based on the invalid assumption that there is no adult female mortality from fall to spring. Hence, the actual calf survival rate (total calves in spring – total calves in fall) is overestimated. In October 1977 we observed only 26 yearlings (i.e. 16 months old):100 cows; however, because of biases (Davis and Valkenburg 1978), we calculated a more like estimate of 43 yearlings:100 cows.

Estimates for the 1978 calf cohort were 68:100 at the peak of calving and 52:100 at he end of June – a 23% decline compared to 26% in 1976. The ratio declined to 42:100 by October. The mean herd calf/cow ratio in April 1978 (adjusted as in 1976 to allow for 23-month-old animals being lumped with cows) was 29:100 or a 31% decline from October. Calf survival on the arctic coast near Point Lay was particularly low (19.5:100). The ratio south of the Brooks Range was higher than the herd mean (35.2:100). A clue to the poorer calf survival on the coastal plain was our discovery of several dead or moribund calves near Point Lay. All had considerable numbers of nasal bot fly (*Cephenomyia trompe,* Modeer) larvae in the throat and/or heavy warble fly (*Oedemagena tarandi,* L.) larvae infestations. One calf supported 1900 to 2000 warble fly larvae by actual count and a second was visually judged to have a similar number. Winter temperatures and snow accumulation were considered less severe than average by our field crew and local residents.

Yearling recruitment in 1979 was difficult to calculate because most data were obtained from fixed-wing aircraft and only calf percentages in the samples could be determined. The herd was sampled in 6 locations between March 17, 1979 and May, 12, 1979 and the unweighted percentages of short yearlings ranged from 14 to 41% ($\bar{x}$ = 26.2 and s.d. = 10.9). The weighted mean was 23.4%. If the samples were representative of the

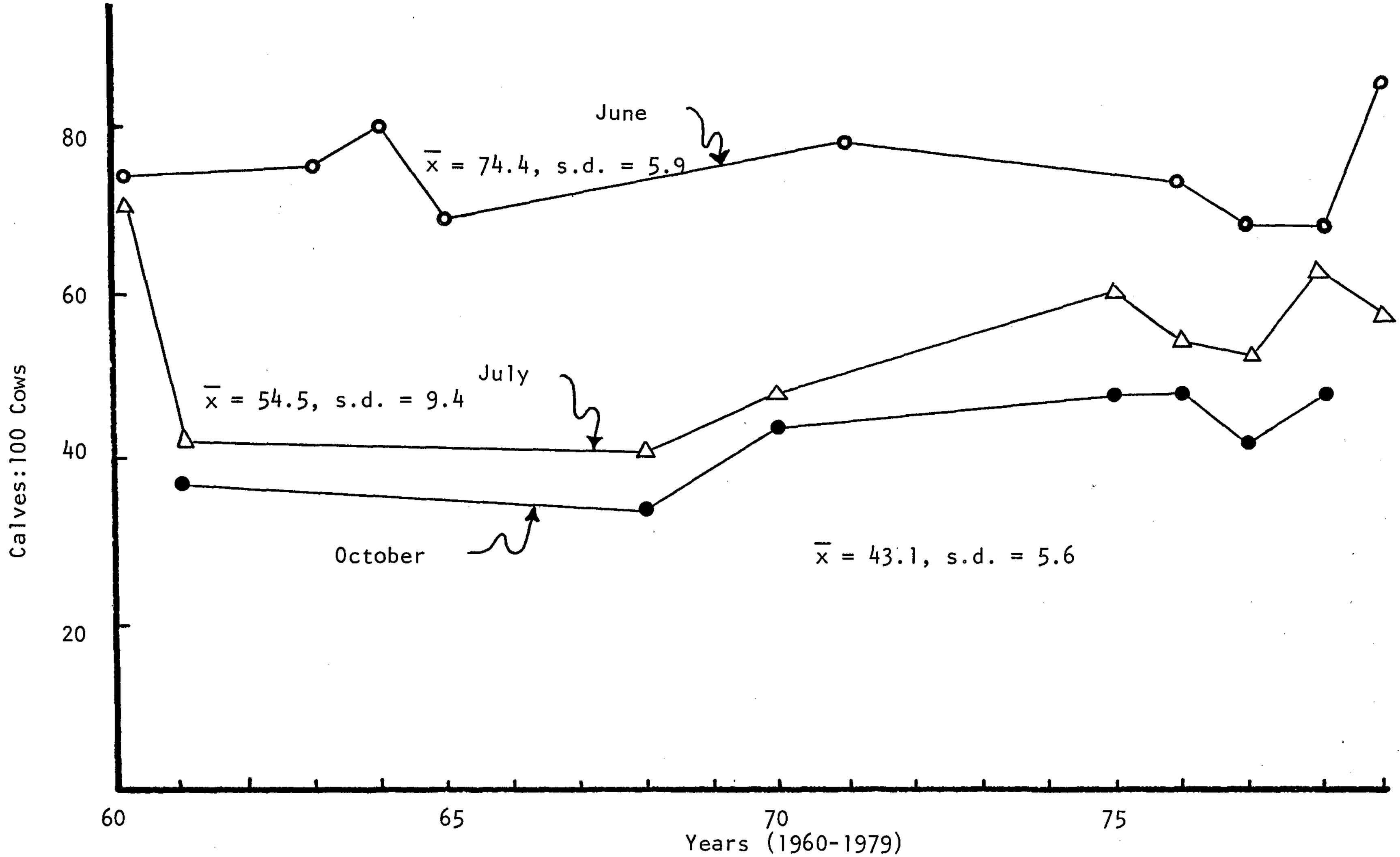


Fig. 2. Calves:100 cows in the Western Arctic Caribou Herd during early June, July, and October 1960-1979.

herd, the overwinter survival of calves must have been excellent considering the high percentage of short yearlings observed.

### 4.4. Predation and natural mortality

Predation, primarily by wolves, was hypothesized as the second largest mortality factor (second to human-induced mortality) operating on the WAH in 1975 (Alaska Department of Fish and Game 1976, Davis and Valkenburg 1978). The conjectured level of wolf predation has been widely discussed (Davis et al. unpubl, Haber 1977, Doerr 1979, Stephenson unpubl., Stephenson and James in press), but few data are available to substantiate the estimates. We believe that wolf predation on the WAH greatly diminished between 1976 and 1979. This reduction is thought to have occurred because of changes in spatial distribution between the caribou and wolves and also because of fewer wolves. Beginning in 1976–1977, approximately half the WAH has wintered annually on the arctic coastal plain where wolf density is extremely low (Stephenson and James in press). Although some areas of relatively high wolf abundance remain in the southern portion of the herd's range, there has been an apparent regional decline in wolf numbers. Possible explanations include substantial legal and illegal hunting, the widespread occurrence of rabies and other canine diseases, and a general decline in the abundance of caribou and moose. Aerial surveys of wolves substantiated their low density on the arctic slope winter range (Stephenson and James in press). Supporting data for the reduced wolf abundance in some southern portions of the herd's range involve inference from other indices. During aerial surveys for caribou, the frequencies of sighting wolves, wolf-killed caribou, and wolf tracks have declined substantially since 1975–1977 (ADF&G files). Deaths of wolves from rabies, in one instance decimation of a pack, were documented twice in arctic Alaska during this period (Chapman 1978, Stephenson pers. comm.). Other canine diseases may have been involved because many village dogs reportedly died during this period. To a degree, wolf harvest levels also support the contention of lowered wolf abundance. A similar situation of lowered wolf abundance and increased caribou recruitment after 1976–1977 has been observed in the range of the Central Arctic Herd which is contiguous with the WAH (Cameron and Whitten, pers. comm.).

### 4.5. Other factors influencing population dynamics

We acknowledge that other factors may affect caribou populations. Many of these, including ingress by reindeer, immigration–emigration, disease, parasites, range condition, and weather have been discussed previously (Davis and Valkenburg 1978, Doerr 1979). There is no new evidence that any of these were major factors in the recent decline and subsequent increase of the herd.

## 5. DISCUSSION

In 1975, when a dramatic decline of the WAH was first documented, we hypothesized that human exploitation and predation were greatly exceeding recruitment to the herd. Opposing views were that: 1) no decline had occurred; 2) the decline was attributable to emigration, primarily to the Porcupine Herd; 3) the herd was experiencing a "normal" cyclic decline (or some other occult phenomenon), and further that predation and subsistence hunters had no, or only beneficial, effects; and 4) any decline was due to forage deficiencies, and that, if anything, more hunting and predation were necessary to facilitate range recovery.

For those who believe in a cause-and-effect world, the logical prediction to follow our original hypothesis was that the herd would increase if human harvest and predation were eliminated or adequately reduced. An opposing occultist prediction was that the population trend would continue in a given direction regardless of extrinsic changes. Available data strongly suggest that the herd has increased coincident to reduced mortality due to humans and wolves. Obviously some minimum level of yearling recruitment is essential for herd growth even under conditions of no exploitation by humans or predators. If, however, increased yearling recruitment occurs simultaneously to reduced exploitation, and herd growth (r) becomes positive, it is a coincidence difficult to explain using any of the alternative arguments. Further, it seems improbable that forage conditions could deteriorate and recover rapidly enough to account for the drastic short-term decline and subsequent recovery, particularly if herd growth is sustained for several years. We acknowledge that extrinsic factors such as weather must be considered, but the fall and rise of this herd correlates so closely to the level of exploitation that logic argues that exploitation must be the causative force in this situation.

The decline of the WAH is by no means unparalleled. We constructed Tab. 2 to illustrate the similarity of the recent WAH decline with the decline of caribou in northern Canada from 1949 to 1956 (cf. Tab. 24 in Kelsall 1968: 201). The basic difference between Kelsall's scenario and ours is that we adjusted natural mortality rate upward from his assumed constant of 5% to values of from 7% to 9%. Our adjustment was made to reflect the role of wolf predation in northwestern Alaska. Our findings suggest that Bergerud's (1978) mortality rates for adult caribou of 7–13% are more realistic. Also, in contrast to Kelsall, we lowered the deficit to human kill

Tab. 2. A possible scenario for the decline of the Western Arctic Caribou Herd, 1970 through 1976.

| Year | Spring population estimate | Natural[1] mortality (%) | Human kill | 20% crippling loss | Spring[2] population less deficit | Increment after deficit (%) |
|---|---|---|---|---|---|---|
| 1970-71 | 195000 | (7) 13650 | 25000 | 5000 | 155850 | (14) 21819 |
| 1971-72 | 177669 | (7) 12437 | 25000 | 5000 | 139732 | (14) 19562 |
| 1972-73 | 159294 | (8) 12744 | 27500 | 5500 | 118500 | (14) 16590 |
| 1973-74 | 135090 | (9) 12158 | 27500 | 5500 | 94882 | (14) 13284 |
| 1974-75 | 108166 | (9) 9735 | 22500 | 4500 | 77294 | (14) 10822 |
| 1975-76 | 88115 | (9) 7930 | 22500 | 4500 | 57235 | (14) 8013 |
| 1976-77 | 65248 | | | | | |

[1] The percent natural mortality is varied from 7% to 9% based on relative wolf abundance (Fig. 1) and Bergerud's (1978) calculated natural mortality rates of 7% to 13% depending on wolf abundance.
[2] Calculated by: deficit = natural mortality + (0.85)(human kill + crippling loss).

and crippling loss by 15% because we assumed that 15% of the harvest came from the calf cohort between fall and spring. We assumed a liberal 14% recruitment rate, calculated by increasing the mean yearling percentage for 1968–1978 by an adjustment factor of 1.4. This compares closely to Kelsall's (1968) observed 6-year mean recruitment rate of 14.9% when 2% to 4% less natural mortality was presumed.

Kelsall's (1968) table suggests an exponential growth rate of r = –0.15 during the decline from a pre-calving population of 668000 in 1949 to 270569 in 1955. The WAH declined from a pre-calving population of 195000 in 1970 to about 65248 in 1976 (r = –0.18). If estimates of the post-calving herd size are used (see Fig. 1) the decline from 1970 to 1976 was 242000 to 65000–75000 or r = –0.22 to –0.20. In contrast the apparent growth of the WAH from 1976 (75000+) to 1979 (113000+) was r = 0.14. The 1976 estimate is a conservative estimate and the population could have been as much as 10% larger. The 1979 estimate may also be conservative.

It is instructive to review Kelsall's (1968) analysis of the Canadian decline. In discussing it he stated, "Of first importance was the human kill and attendant crippling loss, which alone appear to have removed more caribou than were added to the population between 1949 and 1955." He elaborated by designating human kill of caribou as the primary limiting factor and stating that if the human kill of caribou had been substantially less no crash would have occured.

Following this decline, the Canadian government encouraged subsistence hunters to reduce harvest and a wolf control program was instituted. Yearling recruitment subsequently increased and the population grew.

The parallel between the decline of caribou in Canada and that of the WAH is such that one wonders if we have learned anything about factors limiting caribou herds and if caribou management has improved in the past 2 decades.

## 6. CONCLUSIONS

Population size of Alaska's Western Arctic Caribou Herd declined from 242000 in 1979 to a minimum of 75000 in 1976 (r = –0.20). It has increased to 113000+ in 1979 (r = 0.14).

The 1970–1976 decline occurred primarily due to excessive exploitation by subsistence hunters, including substantial wounding loss and waste, and considerable predation losses, primarily from wolves. Although few data are available for this period, yearling recruitment was probably sufficient to sustain the herd, even at a moderate level of human exploitation.

Three main factors have allowed the population to grow since 1976. Harvest was reduced from an annual mean of 25000 caribou of either sex to 3000 to 4000 comprised mostly of bulls. Wolf predation decreased due to changes in the winter distribution of caribou and decreased numbers of wolves. Finally, yearling recruitment increased.

Calf natality, determined by field observations at calving, was constant from 1960 through 1979 ($\overline{x}$ =

74.4 calves:100 cows, s.d. = 5.9). During the same period, July calf/cow ratios showed no statistically significant changes ($P < 0.05$). However, calf/cow ratios in fall have increased significantly ($P < 0.10$) and though calf/cow ratios in April have only been determined since 1976, they reflect increased calf survival. Natality has probably been density independent. Survival has been inversely related to density but mortality factors have not been constant. Mortality from wolf predation and hunting decreased concurrently. The influence of predation on calf survival is unknown, as are the indirect effects of hunting, such as orphaning and pursuit by snow machines.

Efforts to analyze the population dynamics of the WAH from 1960 through 1979 suggest that, for probable data points to fit, herd size up to and including 1970 was larger than censuses indicate, human-induced mortality was considerably lower, recruitment rates were much higher than available data suggest, natural mortality rates were much lower than our estimates, and/or ingress was substantial. The degree of ingress necessary to make the data fit seems least probable. Underestimates of recruitment are probable, but were likely not of sufficient magnitude to account for all inconsistencies. Although magnitude of human-induced mortality was intermittently "truthed," data for most years were subjective. Rates of natural mortality have never been documented conclusively, but most estimated rates seem defensible. Some modelers favor the assumption that initial populations were larger, but reasonable counter arguments can be made.

**Acknowledgements**

During a protracted study such as this one, so many people contribute that appropriate acknowledgment becomes unwieldly. We simply express our thanks to all who contributed and particularly thank J. Doerr and ADF&G biologists C. Grauvogel, D.A. Johnson, and H. Melchoir. R.D. Cameron reviewed the manuscript. The work was funded through Federal Aid in Wildlife Restoration Projects W-17-8 and 9 and National Petroleum Reserve-Alaska 105-c Studies.

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