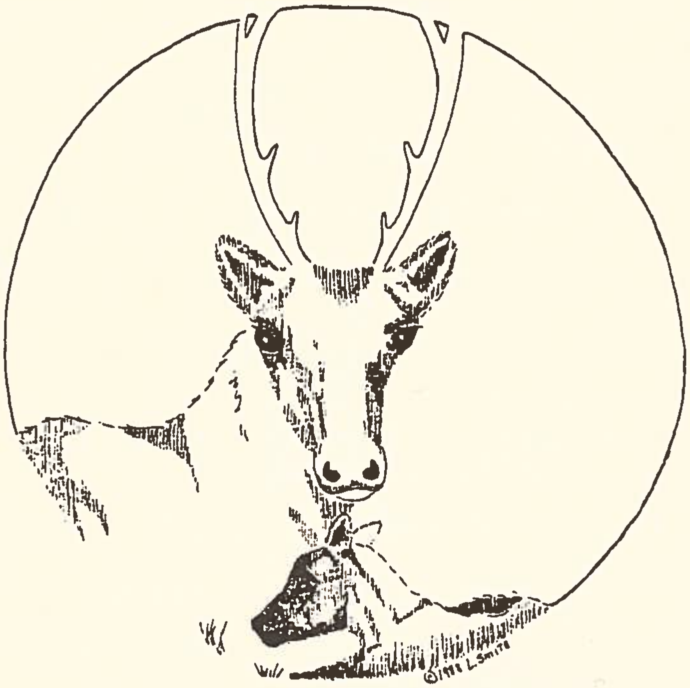
REPRODUCTION AND CALF SURVIVAL



Proceedings of the 3rd North American Caribou Workshop

Chena Hot Springs, Alaska

4 - 6 November 1987

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A Cree Indian Proverb:

"NO MAN KNOWS THE WAY OF THE WIND AND CARIBOU"

This volume is dedicated to the caribou and their ways, to those who endeavor to understand them, and to the belief that understanding will bring forth the wisdom to ensure that those ways are preserved.

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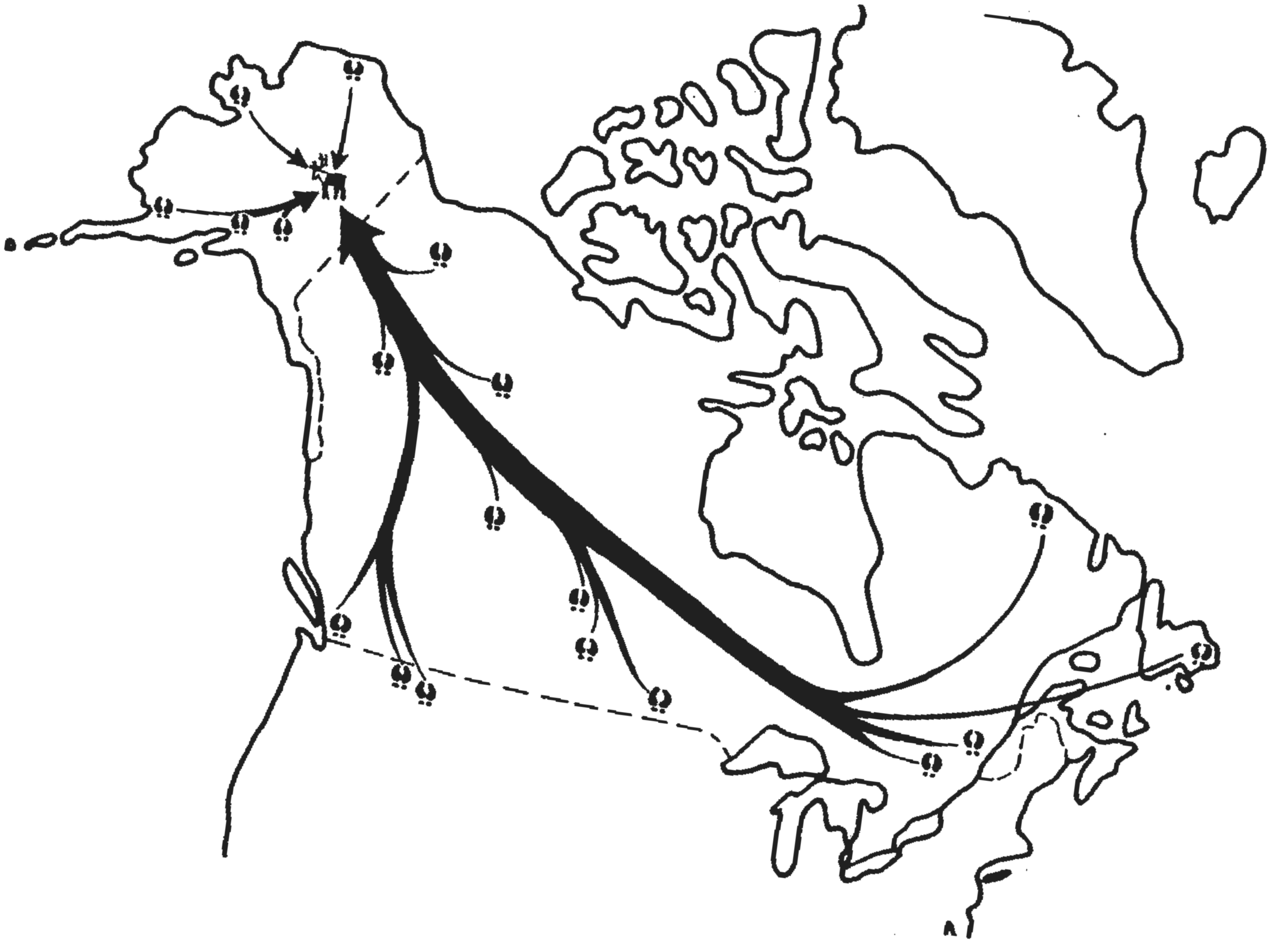

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PREFACE

As organizers of the 3rd North American Caribou Workshop (NACW), we found ourselves pondering rhetorical questions regarding the value of such meetings and the future of the NACW Proceedings as a series. Is there indeed a need for frequent NACW's? Will the NACW's compete with the International Reindeer/Caribou (R/C) Symposia? Are not the scientific journals alone adequate for communicating knowledge and ideas on caribou?

Clearly, there is need for a forum with a focus on caribou research and management in North America. That forum should be informal and complement the R/C Symposia and journals. Appropriately, the goal of past NACW's was to facilitate the timely exchange of preliminary data and to promote discussion of ongoing projects and issues. This goal remains appropriate, and meeting it requires that NACW's continue to (1) attract researchers, managers, and users who would otherwise be unable or unwilling to communicate by other means, and (2) publish a proceedings so that contributions are readily available.

In keeping with tradition, a theme was selected as the focus for the 3rd NACW presentations and discussions. The consensus among those polled early in the planning stages was that this meeting should emphasize reproduction and calf survival--a timely and appropriate subject, given the keen interest in the productivity of caribou herds subjected to predation and human use, and concern about impacts of industrial development on caribou populations.

Unlike the previous 2 proceedings, papers submitted for publication in this volume were not formally refereed. We reasoned that more flexible standards of publication would encourage wildlife managers and researchers to contribute findings that would otherwise be unavailable in the literature. Also, we had hoped that the time required to publish the Proceedings would be reduced. And, finally, authors would not be constrained from publishing their results elsewhere.

However, deleting the peer review process had its liabilities. The quality of papers varied tremendously, and we often found ourselves in that gray area between the compiling and reformatting duties of editors and the substantive reviews that normally are the responsibility of referees. As a result, the publication process was somewhat awkward and quite time-consuming.

On the other hand, foregoing peer review certainly did not discourage, and may well have enhanced, the level and scope of participation. Of the 35 oral or poster presentations, 12 were related to reproduction and calf survival, 9 were on methods of population assessment, and 14 dealt with a wide range of other subjects. Overall, 13 papers were submitted as full-length manuscripts and 17 as standard or expanded abstracts. The response speaks well for the enthusiasm of those working with caribou.

Perhaps a better policy for publishing the NACW Proceedings would involve a compromise: peer review, but with no requirement for compliance by the author. This would maintain responsibility for content with the authors, who would benefit from the insights and suggestions of others, and the editors would be free to concentrate on coordination and organization.

We look forward to the 1989 NACW in Newfoundland, with its continuing discussion of findings, an informal exchange of ideas, and the occasional lively debate.

Raymond D. Cameron

James L. Davis

> "All errors associated with the retyping and the editorial work on style and English are the responsibilities of the editors. As the manuscripts have not been edited for scientific content, inconsistencies or blunders in this respect should be blamed on the authors."

E. Reimers, E. Gaare, and
S. Skjenneberg, editors,
Proc. 2nd Int. Reindeer/
Caribou Symp.

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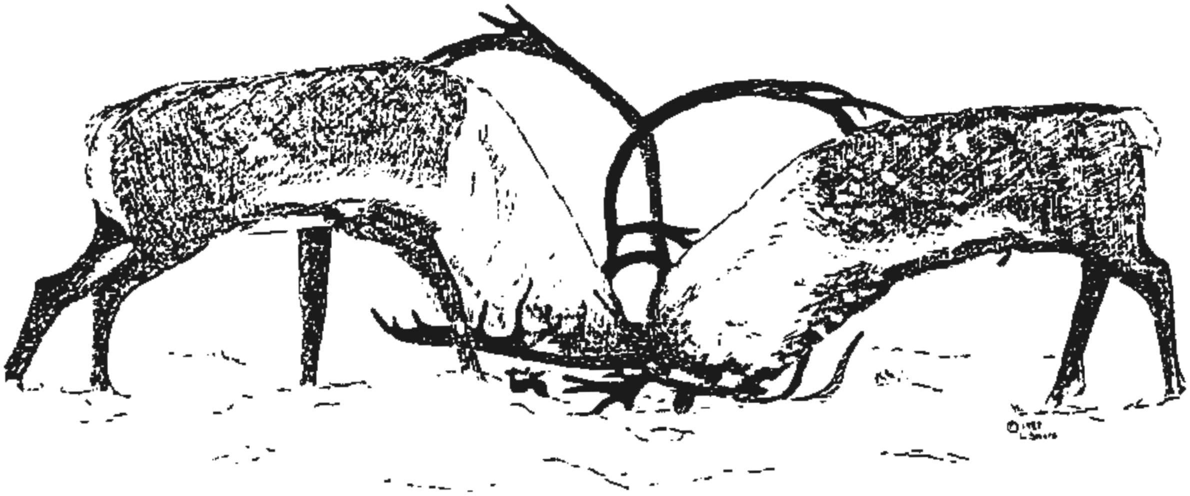

CONCEPTION AND PARTURITION

VARIATIONS IN INITIAL CALF PRODUCTION OF THE CENTRAL ARCTIC CARIBOU HERD

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Abstract: Caribou (Rangifer tarandus granti) were surveyed annually by helicopter from 1978 to 1987 in a 1,700 km^2 portion of the calving grounds of the Central Arctic Herd. Calf:cow ratios in early June varied between 56 calves:100 cows in 1986 and 91 calves:100 cows in 1983; during postcalving, trends in the percentage of radio-collared females with calves were similar. As the calving grounds are virtually predator-free, and because consistently few dead calves were observed, it appears that differences in the calf:cow ratio are primarily attributable to variations in conception rate and/or in utero survival. The relatively low calf:cow ratio recorded in 1986 correlated with poor body condition of adult females captured ca. 1 month before calving, suggesting that reproduction for that year was influenced by nutritional status.

Key Words: calving, Central Arctic Herd, mortality, natality, Rangifer

The pregnancy rate of adult (≥3 years old at calving) barren-ground caribou (Rangifer tarandus granti) reportedly ranges from 48% to 90% (Skoog 1968, Dauphiné 1976, Bergerud 1983). The proportion of females with viable calves immediately after parturition varies with the conception rate, and the incidence of abortion, stillbirths, and lethal birth defects. Subsequent causes of neonatal mortality include predation, abandonment, accidents, starvation, and disease. We define "initial" calf production as the calf:cow (≥2 years old) ratio 1-2 weeks postpartum. This represents the upper limit of recruitment of that cohort and, as such, is an important indicator of the growth potential of the population.

In this paper, we report estimates of initial calf production of the Central Arctic Herd (CAH) (Cameron and Whitten 1979) over a 10-year period based on helicopter surveys of the calving grounds (Whitten and Cameron 1985) and observations of the reproductive performance of radio-collared females.

We are grateful to K. R. Whitten, J. R. Dau, and C. S. Gewin for assistance in data collection and analysis. The work was funded primarily through Federal Aid in Wildlife Restoration Projects W-17-10/11, W-21-1/2, and W-22-1 through W-22-7. Supplemental support was provided by ARCO, EXXON, SOHIO/BP, and CONOCO. J. L. Davis offered helpful comments on the manuscript.

METHODS

On 11-14 June 1978-87, at least 1 week after the peak of calving, we surveyed a 1,700-km^2 portion of the CAH calving grounds by helicopter. We searched within 11-13 north-south strip-transects, each 3.2 km wide and 41 km long (Fig. 1), and recorded the sex/age composition (i.e., bulls, cows ≥2 years old, calves, and yearlings) of all caribou observed (Cameron et al. 1985, Whitten and Cameron 1985).

Between early June and late August 1980-87, 9-40 radio-collared adult (≥3-year-old) females were relocated at least once by fixed-wing aircraft (Whitten and Cameron 1983, Cameron et al. 1986). For each sighting, the presence of a calf at heel was recorded.

RESULTS AND DISCUSSION

Calf:cow ratios determined from calving ground surveys in 1978-87 varied from 56 to 91 calves:100 cows. By comparison, the 1980-87 percentages of radio-collared cows observed with calves (the equivalent of calf:cow ratios) ranged from 64 to 100 (Table 1).

The 2 data sets are not entirely comparable for several reasons. First, much radio-tracking was done well after the peak of calving, and

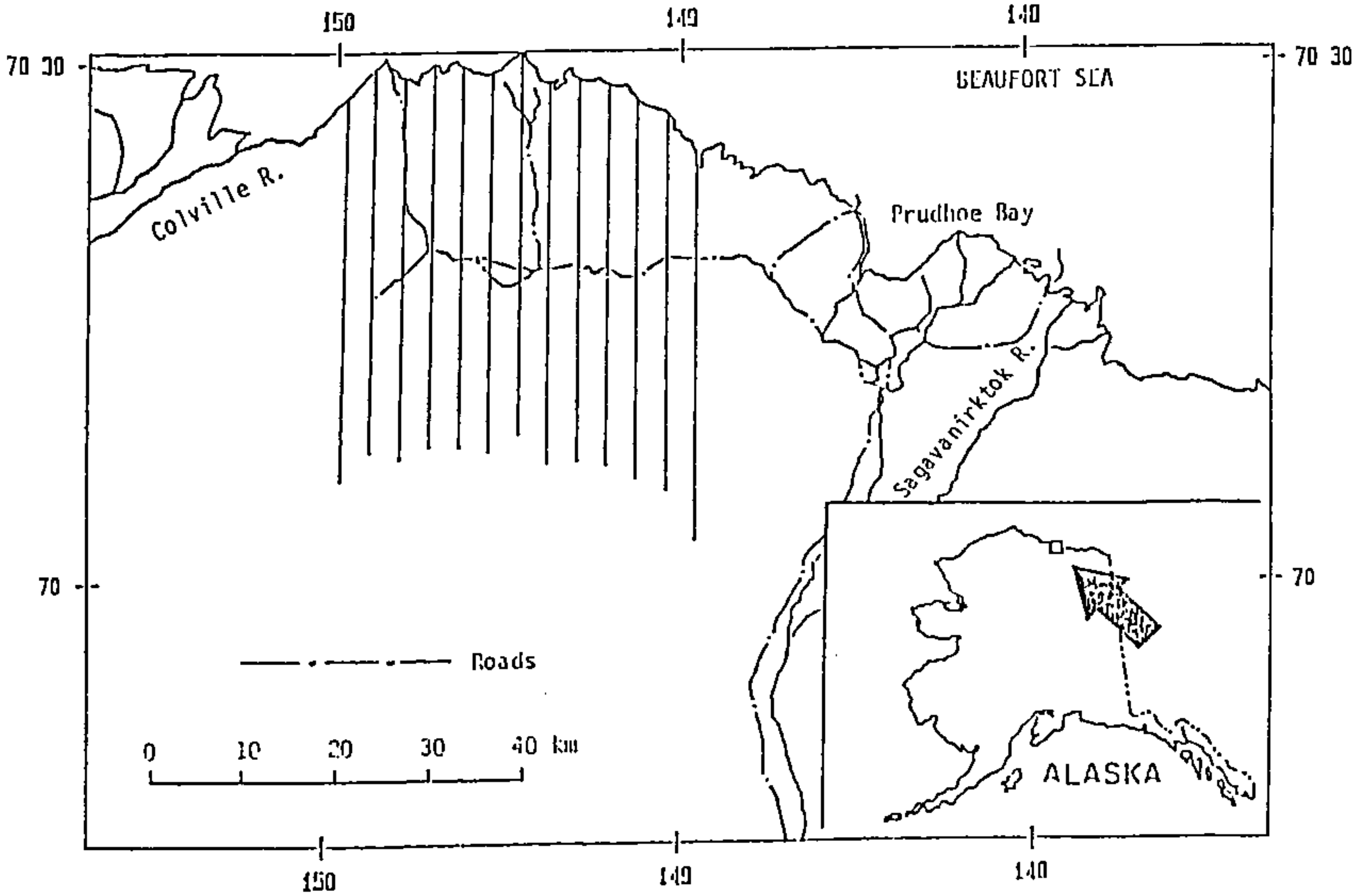

Fig. 1. Centerlines of strip-transects surveyed by helicopter, 11-14 June 1978-87. Note: Westernmost 2nd and 3rd transects not flown in 1978.

Table 1. Estimates of calf production in the Central Arctic Herd, Alaska, 1978-87.

	Strip-transect surveys[a]		Radio-collared females[b]	
Year	No. calves/ 100 cows[c]	n	% with calves[d]	n
1978	85	771[e]	--	--
1979	85	1,162[e]	--	--
1980	67	509	89	9
1981	88	1,361	90	20
1982	69	1,021	87	31
1983	91	1,796	100	22
1984	89	2,682	79	34
1985	88	2,344	82	28
1986	56	881	64	28
1987	76	991	80	40

[a] See Fig. 1.
[b] Females ≥3 years old within the Central Arctic Herd at large.
[c] Females ≥2 years old.
[d] Within ca. 5 weeks after the peak of calving.
[e] Excludes caribou in groups with 1 or more unclassified adults.

observations of females without calves would have included mortality that occurred subsequent to the strip-transect surveys. Second, in the strip-transect observations, all females older than yearlings were classified as cows for calculating the calf:cow ratio, whereas all radio-collared cows were ≥3 years old. Third, strip-transect surveys were centered on a calving concentration area (Whitten and Cameron 1985, Dau and Cameron 1986) and presumably excluded most nonparous females present in the general region, thereby overestimating calf production. Finally, among-year differences in the patterns of snow ablation and flooding strongly influenced the use of coastal vs. inland habitats during calving (Whitten and Cameron 1985), and possibly also affected the relative distribution of parous and/or nonparous females between the 2 areas.

Despite the several sources of potential sampling error, the 2 sets of independent estimates of calf production are correlated (1980 estimates excluded because of the particularly small sample of radio-collared females: $r = 0.71$, $\underline{P} < 0.1$). Most importantly, the extremes were apparent from both samples in the same 2 years: 56 and 64 in 1986, 91 and 100 in 1983 (Table 1). Thus, while the individual values may not be entirely representative of the herd at large, the paired estimates, overall, are in reasonable agreement.

The variation in initial calf production is apparently not attributable to annual differences in predation rate. Golden eagles (Aquila chrysaetos) are rare on the CAH calving grounds, and no wolves (Canis lupus) or grizzly bears (Ursus arctos) have been observed during our helicopter surveys--either in the study area (Fig. 1) or in other areas to the east that have been surveyed less frequently and less intensively over the past decade. Of the few dead calves encountered during our surveys (see below), all were intact, and in no case was there evidence of predator-related mortality. In summary, we are confident that predation has been negligible on the CAH calving grounds in general, and within our study area in particular.

Likewise, it appears that variations in early post-natal mortality are insufficient to account for the observed annual differences in calf production. No more than 4 dead calves have been observed during any one survey of the study area. However, because surveys were conducted ca. 1 week after most calving occurred, frequently under poor sighting conditions (e.g., mottled snow cover), and because searches for dead calves were of an opportunistic nature, we cannot entirely rule out the possibility of annual differences in the rate of early post-partum mortality; but the circumstantial evidence indicates that such an effect was minimal.

It appears, then, that the variation in CAH calf production is attributable to changes in the conception and in utero survival rates, but the relative influence of these 2 factors is not readily apparent. Dauphiné (1976), Reimers (1983), and Skogland (1985) reported a direct relationship between fall body weight/condition and pregnancy rate. However, Dauphiné (1976) and Reimers (1983) found low rates of prenatal mortality, irrespective of nutritional status during the previous fall or winter, whereas Skogland (1985) detected significant fetal mortality during late gestation among females on low-quality winter ranges. It is noteworthy that in 1986, the year of lowest CAH calf production, all females collared ca. 1 month before calving were in exceptionally poor condition--in fact, obviously thinner than any others we had handled since 1977. This strongly suggests that the apparent low natality rate was related to the nutritional status of females during the previous fall and/or winter. Ironically, however, insect activity during summer 1985 was unusually low, theoretically enhancing foraging opportunity, and winter snow conditions in 1985-86 were unremarkable. The specific cause of the observed change is, therefore, in question.

At the very least, these data on the CAH indicate that substantial variations in calf production can occur in mainland populations of barren-ground caribou in the absence of predation. While the exact response mechanism is uncertain, variations in body condition, and therefore energy retention, emerge as the likely cause of the changes in reproductive performance. Hypothetically, any environmental change that depresses energy intake or increases energy expenditure can adversely affect calf production and, hence, the growth potential of a caribou herd.

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DISTRIBUTION AND MOVEMENTS OF CENTRAL ARCTIC HERD CARIBOU DURING THE CALVING AND INSECT SEASONS

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Abstract: Several studies of the effects of oil development on caribou (*Rangifer tarandus granti*) distribution and movements in northern Alaska were sponsored by the oil industry between 1981 and 1985. These studies included intensive aerial tracking of radio-collared caribou (1983), extensive aerial transect surveys during calving (1984), satellite tracking of a collared cow (1984, 1985), and site-specific ground observations of caribou movements in relation to oilfield facilities and activities (1981-85). All studies were done in anticipation of permit needs or in compliance with oilfield-unit operating agreements with regulatory agencies. Funding was provided by ARCO Alaska, Inc., the Kuparuk River Unit Owners, and the Lisburne Unit Owners. Some surveys were conducted in cooperation with the Alaska Department of Fish and Game (ADF&G). This paper synthesizes data obtained from May through August, when contact is greatest between Central Arctic Herd (CAH) caribou and oil development in the Prudhoe Bay region.

The study area was that portion of the Arctic Coastal Plain between the Colville and Tamayariak Rivers, within approximately 120 km of the Beaufort Sea. The Prudhoe Bay, Kuparuk, and Milne Point Oilfields are in the western half of the study area, within 25 km of the coast between the Colville and Sagavanirktok Rivers. Several studies were conducted at specific sites within the Kuparuk and western Prudhoe Bay Oilfields (for most locations, see Curatolo and Murphy 1986).

The 1983 radio-telemetry program and the 1984 calving distribution surveys employed Piper PA-18-150 and Cessna 185 aircraft. From 23 May to 10 August 1983, 1,205 locations were obtained for 34 caribou (25 cows, 2 2-year-olds, 7 yearlings) that had been radio-collared by ADF&G. During the 1984 calving study, sampling was primarily by aerial survey (at

90-150 m agl) of 1.6- and 3.2-km wide strip transects from 29 May through 12 June, but radio-collared caribou occasionally were tracked as well. The satellite telemetry studies in 1984 and 1985 have been described by Curatolo (1986). Several of the site-specific studies of movements and corridor-crossing success during the midsummer insect season (late Jun-early Aug), 1981-85, were described previously by Curatolo and Murphy (1986) and by Murphy and Curatolo (1987).

During the 1983 and 1984 calving seasons, cows and calves were clumped in 2 "concentration areas" described previously (Oliktok Point/Kuparuk River and Bullen Point/Staines River), although lower densities of parturient caribou were observed elsewhere on the coastal plain and in the foothills. Fewer than 5% of all caribou observed on the calving grounds were adult bulls. In both 1983 and 1984, numbers of adults and yearlings increased in both concentration areas to maxima near the end of calving (mid-June). However, some inland movements from the eastern concentration area occurred on about 10 June of both years. The mean distance between daily locations for 9 radio-collared cows during 7-10 June 1983 was 5.8 km (n = 12); the greatest distance was 14.5 km in 19 hours.

Early in the 1984 calving period, caribou (including pregnant cows) were attracted to areas of accelerated snowmelt (caused by dust) downwind of roads in the Kuparuk Oilfield. In contrast, few caribou were present within 3-5 km of the Oliktok Point and Milne Point Roads during and after the peak of calving in that year. This localized avoidance was especially marked for cows with calves (Fig. 1). Both roads were in use at the time, but the Milne Point Road had very little traffic. Few caribou, and no radio-collared individuals, were observed in that portion of the Prudhoe Bay Oilfield between the Kuparuk and Sagavanirktok Rivers during the calving period.

Site-specific behavioral observations and satellite telemetry data indicated that daily movement rates were relatively low from the end of the calving period (mid-June) until the onset of the insect season (early July). Avoidance of human activity by cows with young calves appeared to persist throughout that period, but abated during insect season when

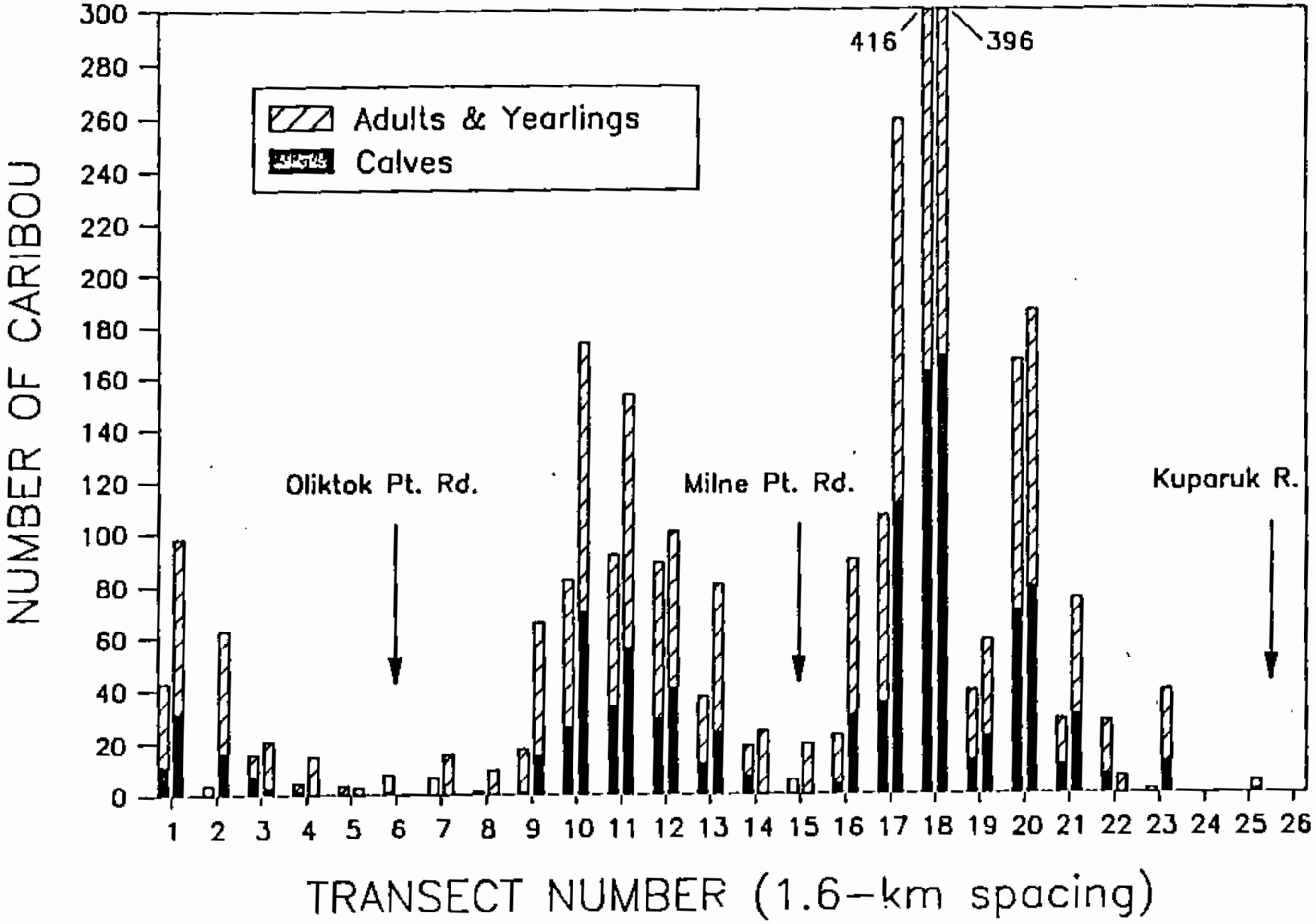

Fig. 1. Numbers of caribou observed in 1.6-km wide, north-south aerial strip transects (100% sampling intensity) north of the Spine Road in the Kuparuk, Milne Point, and western Prudhoe Bay Oilfields, Alaska, 10 and 12 June 1984. For each transect, left and right bars indicate 10 and 12 June counts, respectively (transects 24-26 not surveyed on 10 June). Mean (±SD) transect length = 19.0 (±3.1) km inland from the coast.

movement rates and crossings of pipeline/road corridors increased due to harassment by mosquitoes and oestrid flies.

During July, caribou movements were influenced primarily by mosquitoes, which caused caribou to aggregate and move northward to relief habitat on or near the coast. Collared caribou were located nearer the coast during the mosquito season, especially when mosquitoes were active, than during any other observation period (Table 1). The location of mosquito relief habitat was not static. Caribou moved toward the coast only as far as necessary to escape harassment on any given day, and moved inland when mosquito activity abated.

Table 1. Changes in mean (±SD) distance (km) from the Beaufort Sea coast of 34 radio-collared caribou, Central Arctic Herd, 1983.

Period	Distance (km)	n
Calving (23 May-10 Jun)	26.1 (22.5)	132
Postcalving (22 Jun-2 Jul)	25.3 (19.8)	72
Mosquito season (3-25 Jul)	6.6 (7.1)	764
Mosquitoes inactive	10.0 (7.7)	402
Mosquitoes active	2.7 (3.7)	362
Oestrid fly season/August dispersal (26 Jul-10 Aug)	29.9 (20.0)	237

During the 1983 mosquito season, the 34 radio-collared caribou were found within 2 separate areas, one east and the other west of the Sagavanirktok River (Fig. 2). By tracking the collared individuals, we were able to locate the majority of the herd, due to the aggregations that formed, and to estimate the total numbers of caribou in each of the 2 areas. Based on the consistency of successive counts, we concluded that the eastern component of the herd numbered at least 4,300 caribou and the western component at least 4,900 caribou. The minimum areas occupied during that

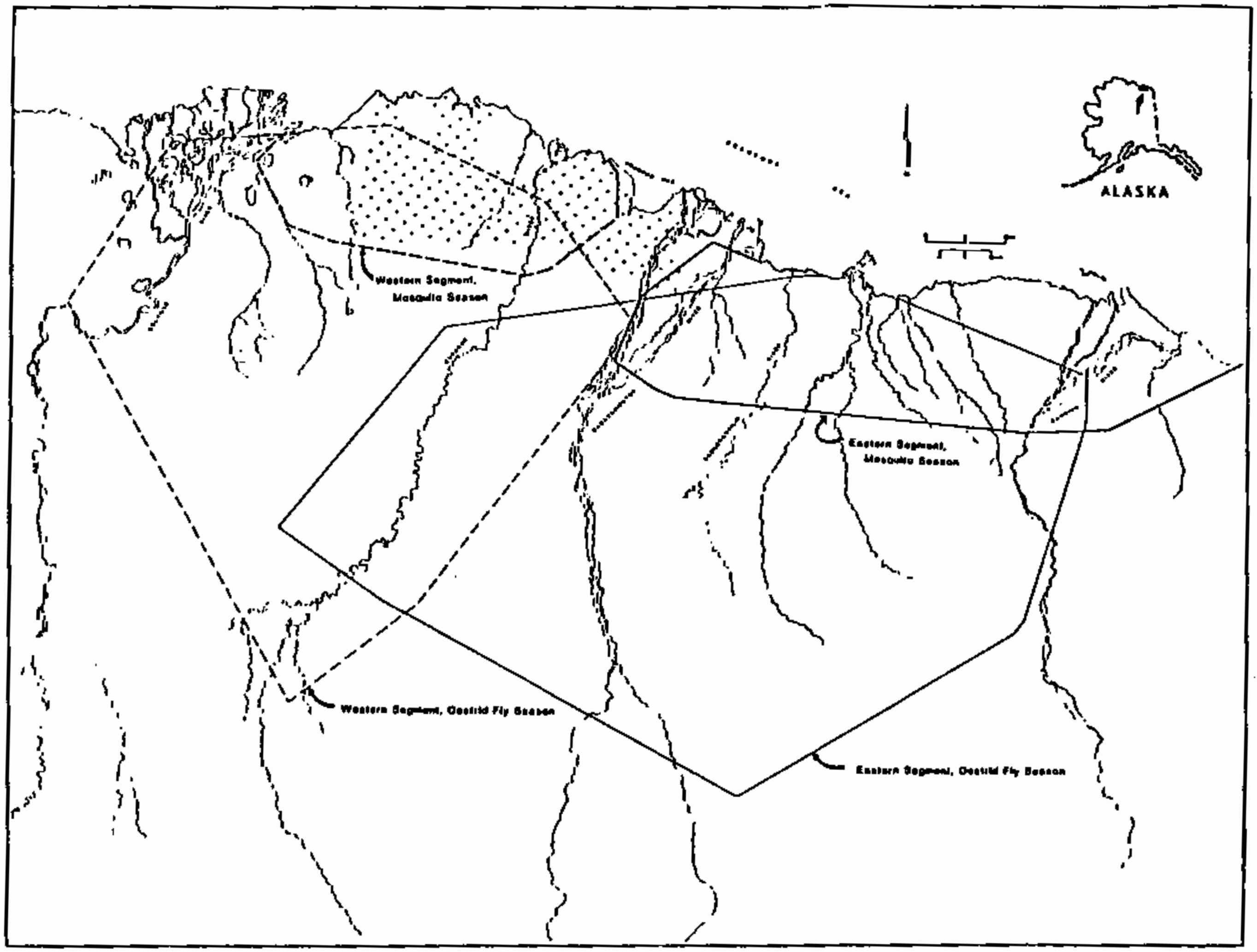

Fig. 2. Convex polygons enclosing all locations of 34 radio-collared CAH caribou during the mosquito (3–25 July) and oestrid fly (26 July–10 August) seasons, 1983. Western and eastern components contained 10 and 24 collars, respectively. Stippling indicates extent of oilfield development.

period were 3,000 km^2 and 1,750 km^2 on the east and west, respectively; maximum inland movement was 33 km. No overlap of the 2 ranges was seen until the oestrid fly season (August dispersal), when the eastern and western ranges increased to 10,960 km^2 and 7,760 km^2, respectively, and the use of coastal relief habitat decreased substantially. By the end of our observations, maximum inland movement had increased to 113 km. The minimum total area used by the CAH during the combined insect seasons was approximately 18,300 km^2. The location of summer range appeared to be related strongly to calving location. Of the collared cows tracked in 1983, 92% spent the mosquito season on the same side of the Sagavanirktok River where they had calved.

Although large groups (>1,000 caribou) closely approached the central Prudhoe Bay Oilfield (a densely developed area with many low-elevation pipelines) in both the 1983 and 1984 mosquito seasons, no large-scale movements through the field were observed. In contrast, such movements were observed frequently through the newer Kuparuk Oilfield (in which all pipelines are elevated at least 1.5 m) in response to changing levels of mosquito activity. During the 1982-85 insect seasons, >86,000 caribou were observed in the western Kuparuk Oilfield, and 54,500 of those were classified by sex and age: 45% cows, 25% calves, 12% yearlings, and 18% bulls. Although movements were often delayed or deflected locally near human activity, caribou encountering developed areas in the Kuparuk Oilfield were able to achieve access to and from mosquito-relief habitat.

Key Words: calving, caribou, Central Arctic Herd, distribution, insect harassment, movements, oil development, radio telemetry, Rangifer

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DISTRIBUTION OF RADIO-COLLARED CARIBOU FROM THE DELTA AND YANERT HERDS DURING CALVING

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Abstract: Each year from 1980 through 1987, we located 9-55 radio-collared female caribou (Rangifer tarandus granti) and 1-10 radio-collared male caribou from the Delta and Yanert Herds during the calving period. All but 3 of the Delta Herd females were collared at 8-12 months of age. Of 186 calves born to the radio-collared Delta and Yanert Herd females, 183 were apparently born in 2 disjunct areas totaling about 2,500 km^2. Most ($\geq$50%) radio-collared Delta females calved within a previously defined "major calving area" in only 1 of 8 years, and only 1 female exhibited affinity to a specific calving site. In 1984 and 1987, major unexplained shifts in calving distribution occurred in the Delta Herd. Distribution of caribou during calving is discussed in relation to sex, reproductive status, previous experience, snow conditions, and predator numbers.

Key Words: calving, caribou, Delta Herd, radiocollar, Rangifer

Calving grounds are perhaps the most predictably used portion of a caribou (Rangifer tarandus) herd's annual range (Skoog 1968:121, Thomas et al. 1968, Bergerud 1974, Brown and Theberge 1985, Paré and Huot 1985, Cameron et al. 1986, Davis et al. 1986, Gunn and Miller 1986, Hatler 1986). However, major exceptions to calving ground fidelity have been reported (Cameron et al. 1986, Davis et al. 1986, Valkenburg and Davis 1986). In addition, fidelity varies among individuals (Edmonds and Bloomfield 1984, Paré and Huot 1985, Hatler 1986). Davis et al. (1986) discussed patterns of range use (including apparent anomalies) of the

Delta and Yanert Caribou Herds (DCH and YCH) between 1950 and 1985 and compared those patterns with existing theoretical models of caribou socioecology. In this paper, we present 2 years of additional data and summarize the calving distribution of radio-collared Delta and Yanert caribou for the entire period. We also discuss the implications of our results to caribou management and ecological theory.

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METHODS

Caribou Capture and Collaring

From January 1979 through April 1987, we captured and radio-collared (collars from Telonics, Inc., Mesa, Ariz.) 61 female caribou in the DCH and 8 in the YCH. DCH females were collared at 8-12 months of age, except for 3 which were collared as adults; all YCH females were collared as adults. Collars were replaced every 3-4 years. Most caribou were immobilized by darting with M99 (Valkenburg et al. 1983) or Wildnil (3 mg/ml Carfentanil Citrate, Wildlife Laboratories, Fort Collins, Colo.) from a helicopter. The remaining caribou were captured with a shoulder-held net gun (Valkenburg et al. 1983) and handled without chemical immobilization or sedation. Unless otherwise stated, the terms DCH caribou and YCH caribou refer to caribou that were radio-collared within the respective ranges of the 2 herds (Fig. 1) (Figs. follow Lit. Cit.).

Relocating Radio-collared Caribou and Determining Reproductive Status

Davis et al. (1986) described the methods used to relocate caribou during the calving period, 1979-85; methods used in 1986 and 1987 were similar.

We relocated caribou with a Piper Super Cub or a Bellanca Scout aircraft on 14, 15, 17, and 28 May 1986 and on 14, 15, 20, 27, and 31 May 1987. Each female ≥ 24 months old was located and observed 1-3 times per year. For 75-80% of the relocations, reproductive status of the female was judged from the presence or absence of a distended udder (Bergerud 1964); otherwise, the presence of hard antlers or a calf was accepted as evidence of pregnancy. In 4 of 294 cases (all in 24-month-olds), we were unable to judge reproductive status. Radio-collared males and yearling females were relocated at least once during the last 2 weeks of May each year. On 30 May and 2 June 1987 we used helicopters (Allouette A-star and Bell Jet Ranger) to obtain sex and age composition and pregnancy data (as above).

Calving Location of Radio-collared Females

Calving location is defined as the site where a female was first found with a newborn calf. In years when a pregnant female was never seen with a newborn (i.e., some newborns died before being observed), calving site was defined as the location where observed on the date closest to the peak of calving. Peak calving date was estimated as the day(s) when approximately half of the pregnant females in the herd had calved. Calving distribution was defined as the area within a convex polygon which connects the outermost calving locations for all radio-collared females in a given year.

Data Analysis

During radio-tracking flights, locations of caribou were recorded on topographic maps (USGS, scale 1:250,000). Subsequently, locations were electronically digitized by latitude and longitude and then transferred to a computer file (DBase III, Ashton-Tate, Torrance, Calif.). Other information was later entered into each record. We replotted location data using a Hewlett-Packard 7475A plotter and a computer graphics program developed by J. Venable (Alaska Department of Fish and Game, Fairbanks). Statistical testing for non-independent ratio estimates was by Student's t-test (Cochran 1977). Significance level is presented in the narrative.

RESULTS

Size of Delta and Yanert Calving Areas and Range Size of the Herds

From 1980 through 1987, 183 of 186 calves born to the DCH and YCH females were found in 2 disjunct areas (Figs. 2-9): the Little Delta River/Delta Creek area (Area 1, 2,020 km^2) and the Yanert/Wood River area (Area 2, 450 km^2). Two of the 3 calves found outside Areas 1 and 2 were produced by primiparous DCH cows (age 36 months) in an area used by the herd during the preceding winter. The third calf was with a YCH female on a plateau south of the Yanert River.

Between 1980 and 1987, the total range of the DCH increased from 8,000 km^2 to 10,800 km^2. Range of the YCH was about 1,500 km^2 and overlapped that of the DCH.

Fidelity to Calving Areas

The discussion that follows requires familiarity with the DCH's historical main calving area (MCA), which consists of 2 adjacent areas separated by a timbered river valley about 2 km wide (Fig. 2). The MCA was identified as the DCH's traditional calving area by extensive aerial surveys conducted from the late 1950's through the mid-1970's (Skoog 1968; Hemming 1971; ADF&G 1976; M. Buchholtz and L. Jennings, retired ADF&G employees, pers. commun.).

Intensive monitoring of calving distribution in the late 1970's and early 1980's seemed to confirm the fidelity of the DCH to the MCA (Davis and Preston 1980; Davis and Valkenburg 1981, 1983, 1984; Davis et al. 1982; ADF&G 1986). Investigators estimated that 75-90% of all calving occurred within the boundaries of the MCA in 1979, 1980, and 1983, and failure of the DCH to calve within the MCA in 1981 and 1982 was attributed to late snowmelt. In summary, from the late 1950's through 1980 calving apparently occurred annually within the MCA, with little or no calving elsewhere.

From 1980 to 1987 over 98% of all parturient radio-collared DCH females calved within Areas 1 and 2 (Figs. 2-9). However, a majority (>50%) of the radio-collared females have not calved within the MCA in any year after 1983. In 1982 and 1983 deep snow (>10 cm) covered the MCA throughout May, and most caribou calved on the northern periphery of the area where snow was patchy or absent (Figs. 4 and 5). In 1986, 12 of 29 parturient DCH females calved within the MCA, and at least 5 more moved onto the MCA within several days after they had calved. In 1987, about 50% of the collared parturient DCH females calved on the upper Wood River within the area normally used by YCH females (Area 2).

We first detected calving in Area 2 by DCH caribou in 1983 when 2 parturient and 2 nonparturient females ($\geq$24 months old) were observed there during the period of calving. In 1984, 4 of 24 parturient and 3 of 12 non-parturient females ($\geq$24 months old) used Area 2 (note: numbers differ slightly from those reported by Davis et al. 1986 due to slight changes in definition of calving date and calving areas). From 1982 through 1987, Area 2 was frequented during the calving period by both radio-collared DCH caribou 12-24 months old and uncollared caribou 12-24 months old.

The 8 YCH females usually calved in Area 2, but there were notable exceptions. In 1 year a YCH female calved on a high plateau south of the Yanert River. A second YCH female (No. 102368) calved in Area 2 in 1981 and 1982 and then calved in Area 1 from 1983 through 1987 (Fig. 10). A third YCH female (No. 102366) calved in Area 2 and remained year-round in the Yanert River drainage from 1981 through summer 1985. She did not produce a calf in 1986, and from November 1985 through 2 May 1987 she remained south of the Alaska Range in the upper Nenana and Susitna River drainages with about 200 caribou assumed to be members of a discrete resident herd (Pitcher 1987). Between 2 and 15 May 1987, she traveled >70 km across the crest of the Alaska Range and returned to Area 2 where she calved.

Selection of Calving Areas by Primiparous vs. Multiparous Females

Within Area 1, primiparous DCH females were no more likely to calve outside the MCA than multiparous females ($\underline{P} > 0.1$; t = 0.33, d.f. = 44) (Fig. 11). Excluding replicates, 13 of 37 (35%) of the primiparous females calved outside the MCA and 14 of 37 (38%) of the multiparous females calved outside the MCH.

Location of Nonparturient Females During Calving

During the peak of calving from 1979 through 1987, 82% of the 99 locations of nonparturient radio-collared DCH females $\geq$12 months old were within Areas 1 and 2 (Figs. 2-9). Yearling DCH females were no more likely to be outside (36 inside vs. 43 outside) Areas 1 and 2 than nonparturient DCH females older than yearlings (45 inside vs. 56 outside) ($P > 0.1$, $t = 0.43$, d.f. = 57) (Fig. 12). In contrast, 4 of 6 locations of nonparturient YCH females were outside Area 2 in the Yanert River valley in lowland spruce (*Picea* spp.) forest.

Calving Site Affinity of Females

We verified affinity to a specific calving site by 1 DCH female (Fig. 13), but we may have underestimated birthing site affinity because our surveys were too infrequent to ascertain most birth sites. However, most workers experienced with barren-ground caribou behavior believe that affinity for birth sites is low.

Distribution of Males During Calving

Eight of 30 locations of radio-collared DCH males during May were within Area 1, and none were within Area 2. Until June most males remained on winter ranges at lower elevations (often in spruce woodland or muskeg habitat) to the north and northwest of Area 1; YCH males also remained on their winter range, occupying similar habitats in the lower Yanert valley. Furthermore, the sex ratio from composition samples on the calving areas never exceeded 5 males:100 females in late May, whereas samples during the rut indicated 40-50 males:100 females in the DCH and 70:100 in the YCH.

DISCUSSION

Fidelity to Calving Areas

Clearly, the 640 km^2 MCA has remained an important calving area for the DCH. Furthermore, during the 8-year study period, the vast majority of parturient DCH females have calved in the 2,020 km^2 of Area 1, which encompasses the MCA. That most DCH females did not calve within the MCA between 1980 and 1987 may reflect a change in calving distribution, an increase in herd size, improved knowledge resulting from the use of radiocollars, or a combination of these factors. Between the late 1950's and 1979 the DCH was considerably smaller (2,500-5,000) than it was in 1985-87 (7,000-8,000). Prior to 1980, major shifts in calving distribution, as in 1984 and 1987, could have gone undetected because surveys were relatively infrequent.

The major shifts in calving distribution of the DCH contrast with conventional concepts of calving tradition and herd identity (c.f. Skoog 1968, Davis et al. 1986, Gunn and Miller 1986). In reporting the 1984 shift in calving distribution, Davis et al. (1986) noted that most females returned to Area 1 in 1985 and 1986. Most of these females again used Area 2 in 1987 when snowmelt was particularly early, although virtually all DCH females were present on, or in close proximity to, Area 1 during early May. The caribou that eventually calved in Area 2 moved there along the route used since the early 1980's for postcalving movements. In addition, many females that had never previously used Area 2 for calving went there in 1987. The "Yanert" female (No. 102368) that "moved" to the DCH in 1982 was not one of those.

A possible explanation for the 1987 shift in distribution during calving may be that caribou concentrated near the retreating snowline, perhaps minimizing predator contact while allowing access to emerging _Eriophorum_ spp. buds. Snowmelt was indeed early in 1987, which could partially explain why caribou that calved in Area 1 concentrated farther south than ever observed before (i.e., closer to high mountains). The conditions presumably present in southern Area 1 and being sought by calving caribou were probably also present in Area 2 (albeit Area 2 has more low-elevation forest and a greater abundance of alternative prey for wolves (_Canis lupus_) and bears (_Ursus arctos_) than the southern portion of Area 1). Wolf and grizzly bear densities appear to be comparable in both areas.

Influence of Sex, Reproductive Status, and Individual Experience on Calving Distribution

The pronounced difference in the distribution of radio-collared bulls and cows during the calving period suggests that the sex of individuals has the greatest influence on their distribution. More than 98% of the parturient females and 82% of the nonparturient females (regardless of age and calving tradition) went to Areas 1 and 2 during calving; this contrasts with less than 30% for the males. Reproductive status is apparently the next most important influence on calving distribution; over 98% of the parturient radio-collared females were found in Areas 1 and 2. Previous pregnancy may also influence calving distribution of individuals; 2 of 3 radio-collared pregnant caribou that did not calve in Areas 1 and 2 were primiparous 3-year-olds.

The observed distribution of pregnant and nonpregnant YCH females supports the premise that, as parturition approaches, pregnant females forego feeding in areas of high phytomass of nutritious plants in favor of higher elevation, more open habitat to avoid predation. Five of 10 locations of nonparturient YCH females during calving time were in the Yanert River valley, which was not used by pregnant, radio-collared females during calving. In the Yanert valley (elevation about 900 m), dwarf birch (Betula spp.) and willow (Salix spp.) leaves emerge by about 25 May in most years, in contrast to a 10-day later emergence at calving locations (1,500-2,500 m) chosen by YCH cows.

Perhaps most nonparturient Delta females were in the same areas as parturient females because of the greater availability of lowland tundra in Area 1 than in Area 2. However, some nonparturient females used the highest parts of Area 1, and none were found in the lowest parts (300-400 m), which were frequented by radio-collared adult males and male yearlings. Presumably, quantity, quality, and diversity of new plant growth were greatest at the lowest elevation.

The preference of DCH females for open habitats, regardless of their reproductive status, could have a phylogenic basis or be a conditioned response to predators. Bergerud (1974) hypothesized that predator harassment acts as an environmental trigger which causes barren-ground caribou to seek open habitats and form large groups during calving. Observations from the Fortymile Caribou Herd (FCH) may or may not be consistent with this hypothesis. Calving distribution of the FCH has varied annually during the past 10 years, and calving has not consistently occurred in the most open habitat (Valkenburg and Davis 1986). There may be no area within or adjacent to the range of the FCH where predator numbers are low, which suggests no advantage to a specific calving area (however, open habitat should still enhance predator detection). Present data are insufficient to critically test the hypothesis for either the DCH or FCH.

Calving Site Affinity

Radio-collared DCH and YCH females apparently did not exhibit as much affinity to birthing sites as has been reported for woodland caribou (*R. t. caribou*) (Edmonds and Bloomfield 1984, Hatler 1986, Paré and Huot 1986). Only 1 DCH female clearly exhibited site affinity. It is possible, however, that others exhibited such affinity undetected. Apparently, individuals with different behavioral tendencies may exist within a herd (Davis et al. 1986). Whether these tendencies are inherent in individuals or are facultative responses to the environment is an interesting question. A changing calving strategy by individuals (i.e., from site affinity to non-affinity or vice-versa) could be construed as evidence of facultative responses.

CONCLUSIONS

Because of progressive development in the North, it has become increasingly important that we learn how and why caribou select calving areas. It has proven difficult to learn what motivates caribou because both environmental and phylogenic factors are likely involved, as well as variation in individual behavior. With more data on the movements of radio-collared caribou, it has become increasingly apparent that short-term, and perhaps long-term, shifts in calving distribution are to be expected. Calving grounds are less easily delineated than previously believed, and infidelity of individual females to a designated calving area may be more frequent than implied in the literature. The above observations have important management implications. For example, census techniques may have major limitations if based on the assumption that all females in a herd use a traditional calving area or that all calving occurs in a continuous distribution. Also, recognition that calving distribution may shift appreciably between years should be considered in formulating strategies to mitigate the impacts of development on caribou. For instance, moderate protection of calving habitat over a larger and/or discontinuous area may prove more beneficial to caribou than inviolate protection of a relatively small area.

It is important to maintain access to larger areas for calving than those that may be identified at a narrow time interval. Empirical evidence is mounting to show that changes in snow condition and population size are only 2 of many possible variables that are apt to affect calving distribution.

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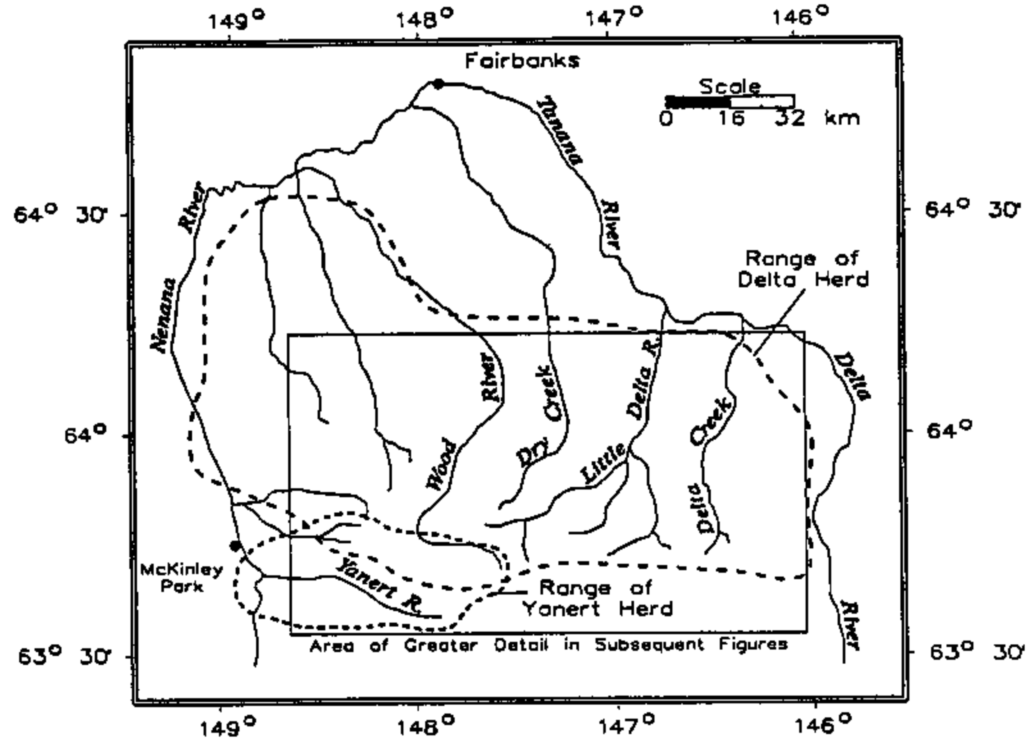


Fig. 1. Study area.

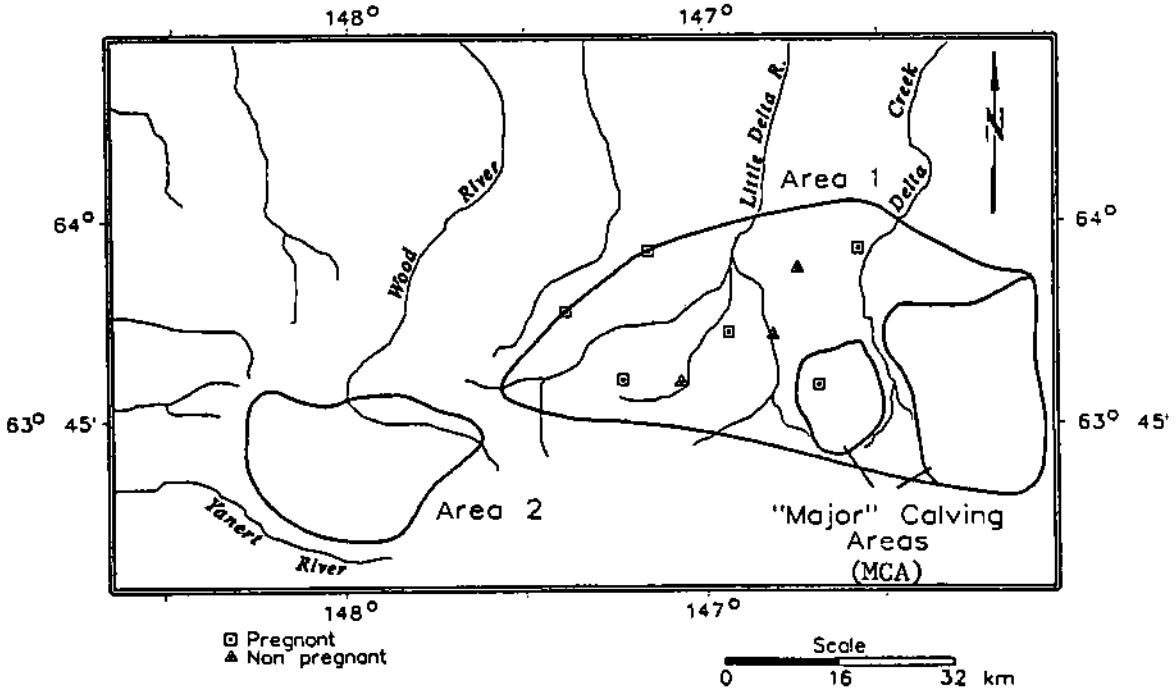


Fig. 2. Approximate calving locations of radio-collared parturient and nonparturient female Delta caribou older than yearlings in 1980, and locations of previously recognized "major" calving areas.

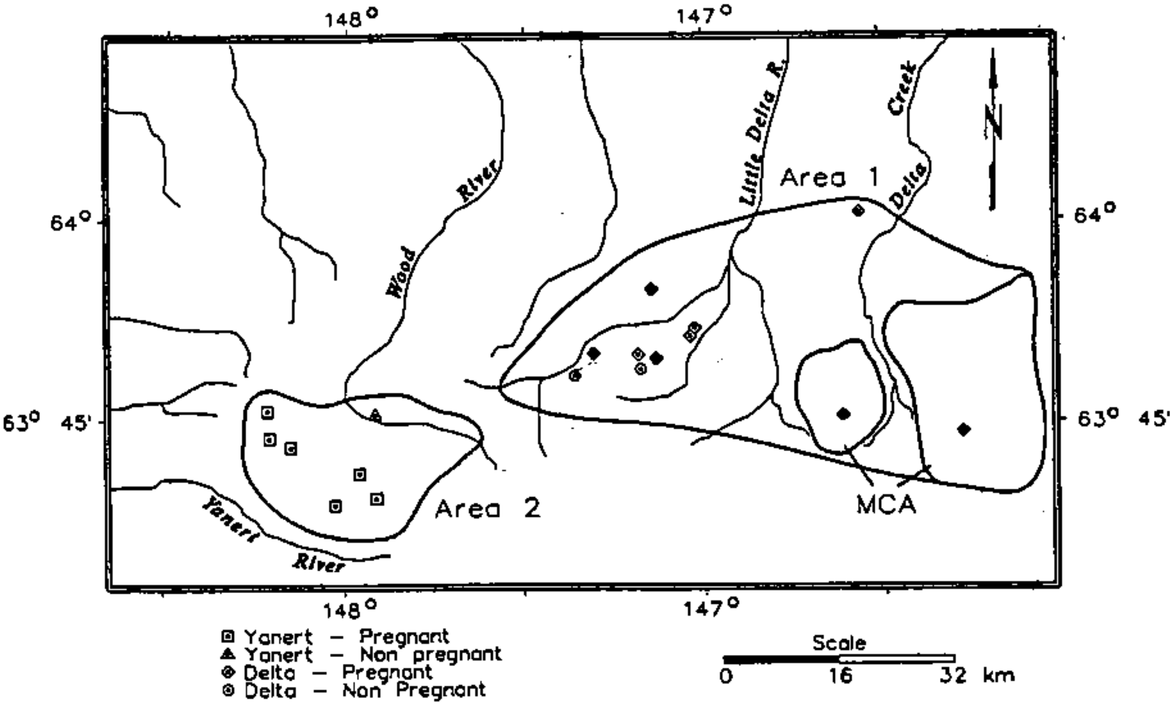


Fig. 3. Approximate calving locations of radio-collared parturient and nonparturient female Delta caribou older than yearlings in 1981.

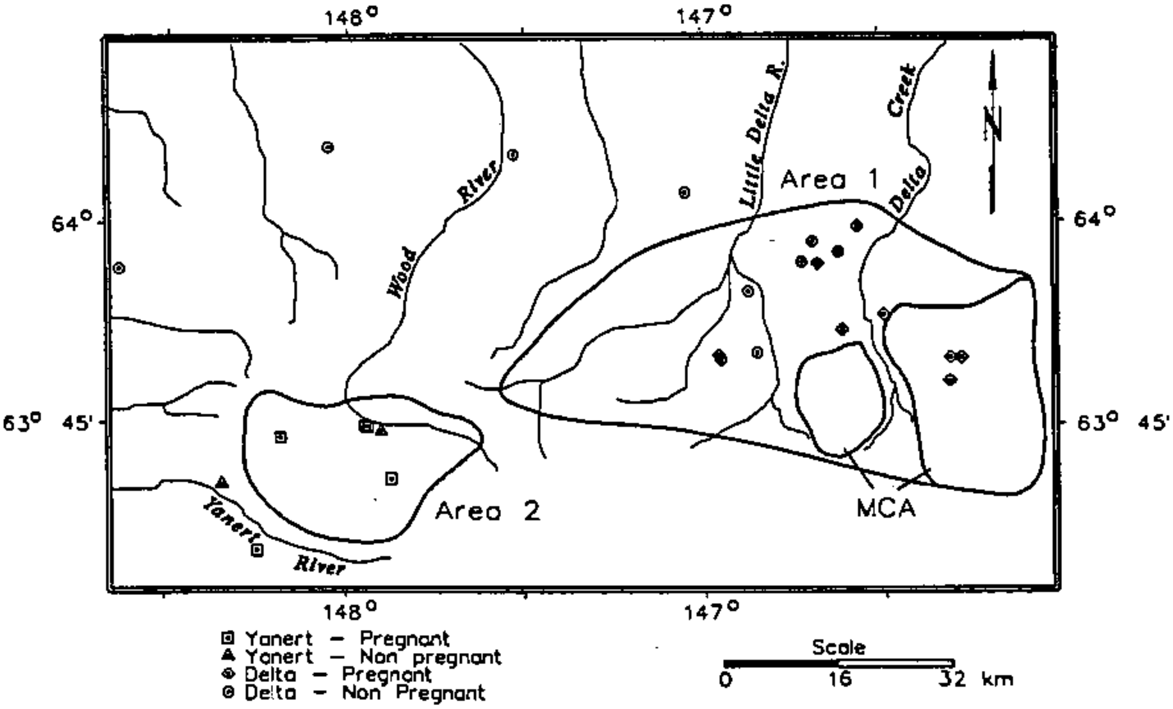


Fig. 4. Approximate calving locations of radio-collared parturient and nonparturient female Delta caribou older than yearlings in 1982.

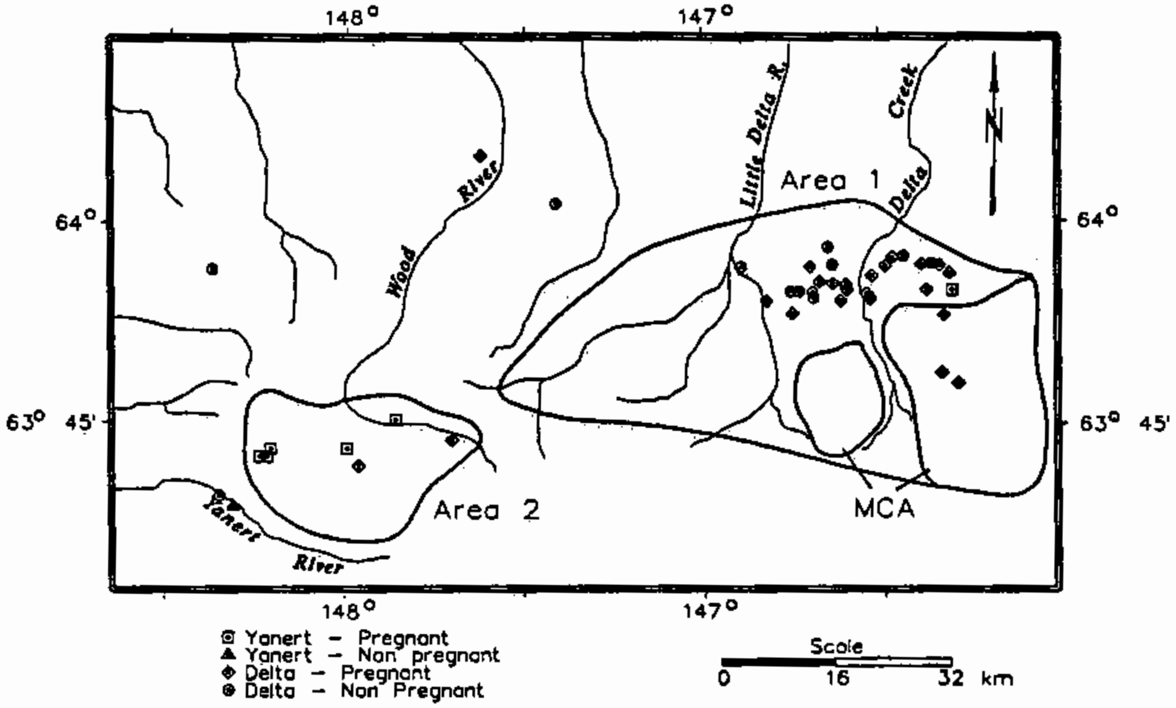


Fig. 5. Approximate calving locations of radio-collared parturient and nonparturient female Delta caribou older than yearlings in 1983.

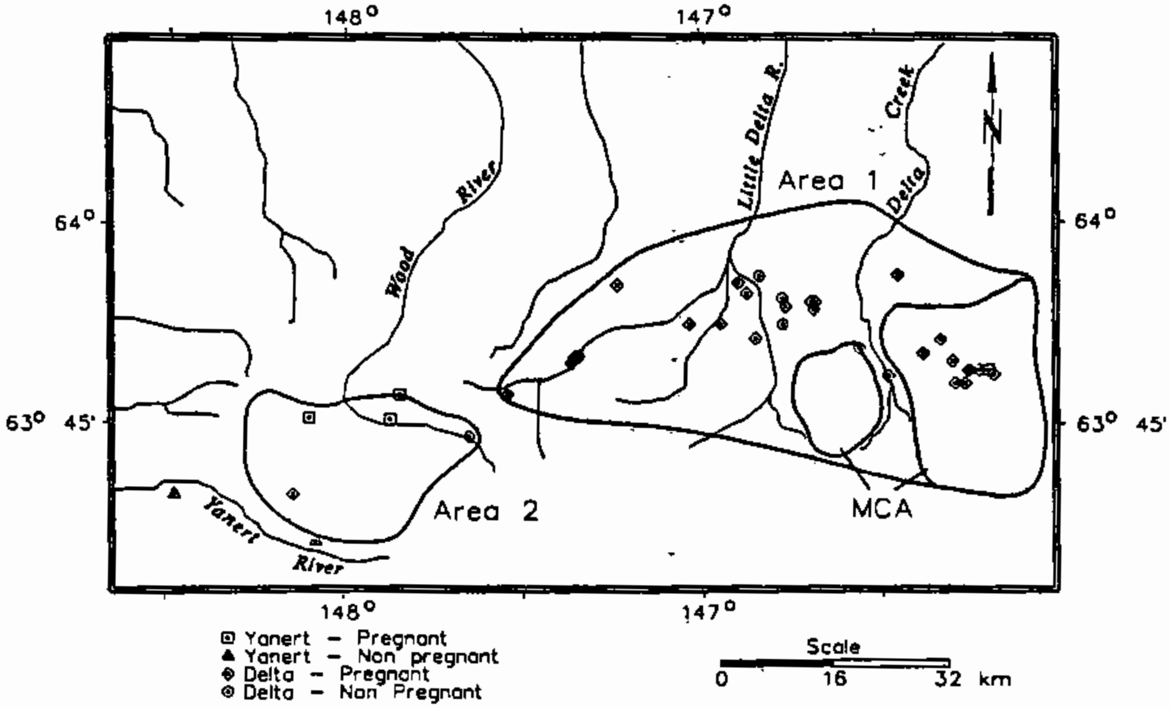


Fig. 6. Approximate calving locations of radio-collared parturient and nonparturient female Delta caribou older than yearlings in 1984.

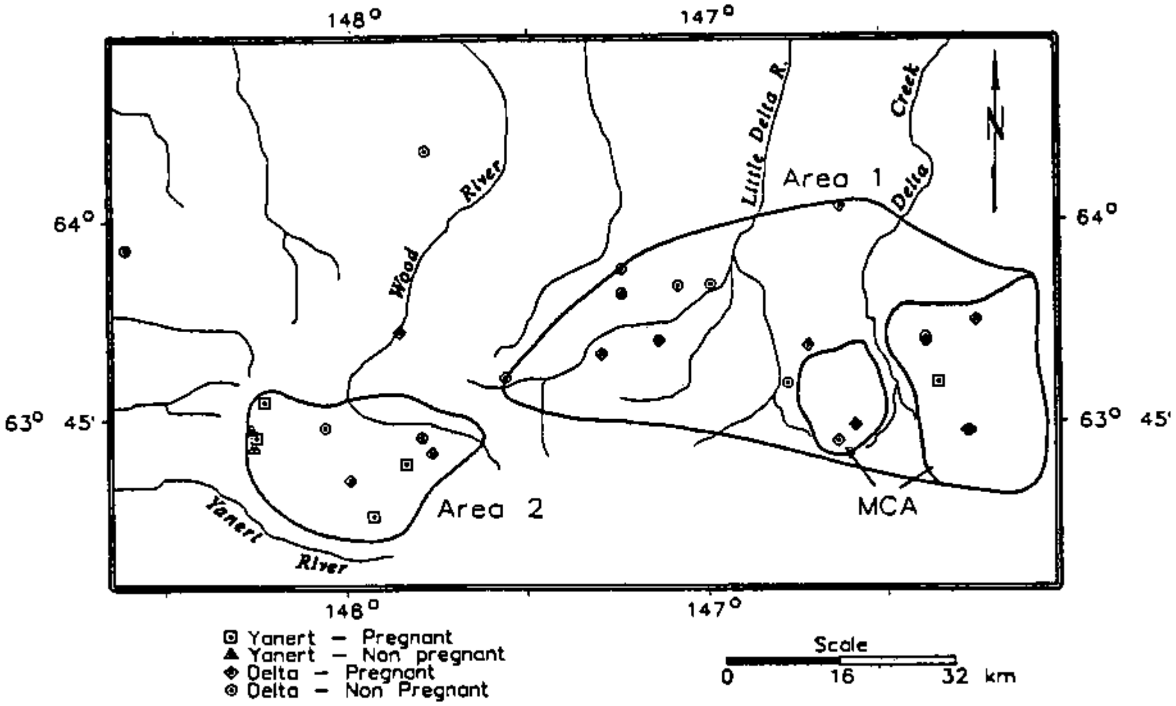


Fig. 7. Approximate calving locations of radio-collared parturient and nonparturient female Delta caribou older than yearlings in 1985.

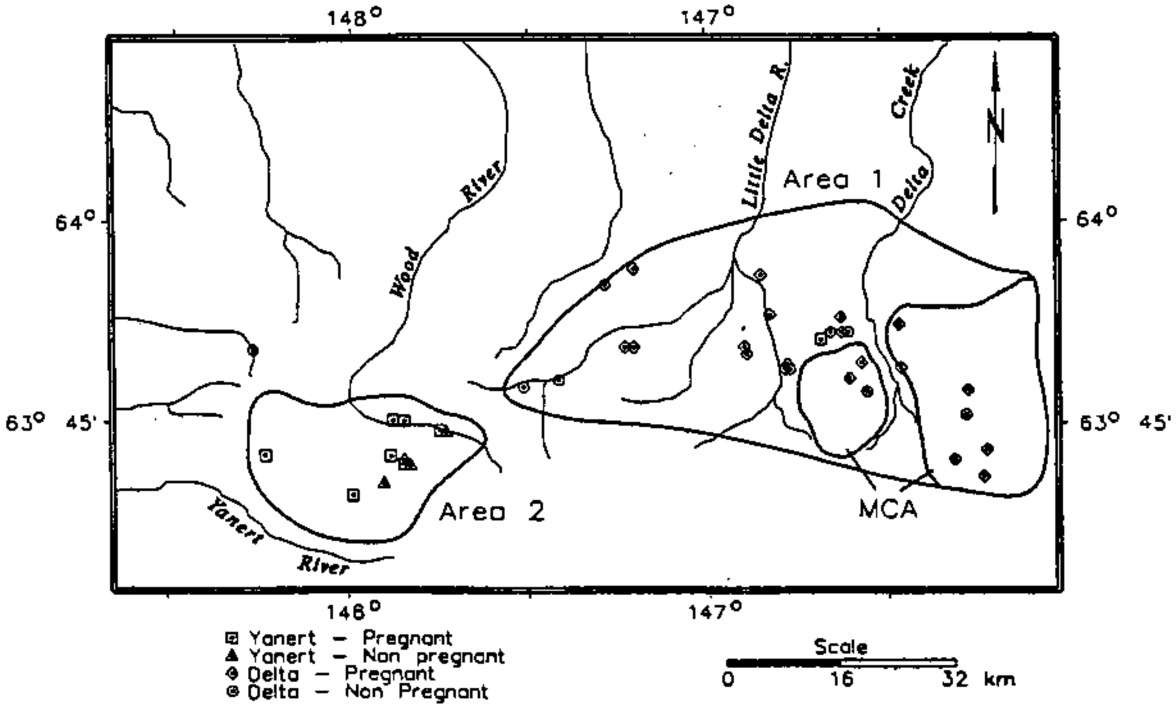


Fig. 8. Approximate calving locations of radio-collared parturient and nonparturient female Delta caribou older than yearlings in 1986.

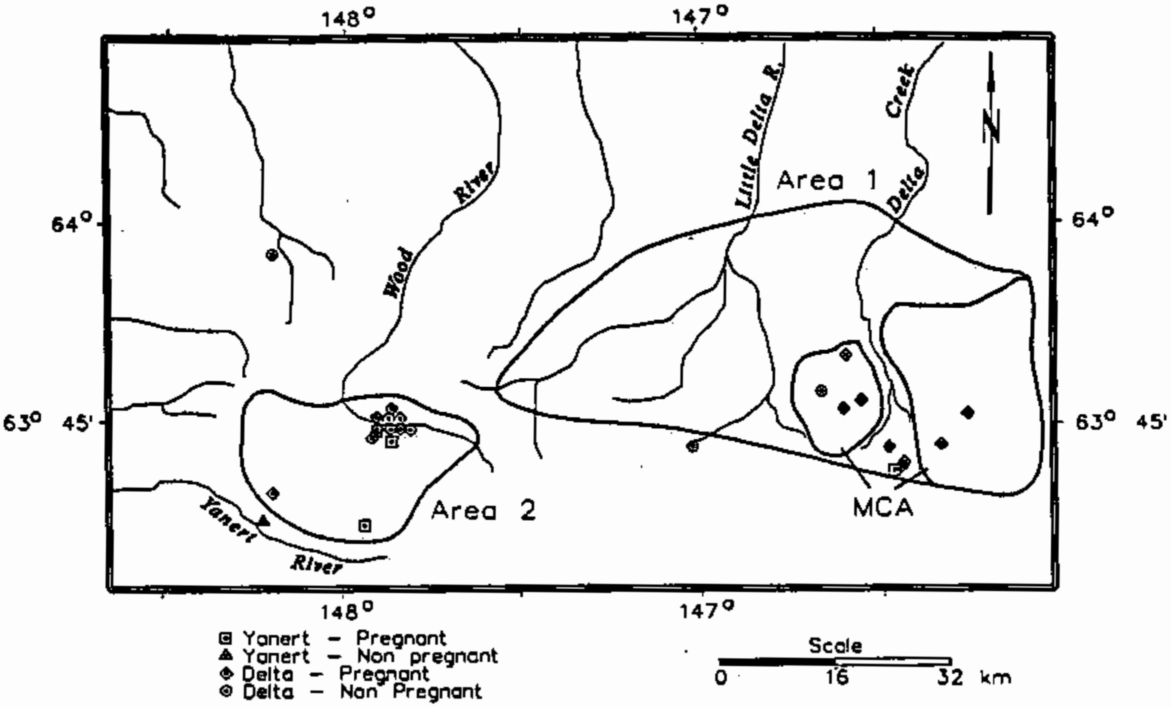


Fig. 9. Approximate calving locations of radio-collared parturient and nonparturient female Delta caribou older than yearlings in 1987.

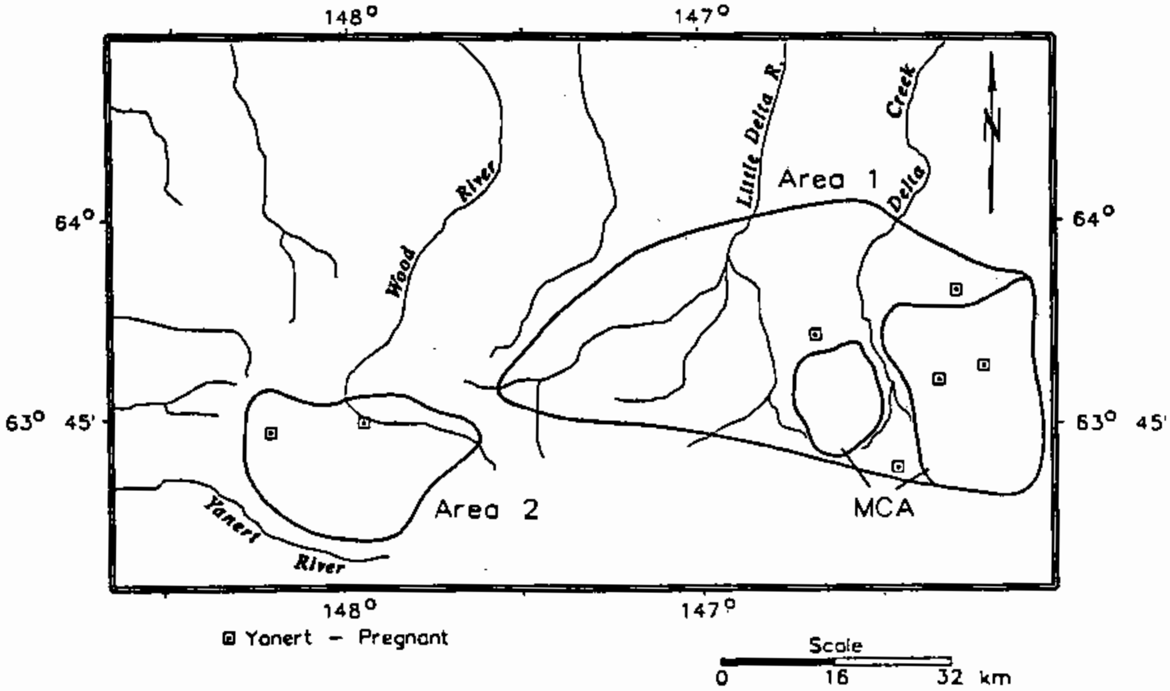


Fig. 10. Approximate calving locations of female no. 10236S, 1981-87.

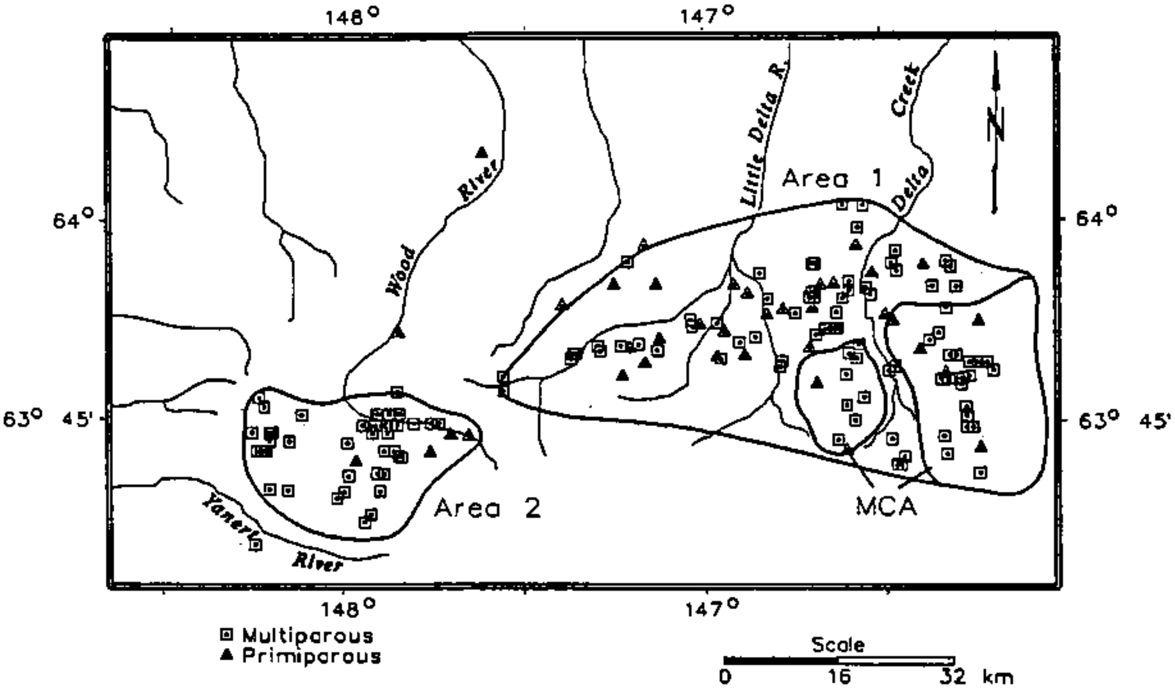


Fig. 11. Approximate calving locations of primiparous and multiparous radio-collared female Delta and Yanert caribou, 1980-87.

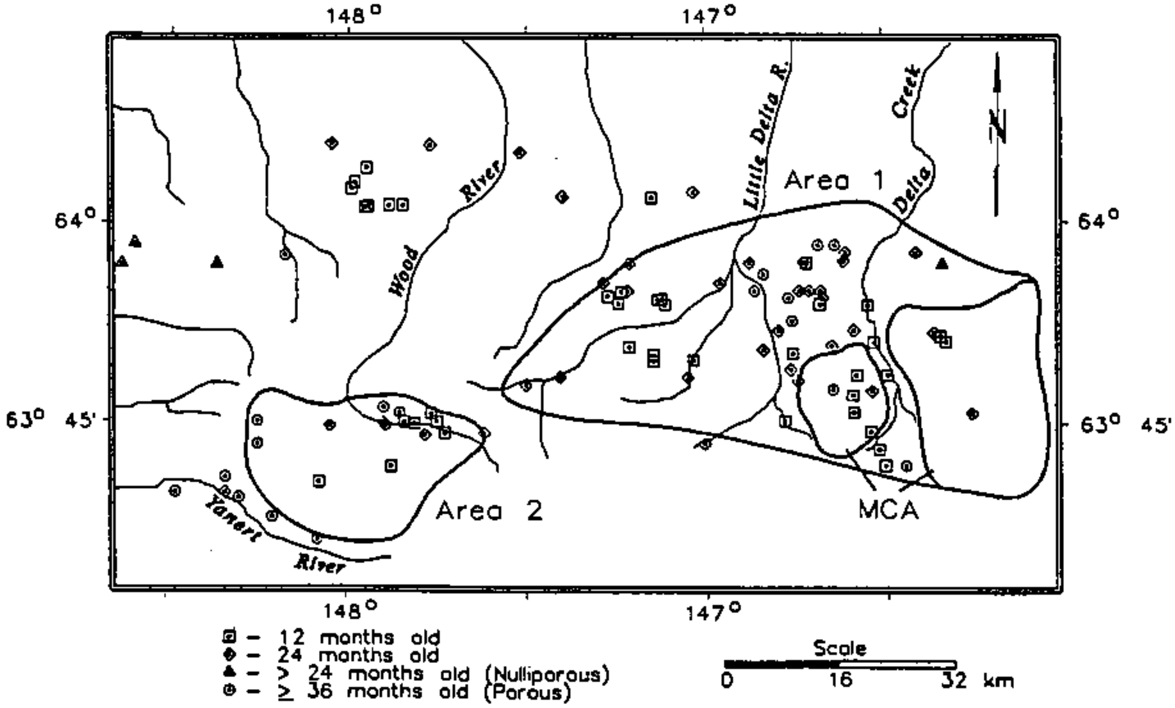


Fig. 12. Approximate locations of radio-collared nonparturient female Delta and Yanert caribou during the peak of calving, 1979-87.

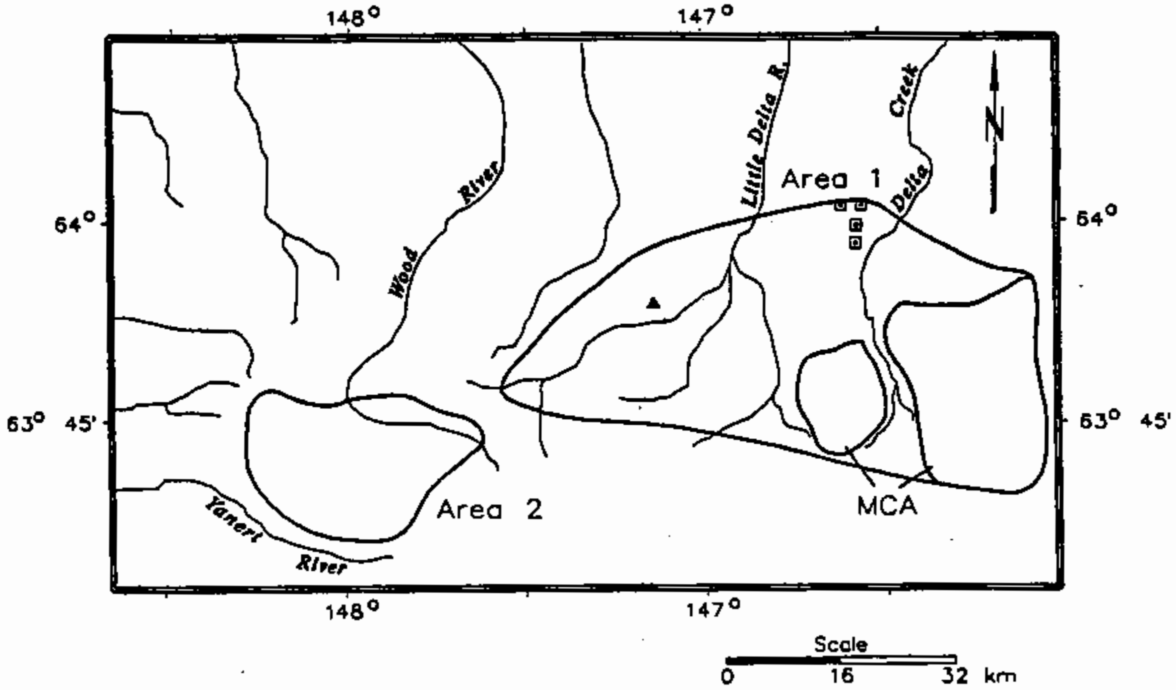
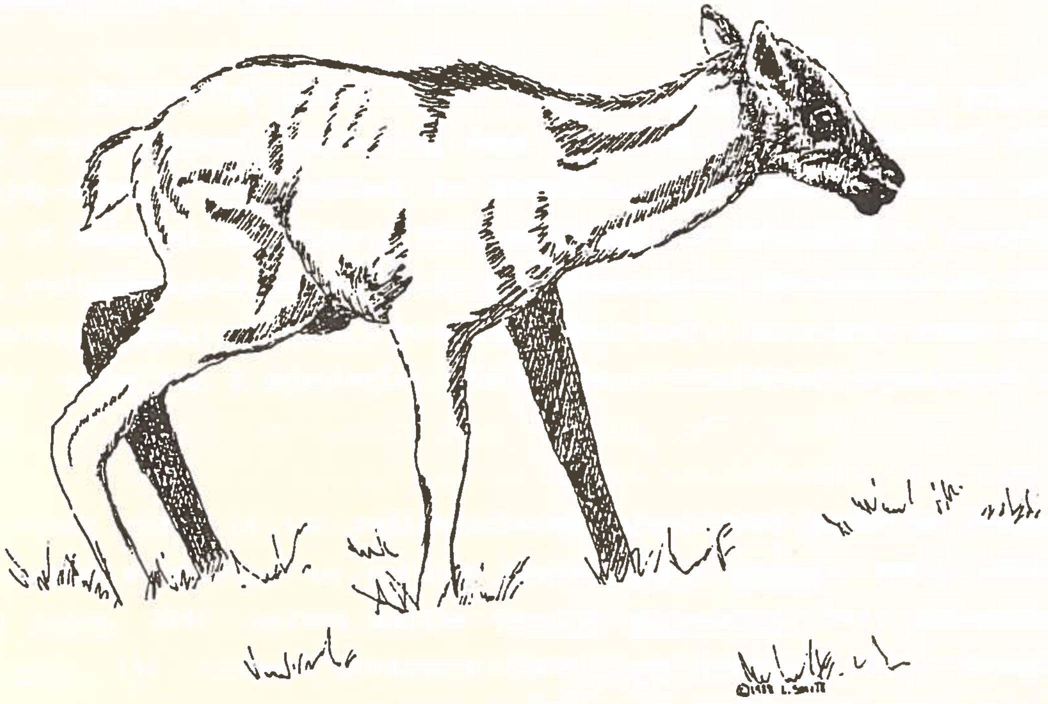


Fig. 13. Approximate locations of female no. 101972 during the peak of calving, 1980-84.

PART II



SURVIVAL

NEONATAL MORTALITY IN THE DENALI CARIBOU HERD

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Abstract: During May 1984-87, 224 caribou (Rangifer tarandus granti) calves were captured within 1-5 days of birth and instrumented with mortality-sensing radiocollars to determine the extent, timing, and causes of neonatal mortality. Throughout May, we attempted to visually locate radio-collared calves daily and investigated mortalities as soon as possible (usually within 5 hours of detection). Mortality rates were compared using the Z statistic; results were considered significant at $\alpha < 0.10$.

Eighty-eight (39%) of the radio-collared calves died prior to 1 June. Deaths were attributed to grizzly bears (Ursus arctos, 49%), wolves (Canis lupus, 28%), golden eagles (Aquila chrysaetos, 5%), wolverines (Gulo gulo, 1%), unknown predators (16%), and drowning (1%). Grizzly bears accounted for significantly more of the mortality than wolves and unknown predators combined.

The daily rate of mortality attributed to grizzly bears declined from 0.06 for calves 2 days of age to 0.01 for calves 10 days of age; no mortalities beyond the latter age were attributed to grizzly bears. Wolves killed calves between 3 and 13 days of age, with an average daily mortality rate of 0.01. Overall, daily mortality rates for calves were similar during the first 8 days but decreased significantly at 8-9 days of age (0.07 and 0.02, respectively).

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Total mortality was similar in 1984, 1986, and 1987 ($\bar{x}$ = 33%), but was significantly higher in 1985 (56%) following a winter with deep snow which persisted through the calving period. In addition, a 20-cm snowfall occurred immediately after the peak of calving in 1985. In the years of normal snowfall, the neonatal mortality rate (to 15 days of age) was significantly higher for calves born within the first 4 days of the calving period than for those born during the second 4 days, at the peak of calving (0.50 and 0.29, respectively). Neonatal mortality rates for peak and late period calves (born from the 9th day of calving on) were not significantly different (0.29 and 0.34, respectively). In 1985, however, neonatal mortality rates increased with each successive birth period (0.34, 0.56, and 0.80 for early, peak, and late periods, respectively).

In comparing cause-specific mortality rates for calves among years, we determined that mortality attributed to grizzly bears in 1985 was significantly lower for early-born calves than in the other years (0.00 and 0.27, respectively), the same for peak calves (0.11 and 0.12, respectively), and significantly higher for late calves (0.70 and 0.19, respectively). In contrast, mortality attributable to wolf predation in 1985 was the same as in the other years for early calves (0.22 and 0.21, respectively), significantly higher for peak calves (0.23 and 0.07, respectively), and significantly lower for late calves (0.00 and 0.09, respectively). Note that wolf predation on early calves did not increase in 1985 even though there was no grizzly bear predation associated with that cohort. The increases in calf mortality attributed to grizzly bears on late calves and to wolves on peak calves in 1985 were coincident with the 20-cm snowfall during the calving period.

We suspect that these differences in cause-specific mortality rates for 1985 relative to the other study years are attributable to the following: (1) later den emergence of grizzly bears and (2) increased vulnerability of caribou calves following the 20-cm snowfall during the calving period.

Key Words: caribou, Denali Herd, neonatal mortality, predation, *Rangifer*

DECLINE OF PHYSICAL CONDITION AND DECREASE OF RECRUITMENT IN THE GEORGE RIVER CARIBOU HERD

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Abstract: Following an apparent period of abundance at the end of the last century, the caribou (*Rangifer tarandus*) populations of northern Quebec rapidly declined, provoking famine among the native peoples. Caribou remained rare until the early 1960's. Then, an annual growth of 10-15% due to high recruitment permitted the population to exceed 300,000 by the early 1980's.

This report constitutes the first pessimistic information concerning the recent history of the George River Herd. Data on physical condition of George River caribou in 1985-86 were compared with earlier data from Dauphiné and Drolet (1976), Parker (1980), and Huot and Goudreault (1985). These comparisons suggest a deterioration in the condition of adult females in the spring. Live weight has declined from 101.8 kg ± 7.8 kg (S.D.) (*n* = 21) in 1976 to 93.4 kg ± 8.0 kg (*n* = 103) in 1980, and to 85.6 kg ± 7.1 kg (*n* = 23) in 1984-86. Back fat thickness, femur marrow fat, and kidney fat weight have also declined. Mandible length of females 46 months of age and older has decreased from 286.3 ± 7.1 mm in 1963-65 (*n* = 79, Bergerud 1967) to 274.7 ± 8.9 mm (*n* = 60) in 1985-86. Our data on physical condition suggest that female fat reserves in April equal or exceed those in fall. Our explanation for this phenomenon, unique for northern caribou, is based on the recent deterioration of summer habitat, particularly on the calving grounds.

Recruitment has also decreased since 1976. Between 1973 and 1981, the mean ratio of calves per 100 females in fall was 52 (range 46-57). This ratio remained below 40 between 1984 and 1987. Relative calf abundance in spring has also declined since 1977. In April 1987, the population contained only 8.2% ± 1.0% (S.D.) calves. This decrease in gross recruitment is attributed to increased winter calf mortality since 1977, an increase in summer mortality since 1984, and a decrease in the pregnancy rate. Net annual recruitment, estimated by adjusting for harvest rate by humans (2.7-4.3%) and the rate of natural adult mortality (5.3-10.8%), suggests that the herd has declined about 5% annually since 1984.

Probable causes of the recent trend in herd size include the following: a decline in female physical condition, deterioration of the calving ground habitat, delay in birth dates, increased density of caribou over all the range (but mainly on the calving grounds), an increase in the wolf population between 1976 and 1980, and exceptionally deep snow during winter 1980-81.

In addition, our data on net recruitment suggest that the population size of 472,000 (excluding the newborn), derived from the June 1984 aerial census, was an overestimate. We believe that current herd size is approximately 320,000. Our estimates of net recruitment are consistent with the apparent population dynamics of the herd, as illustrated by the results of aerial surveys in 1976, 1980, 1982; and even those in 1986, which we had thought invalid due to certain logistic and weather-related problems. Considering the uncertainty regarding actual herd size, and the significant decline in recruitment observed recently, we suggest that major commercial exploitation be suspended, leaving the harvestable surplus to hunters. Results of the census planned for June 1988 should clarify the status of the George River Herd.

We particularly thank Stuart Luttich, biologist for the Wildlife Department in Goose Bay, Labrador, who carried out most of the spring counts used to determine overwinter calf survival. We also thank Didier Le Henaff, wildlife technician for the Ministere du Loisir, de la Chasse et de la Peche in Quebec City, for his invaluable contribution to the collection of data on George River caribou for more than 15 years. We are grateful to Dr. Jean Huot, from the Biology Department of the Universite Laval in Ste-Foy, who allowed us to use raw data describing physical condition of caribou in 1983 and 1984.

Key Words: caribou, condition, George River Herd, recruitment, Rangifer

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MORTALITY OF DELTA HERD CARIBOU TO 24 MONTHS OF AGE

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Abstract: From 1979 through 1987, we investigated natural mortality between birth and 24 months of age in the Delta Caribou (*Rangifer tarandus granti*) Herd (DCH). Calf:cow ratios were obtained at the end of calving, during the rut, and in April to estimate natural mortality within the 0-5 and 5-12 month old cohorts (MOC's). Mean rates of mortality for the 0-5 and 5-12 MOC's, respectively, were 56% and 5.5%. Natural mortality within the 8-12, 12-24, and >24 MOC's was estimated from data on known-age radio-collared caribou. No natural mortality was observed among 8-12 month old females, compared with a rate of 34% for males. Natural mortality rates for females and males in the 12-24 MOC were 4% and 19%, respectively. Among the >24 MOC's, mean annual natural mortality was 7% for females and 19% for males. Within all age cohorts, natural mortality was higher for males than females, which is consistent with the literature. In contrast, the observation that natural mortality in the 5-12 and 12-24 MOC's was no greater than in the >24 MOC's is inconsistent with the literature on moose and was unexpected. Data on caribou herd size, trend and density, and predator:prey ratios are presented to place the derived mortality rates in context.

Key Words: calf, caribou, Delta Herd, mortality, *Rangifer*, survivorship, yearling

Except for the period from birth to the rut (0-5 months), the ability to empirically estimate age-specific mortality rates of caribou has lagged behind recognition of the utility of accurate mortality rates. Before 1980, few data were available on natural mortality rates of cohorts older than calves. Although mortality rates for the calf cohort (0-12 months) have been frequently inferred by comparing calf:cow ratios at calving with those in late winter or early spring, little insight exists regarding chronology of mortality within the first 12 months of life. Interpreting changes in serial calf:cow ratios is difficult because of seasonal segregation of the various categories of caribou (e.g., gravid vs. non-gravid in addition to all the sex and age cohorts). In short, sampling bias is common.

Before the 1980's, the literature contained little data on natural mortality rates of caribou. Skoog (1968) and Kelsall (1968) suggested that annual natural mortality rates of 5-6% could be expected for caribou older than yearlings when relatively few wolves (Canis lupus) and grizzly bears (Ursus arctos) were present. Bergerud (1971) reported that male Newfoundland caribou (R. t. caribou) had a higher mortality rate (9%) than females (4%). These mortality estimates were based on the authors' familiarity with the herds they studied; satisfactory quantitative techniques were not available at the time for estimating mortality rates. Lacking empirical estimates of mortality for subadult cohorts (generally defined as caribou 12-36 months old), most workers have inferred rates mid-way between those of the calf and adult cohorts.

Most caribou biologists agree that knowledge of the rates and causes of natural mortality is essential for understanding population change and, hence, central to successful management (Klein and White 1978). To model caribou population dynamics realistically, it is essential to ascertain age-specific mortality rates. A Workshop on "Parameters of Caribou Population Ecology in Alaska" (Klein and White 1978) identified age-specific death rates as one of 8 categories of information necessary to understand caribou population dynamics. Workshop participants agreed that ascertaining serial calf:cow ratios is adequate for assessing calf mortality in summer, but may not be adequate for the rest of the year. In addition, there was a consensus that existing techniques were inadequate for measuring age-specific death rates for age classes older than calves. Therefore, we initiated an investigation to evaluate the utility of using radio-collared caribou of known age to estimate age-specific mortality.

The mortality rates of caribou <24 months of age are emphasized in this paper. Specifically, we (1) compare and contrast empirical estimates of natural mortality (i.e., all but man-induced mortality) rates for 3 age cohorts <24 months of age: 0-5, 5-12, and 12-24 months old, respectively); (2) compare natural mortality of caribou <24 months old with that of older cohorts; (3) present data on caribou population density and predator:prey ratios for the period in which natural mortality was estimated; and (4) discuss the implications of our results for modelers and managers of caribou populations.

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STUDY AREA/HERD

Bibliographic information on the DCH and its environment was cited in Davis et al. (1987).

Large predators in the study area include wolves, black bears (Ursus americanus), and grizzly bears. Major prey species present include moose (Alces alces), caribou, Dall sheep (Ovis dalli), beavers (Castor canadensis), snowshoe hares (Lepus americanus), and ground squirrels (Citellus parryi).

Skoog (1968) originally delineated the range of the DCH. Based on subsequent study, Hemming (1971) modified Skoog's delineation and described the physical environment. Little change has been warranted since.

The DCH currently ranges over about 9,600 km^2 on the north slopes of the Alaska Mountain Range between the Nenana River on the west and the Delta River on the east (Fig. 1). The area lies approximately 110 km south of Fairbanks. The Alaska Range consists of rugged, glaciated ridges, 1,830-2,740 m in elevation, interspersed with glacier-capped mountains exceeding 3,660 m. The northern foothills of the Alaska Range are flat-topped ridges, 610-1,370 m in elevation, separated by rolling tussock tundra, muskegs, and lowlands dominated by spruce (Picea spp.). North of the foothills lies the predominantly spruce-covered Tanana Flats. The entire area is drained by the Tanana River.

The study area is largely snow-free from May until October. Annual temperature range is approximately 29°C to -51°C. Annual precipitation averages about 30 cm; snow accumulation averages 0-50 cm and rarely exceeds 80 cm. In the foothills and mountains, ground vegetation is frequently exposed during winter by strong winds.

METHODS

Capture and relocation procedures for radio-collared caribou have been described previously (Davis et al. 1987).

Radio-collaring

In each of 7 years between 1979 and 1987, we radio-collared 7-19 caribou (primarily females) that were 8-12 months old. To eliminate the effect of capture-related mortalities, only those caribou alive 7 days after radio-collaring were included in the sample.

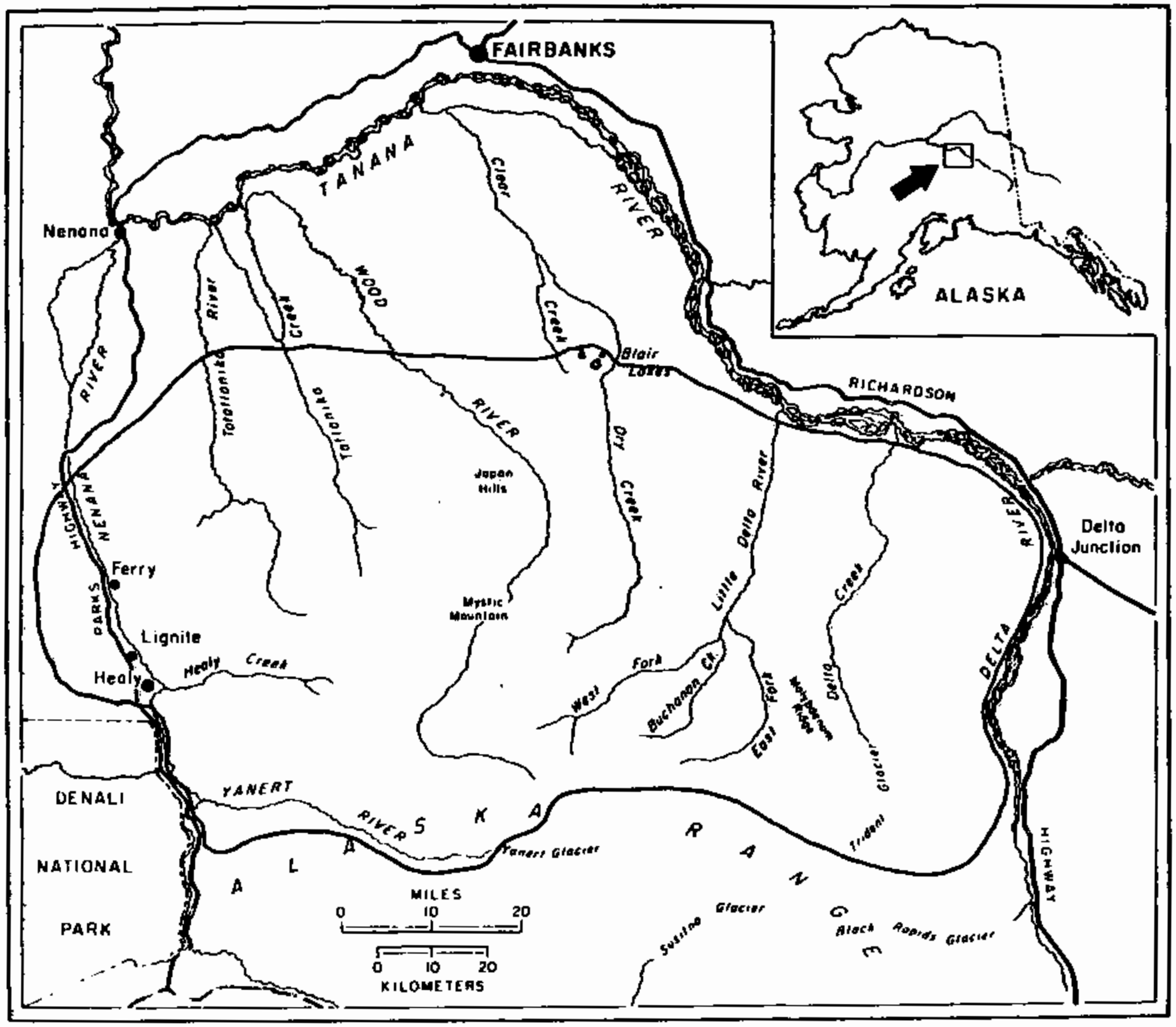

Fig. 1. Study area and distribution of the Delta Caribou Herd.

A helicopter (Bell 206B or Hughes 500C or D) and darting or netting equipment were used for capturing the calves. Immobilizing drugs and doses used from 1979 through 1982 were reported in Valkenburg et al. (1983). Davis and Valkenburg (1985a) reported doses of M99 and its antagonist, M50-50, used from 1983 through spring 1985. In fall 1985 we began using Carfentanil and Naloxone as immobilizing drug and antagonist, respectively; results were summarized by Adams et al. (1988).

All radiocollars (Telonics, Inc., Mesa, Ariz.) were in the 150-151 MHz frequency range and contained movement-sensitive mortality switches. On female calves, collars could be put on tight enough that they would not slip over the head when antlers were shed, but would allow growth of the neck to adult size. On males this was not possible because of their greater neck development as adults. We improvised an expandable collar for males in 1979, but it worked poorly; thereafter, we avoided collaring male calves.

Radio-tracking

Radio-collared caribou were relocated periodically from fixed-wing aircraft; details are in reports summarized in Davis et al. (1987).

When a mortality signal was heard, the collar site was visually located and evidence of mortality was noted. For confirmed mortalities, a helicopter was flown to the vicinity at a later date, the collar was relocated, and the site closely inspected. The caribou remains and adjacent area were investigated to ascertain the cause of death. Samples were obtained from the carcass, and nearby tracks, scats, and hair were noted and photographed.

Natality and Mortality Rates

Calf:cow Ratios: Composition surveys, which yielded calf:cow ratios, were conducted in May, June, October, and April to estimate mortality of the 0-5 and 5-12 MOC's. Details of the methods were presented or cited by Davis et al. (1987). Composition surveys in late May, following the peak of calving, included distended udder counts (Bergerud 1964) which provide an index of natality. Differences in calf:cow ratios over time served as an estimate of the magnitude and chronology of calf mortality.

Radio-collared Caribou: An annual natality rate for radio-collared caribou was obtained by observing each radio-collared cow at least once at or near the peak of calving and noting the presence of a calf, udder distension, and antlers.

We estimated adult mortality rates for radio-collared caribou data using procedures described by Trent and Rongstad (1974). Previously, we compared and contrasted mortality rates using the Trent and Rongstad (1974) procedure with rates calculated using Gasaway et al.'s (1983) method and found only minor difference (Davis and Valkenburg (1985a,b), as did Edmonds (1987) who compared the procedure of Gasaway et al. (1983) with that of Heisey and Fuller (1985).

No statistical tests were conducted to compare mortality rates among the various sex and age cohorts discussed; conclusions are qualitatively based. The mortality rates presented for the various age cohorts apply to unequal time intervals: 0-5 MOC = 5 months, 8-12 MOC = 4 months, 12-24 MOC = 12 months, and >24 MOC = 12 months (i.e., the mean annual rate).

RESULTS

Natality

Herd natality, based on composition surveys, averaged 79 calves:100 cows. The mean birth rate of radio-collared cows ≥36 months old was 82% (Table 1).

Mortality Rates

Observed changes in the calf:cow ratio indicate a mean natural mortality rate of 56% for the 0-5 MOC (Table 2). Our data were inadequate to determine if mortality was similar among males and females within the 0-5 MOC. However, our fall 1988 data showed a sex ratio of 41 males:59 females (we expected 50:50) among the 5-month-old calves, suggesting that males suffer higher mortality within the first 5 months of life.

Table 1. Estimates of natality in the Delta Caribou Herd, 1981-86.

Year	Sample from aerial survey of calving ground % parturient for cows ≥24 mo old (n)	Radio-collared caribou % parturient for cows ≥36 mo old (n)
1981	N.A.	77 (13)
1982	72 (151)	70 (10)
1983	80 (2,052)	77 (22)
1984	82 (482)	90 (31)
1985	N.A.	93 (41)
1986	82 (N.A.)	83 (40)
1987	N.A.	84 (32)
1988	83 (891)	92 (30)
	$\bar{x}$ = 79.0 (4.8 S.D.) 90% C.I. = 79.0 ± 5.6	$\bar{x}$ = 82.0 (8.0 S.D.) 90% C.I. = 82.0 ± 6.35

We observed no natural mortality among 8-12 month old radio-collared females. This is consistent with the low mortality rate of 5-12 month old caribou (both sexes combined) calculated from the serial calf:cow ratios (Table 3). Limited data on radio-collared males 8-12 months old suggest a 34% natural mortality rate (the small sample makes the finding suspect), which contrasts sharply with the low mortality rate of females.

In the 12-24 MOC's, natural mortality rates were 4% and 19% for females and males, respectively (Table 3). For the >24 MOC's, natural mortality was 7% and 19% for females and males, respectively.

DISCUSSION

Mortality

From 1981 through 1988, the mean rate of natural mortality in the DCH was 56% for the 0-5 MOC's, which is consistent with Bergerud's (1978) conclusion that the calf cohort commonly experiences ≥50% natural mortality. However, in contrast to suggestions in the literature and conjecture among caribou workers, we found that the natural mortality

Table 2. Annual percentage change in calf:cow ratio, birth to fall and fall to spring in Alaska's Delta Caribou Herd, 1981-87.

Date	Sample size	Calves: 100 cows	% change in the ratio of calves:100 cows	
			birth to fall	fall to spring
Late May 1981	13RC[a]	77	-47	N.A.
10/2/81	1,095	41		
Late May 1982	10RC	70	-56	-6
10/8 & 11/26/82	1,189	31		
4/20/83	913	29		
Late May 1983	22RC	77	-40	+4
10/4/83	972	46		
4/10 & 13/84	735	48		
Late May 1984	31RC	90	-60	N.A.
10/17/84	835	36		
Late May 1985	41RC	93	-61	-14
10/9 & 12/85	630	36		
4/20/86	853	38		
Late May 1986	40RC	83	-65	N.A.
10/6/86	1,576	29		
Late May 1987	32RC	84	-63	-6
10/5/87	1,682	31		
4/16/88	1,473	29		
			$\bar{x}$ = - 56.0 (9.2 S.D.) 90% C.I. = -56.0 ± 6.7	$\bar{x}$ = -5.5 (7.4 S.D.) 90% C.I. = -5.5 ± 8.7

[a] RC = radio-collared caribou.

rate during the first winter (i.e., 5-11 months of age) was relatively low, with the exception of 8-12 month-old radio-collared males.

Serial calf:cow ratios measure only relative change in the proportion of calves, so they are only an index of the rate of calf mortality. Determining the actual mortality rate of calves requires ascertaining the change in absolute numbers of calves over time. Calf mortality rates estimated from serial calf:cow ratios can be refined by adjusting for the loss of cows during the interval between acquiring ratios. For our data

Table 3. Calculated mean mortality rates for male and female caribou, based on radio-collared caribou, in the 8-12, 12-24, and >24-month-old cohorts, Delta Herd, 1979-87 (after Trent and Rongstad 1974).

Age cohort	No. radio-collared (no. collar-months)	No. man-caused deaths (% mortality)	No. natural deaths (% mortality)	No. total deaths (% mortality)
8-12 mo.	Female 61 (109.5)	0	0	0
	Male 10 (23.8)	0	2(34)	2(34)
12-24 mo.	Female 62 (659)	0	2(2)	2(4)
	Male 7 (63.3)	1(19)	1(19)	2(38)
>24 mo.[a]	Female 64 (2,861)	6(3)	17(7)	23(10)
	Male 18 (308)	8(31)	5(19)	13(50)

[a] Percent mortality represents a mean annual rate.

set, the adjustment for calf mortality overwinter, estimated from October and April calf:cow ratios, would amount to only a couple of percentage points.

An additional complication is that some calves, particularly males, separate from the females during late winter and remain with the adult males, which do not migrate to the calving grounds. Our April composition data always show that bulls are underrepresented, so it follows that calves may be as well. We have no means of objectively correcting for the missed calves, but even a modest elevation of the calf:cow ratio would suggest little difference in overwinter mortality between calves and older cohorts.

Our data from radio-collared caribou suggest that natural mortality of Delta caribou was similar among the 8-12, 12-24, and >24 MOC's. Natural mortality of all cohorts was higher for males than for females, which is consistent with the literature (Bergerud 1978) and our expectations. In contrast, similar mortality rates among >5-month-old calves, yearlings, and adults was unexpected and is inconsistent with the literature on cervids, especially that on moose. When we extrapolate to caribou from the literature, particularly for age-specific mortality and predator-prey relationships, we rely most on the moose literature. We believe this is common among caribou workers. Moose <24 months old clearly experience higher mortality than the mean for adults (Peterson et al. 1984, Ballard et al. 1987).

Implications for Modeling

Bergerud (1971, 1978, 1980, 1983) has repeatedly emphasized that ascertaining mortality rates is essential to understanding caribou population dynamics and therefore to management. Bergerud (1980) pointed out that conventional life table analysis (Banfield 1955, Bos 1973, Miller 1974) has limited usefulness because caribou populations normally have an unstable age structure, resulting from natural variation in calf survival. He suggested using census, recruitment, and harvest parameters to determine natural mortality rates.

Martell and Russell (1983) concluded that Bergerud's alternative may not be practical because it requires accurate determinations of caribou numbers, recruitment, and harvest, all of which may be difficult to obtain. Instead, they suggested radio-collaring calves and following their survival to breeding age to help resolve the inconsistencies in estimates of early mortality rates. In addition, they suggested that cohort analysis may produce a better estimate of the adult mortality rate by avoiding the problem of an unstable age structure. Whitten et al. (1984) discussed the difficulties of using radio-collared calves to obtain calf mortality data that are representative of the herd. The biases contributed by stillbirths, early neonatal mortality, and the selection of calves for collaring are difficult to overcome.

We believe that the use of radiocollars and the application of cohort analysis can overcome the problem of an unstable age structure. However, a caribou population may contain 10-12 male cohorts and 15 or more female cohorts, so large samples of radio-collared individuals are required. Obtaining adequate mortality data from radio-collared caribou may be as difficult as making accurate determinations of population size, recruitment, and harvest required to indirectly estimate mortality rates.

It is imperative to consider our findings on rates and patterns of natural mortality in proper context (Table 4). Extrapolating too broadly from our results may prove counterproductive. Our mortality rates were obtained from a herd that is part of a multi-prey/multi-predator system (Gasaway et al. 1983). Also, during the period of study, growth rate of the herd varied from rapid increase to near stability, resulting from increasing harvest and predation. Nutrition and weather appeared to be favorable during the study period.

Table 4. Range size, population size, density, trend, and predator: caribou ratios of the Delta Caribou Herd, 1979-87.

Year	Size of range km^2	Population size	Population density caribou:km^2	Wolf: caribou	Grizzly: caribou
1979	8,023	3,831	1:2.1	1:101	1:31
1980	8,023	4,321	1:1.9	1:98	1:35
1981	8,023	4,750	1:1.7	1:93	1:39
1982	8,023	6,545	1:1.2	1:111	1:53
1983	9,339	6,170	1:1.5	1:78	1:50
1984	10,007	5,660	1:1.8	1:58	1:46
1985	10,339	7,483	1:1.4	1:63	1:61
1986	10,786	7,204	1:1.5	1:50	1:61
1987	10,786	7,780	1:1.4	1:47	1:61

[a] Assumes 123 grizzlies in 1986 and $\geq$123 prior to 1986 (after Reynolds et al. 1987).

Although there may be some utility in extrapolating to caribou from the conceptual models of moose ecology, we believe the practice may be counterproductive, particularly with regard to patterns of mortality and predator/prey relationships. Clearly, there is no substitute for empirical data.

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THE INFLUENCE OF WOLF PREDATION ON CARIBOU MORTALITY IN YUKON'S FINLAYSON CARIBOU HERD

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Abstract: Mortality from manageable factors (hunting and wolf (*Canis lupus*) predation) was reduced to increase the size of Yukon's Finlayson Caribou (*Rangifer tarandus caribou*) Herd. The influence of wolf predation on this caribou population was assessed by monitoring calf recruitment, as indicated by the percentage of calves in the herd during fall and the rate of adult natural mortality in relation to wolf numbers. We also examined the general influence of winter severity and food limitation. We assumed that the influence of wolf predation on caribou mortality would be evident if other factors remained constant. Between 1983 and 1987, wolf abundance was reduced by aerial hunting to less than 20% of the pre-reduction level. After 1984, calf recruitment increased by 113%, and the rate of adult natural mortality, estimated by the death rate of a radio-collared sample (n = 52) of mostly female caribou (n = 48), decreased by 60%. Both calf recruitment and adult natural mortality rate were significantly (P < 0.01) correlated with the density of wolves. Nutritional factors (food availability), as measured by snow depth and late winter diet, did not appear to play a key role in herd demography. We conclude that wolf predation was the chief cause of mortality in this herd and a driving force in its population dynamics.

Key words: caribou, Finlayson Caribou Herd, mortality, predation, *Rangifer*, wolves, Yukon

Factors influencing caribou (*Rangifer tarandus*) mortality include hunting, predation, forage, weather (including snow conditions and windchill on calves), disease/parasites, and accidents (Kelsall 1968, Skoog 1968).

We believe that, of these factors, the chief causes of mortality among woodland caribou (R. t. caribou) in Yukon are hunting, made possible by road access, and predation, principally by wolves. Our belief is supported by the findings of other studies on woodland caribou in Canada (Bergerud 1978; Fuller and Keith 1981; Edmonds and Bloomfield 1984; Elliot et al. 1984; Gauthier 1984, 1986; Page 1985; Bergerud and Elliot 1986) and on barren-ground caribou (R. t. granti) in Alaska (Davis et al. 1978, 1980; Davis and Valkenburg 1983a,b, 1985; Gasaway et al. 1983). Wildlife managers responsible for maintaining caribou numbers can apply direct strategies to lower hunter- and predator-induced mortality, but have no practical methods to reduce the influences of food availability, severe weather, disease, and parasites.

An intensive management program aimed at increasing the size of Yukon's Finlayson Caribou Herd (FCH) has recently provided an opportunity to assess the influence of wolf predation on caribou mortality. In 1982, the FCH contained 2,000-2,500 animals (Farnell 1982). The percentage of calves in fall was 9.8, and the annual harvest was estimated to be 250 caribou, about 10% of the herd. Our status assessment suggested that this herd was declining by 11% annually due to low productivity and high natural and human-caused mortality. A management goal was adopted to increase the size of the FCH to 5,000 animals, a level that could sustain the hunter demand (200-250 caribou). The management actions taken were: (1) reduce human-caused mortality by restricting hunter harvest, and (2) reduce natural mortality by wolf removal. Subsequent population monitoring over a 5-year period (1982 to 1987) has provided information about the effectiveness of these manipulations.

In this paper we report changes in caribou calf recruitment and adult natural mortality in response to wolf control. We also examine the general influence of winter severity and food limitation as factors possibly affecting FCH population dynamics. We reasoned that the effects of wolf removal on caribou mortality should become evident if the influences of other potential population limiting factors remained constant over the duration of study. If this assumption is correct, lowered wolf predation should have resulted in a short-term (1-2 years) increase in caribou calf recruitment and a decrease in adult natural mortality.

For the purpose of managing woodland caribou in Yukon, we define a "herd" as a discrete population of caribou that inhabits a common winter range (Farnell and Russell 1984). The seasonal movements and distribution of several Yukon caribou herds have been monitored by intensive radio-telemetry studies (Farnell and McDonald 1987). Findings from this work and other studies (Farnell and Russell 1984, Hatler 1986) indicate a strong home range loyalty for the subspecies. At present densities at least, major changes in caribou numbers cannot be explained by shifts between herds as earlier theorized by Skoog (1968) and Haber (1977).

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STUDY AREA

The 19,000 km^2 study area corresponds to the home range boundary of the FCH in east-central Yukon (Fig. 1), and is roughly bordered by the North Canol Road to the west, the St. Cyr Range of the Pelly Mountains to the south, and the Logan Range of the MacKenzie Mountains to the north and east. Most of the FCH winter range lies in the Pelly Plateau and Tintina Trench, where the terrain consists of rolling upland plateaus, hills, and small tableland mountain groups separated by generally broad U-shaped valleys.

Valleys are vegetated by open black spruce (Picea mariana) and lodgepole pine (Pinus contorta) forests. Well-drained upland areas are dominated by white spruce (Picea glauca) and aspen (Populus tremuloides) forest. Paper birch (Betula papyrifera) is scattered throughout the lowlands, and

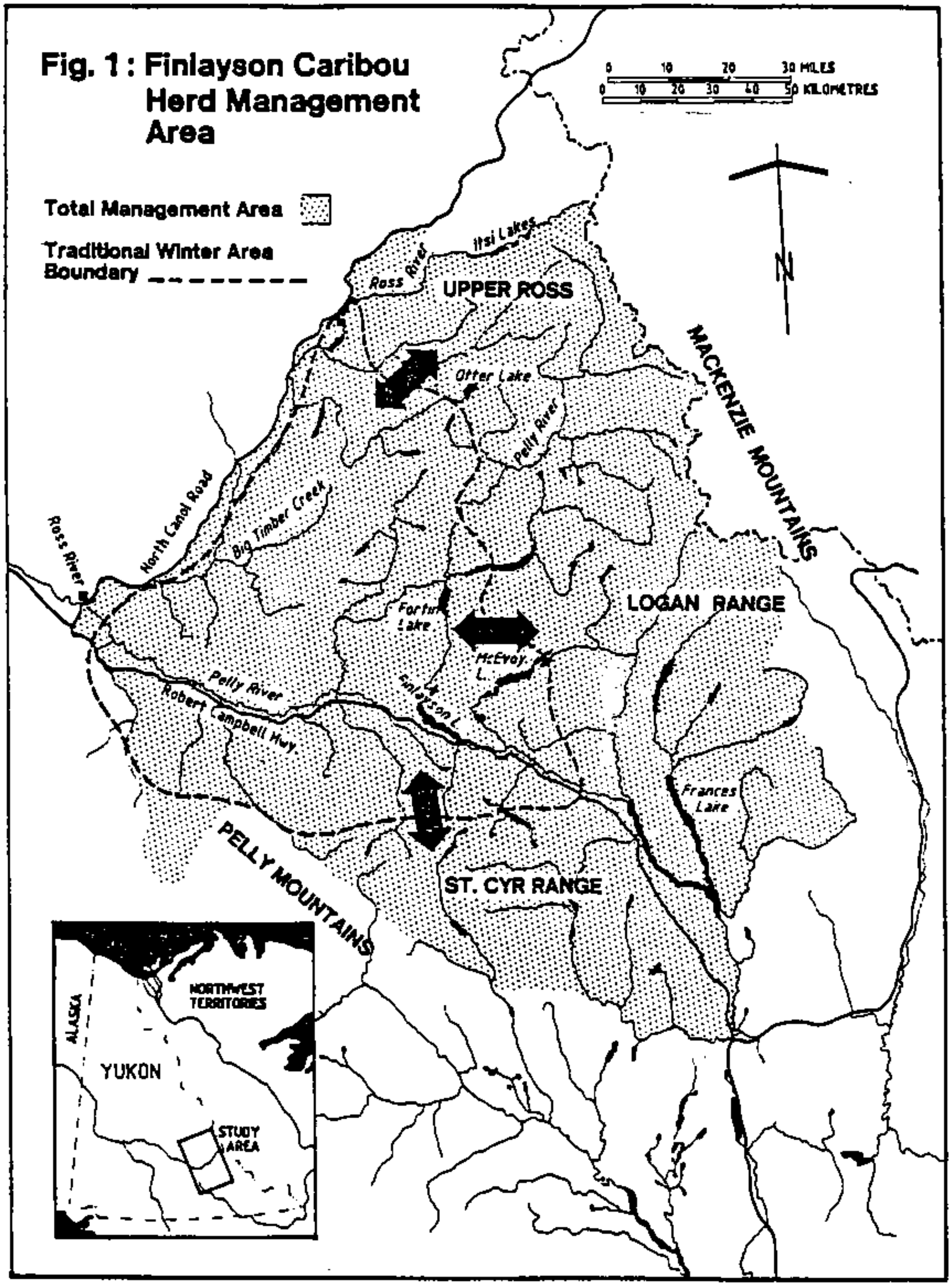

Fig. 1 : Finlayson Caribou Herd Management Area

alpine fir (Abies lasiocarpa) is common in the subalpine areas. Lakes are common in the central study area, providing important travel areas for wintering caribou and wolves.

Relief is moderately high in the St. Cyr Range in the southern study area, with elevations exceeding 1,500 m. The extensive subalpine zone occurs from valley floors to 1,350 m and is mainly vegetated by dwarf birch (Betula glandulosa) and willow (Salix spp.). Lichens, sedge (Carex spp.) tussocks, ericaceous shrubs, and willow dominate the alpine tundra (Oswald and Senyk 1977). The southern flank of the Logan Range, which forms the north and eastern portion of the study area, is characterized by rugged, high, peaked mountains. Most terrain is above treeline (1,350-1,500 m), and subalpine willow and birch form the prevalent plant communities.

Precipitation increases from southwest to northeast in the study area. The St. Cyr Mountains receive about 400-500 mm of precipitation annually, and the northeastern study area receives 750 mm in the Logan Mountain foothills (Oswald and Senyk 1977).

Two other species of ungulates inhabit the region. Moose (Alces alces) are common throughout the study area, and approximately 100 Dall's sheep (Ovis dalli) inhabit portions of the central St. Cyr Range (Lortie et al. 1978). Large predatory mammal species in the study area include wolves (Canis lupus), grizzly bears (Ursus arctos), black bears (Ursus americanus), coyotes (Canis latrans), fox (Vulpes vulpes), wolverine (Gulo gulo), and lynx (Lynx canadensis).

METHODS

Wolf Estimates and Reduction

The wolf population size in the FCH management area was annually estimated by repeated fixed-wing and helicopter surveys (Stephenson 1978) during late winter from 1983 to 1987. These estimates were augmented by observations made by ground personnel stationed in the area during winter.

From 1983 to 1987, we attempted to lower wolf numbers in the FCH management area by shooting entire packs; a helicopter was used for the shooting. Some wolves were also harvested by hunters and trappers. Shot wolves were retrieved whenever possible and skinned; pelts were stretched, dried, and sold on the open fur market. Carcasses were necropsied to determine age and sex, nutritional condition, reproductive history, and food habits. A detailed description of wolf inventory and reduction methods, and wolf necropsy results are found in Hayes and Farnell (1985, 1986, 1987).

Caribou Calf Recruitment

The percentage of calves in the herd during the fall breeding season was our index of recruitment. We assumed that the herd was homogeneously mixed when sampled; therefore, the calf proportions in the sample should have identified major trends in the population. Fall composition counts were conducted annually from 1982 to 1986 during the first week of October. Each year a preliminary radio-tracking survey was flown by fixed-wing aircraft to relocate radio-collared caribou. A helicopter was then used to classify a sample of caribou across the entire herd distribution, as determined from the radiocollar relocations. Caribou were classified as adult female, calf, yearling, immature bull, or mature bull using the characteristics described by Farnell and Russell (1984). Classification counts were made from helicopter overflights on small (<50 caribou) groups and from the ground with 20X spotting scopes on larger groups. Counts were recorded with hand-held, multiple-place tally registers.

Natural Mortality of Adult Caribou

During this study, radiocollars were placed on 4 male and 48 female caribou in the FCH. We deployed 18 radiocollars during late winter 1982, 4 in 1983, and 10 each in 1985, 1986, and 1987. These caribou were all captured by net-gun (Barret et al. 1982, Farnell and Russell 1984) and were therefore not predisposed to predation as a result of using drugs. Radiocollars were constructed of heavy machine belting to which hermetically sealed transmitters were attached. Most transmitters included movement-sensitive mortality switches (Telonics Inc., Mesa, Ariz.). A highly visible vinyl covering was sewn to each radiocollar.

Radio-collared caribou were located from fixed-wing aircraft (C-185 and C-206) from 1982 to 1987 during 4 lifecycle periods: calving (early June), postcalving (mid-July), rut (early October), and late winter (early March). When a mortality was detected audibly (i.e., increased pulse rate of the collar activated by immobility of the animal or by virtue of a stationary signal source between sequential flights), the site was inspected by helicopter and an attempt made to determine the cause of death.

The natural mortality rate (i.e., excluding man-caused mortality) of adult female caribou was calculated using a formula derived by Gasaway et al. (1983). The formula underestimates mortality rates if there is a seasonal peak in mortality near the end of the observation period, or if radio transmitters fail prematurely. And because the formula averages mortality over the entire observation period, a seasonal peak early in the period will cause mortality to be overestimated. The method probably does not ascertain the true natural mortality rate of all sex and age classes (older than calves) but does provide trends and relative rates. We acknowledge that an average sample of 23 collared animals is small in relation to total herd size (1% assuming 2,000-2,500 animals), but it is our only objective means of evaluating natural mortality.

Winter Severity

Winter severity is an important factor affecting caribou survivorship (Russell and Martell 1984), and snow conditions become increasingly adverse as winter progresses. A comparison of severity among winters was assessed by measuring snow depth in late winter at 8 permanent stations along the Robert Campbell Highway, which served as an east-west transect across the winter range of the FCH (Fig. 1). The depth of snow was measured between 5 and 12 March from 1983 to 1986. Snow depth data collected by Water Resources of Canada at Ross River between 26 February and 5 March, from 1975 to 1985, were used as the decade average for comparison with our snow data. The snow depth at Ross River is also indicative of snow conditions on the FCH winter range. Because snow depth generally begins decreasing by April (8% or 3.5 cm on average), the depth in March is probably indicative of the maximum average snow depth that would have influenced caribou in any given year.

Food Limitation

Diet composition in late winter can be used as an index of range condition (Martell and Russell 1987) when combined with data on relative food availability (i.e., snow depth). The late winter food habits of the FCH were examined by composite fecal sample collections made at various locations within the herd's winter distribution from 1982 to 1986. Each composite sample contained 20 fecal pellets, one from each of the first 20 fresh pellet groups observed at each collection site.

Fecal samples were analyzed microhistologically at the Composition Analysis Laboratory at Colorado State University, Ft. Collins. The relative density of plant fragments was based on 100 fields per sample. The results were compiled as percentage frequencies for each plant category (e.g., forbs, lichens, shrubs). The accuracy of fecal analysis is influenced by differential digestibility of the major plant categories (Holechek et al. 1982), and is only a qualitative estimate of the late winter diet rather than actual proportions of plant species ingested. The rumen turnover rate for caribou during winter is about 2 days (White and Trudell 1980). Therefore, each fecal sample should be reasonably representative of the mean forage selection for 20 caribou over an area somewhat larger than that encompassing the actual collection sites. We compared diet composition of the FCH with that of the highly productive Porcupine Herd to assess relative range quality.

RESULTS AND DISCUSSION

Wolf Estimates and Reduction

Initial wolf densities in the study area (11.3 wolves/1,000 km^2) were similar to those reported in central Alaska (Haber 1977, Gasaway et al. 1983) and elsewhere in Yukon (Hayes et al. 1985). The 1983 wolf reductions were carried out in the northern half of the study area only. Our reduction efforts were not uniformly applied until 1984, when the wolf population was decreased to 16% of the pre-reduction level (Table 1). Since then the wolf population has recovered at a fairly constant rate ($\lambda = 2.50 \pm 0.10$) and well above the intrinsic rate of increase (λ 1.15 to 1.46) calculated by Keith (1983).

The rate of increase (from post-removal year 1 to pre-removal year 2) in the wolf population accelerated as wolf numbers declined. It is important to note that the annual rate of increase resulting from a constant annual increment (in absolute numbers) is inversely related to the beginning population size. Ingress undoubtedly played a major role in the annual pre-removal recruitment into the wolf population. Since 1984, an average annual removal of 49 wolves has been required to maintain an average density of 1.77 wolves/1,000 km^2. The intensity of our reduction efforts has remained relatively constant over the duration of the study in terms of money, manpower, and time expended and probably represents the optimal return per unit of effort. To further reduce this wolf population below the levels achieved since 1984 would likely require a substantial increase in effort.

Caribou Calf Recruitment

The percentage of calves in the herd during fall increased from 9.8 in 1982 to 14.9 in 1983 (a 52% increase) after a 49% reduction in wolf numbers (Table 2). Between 1984 and 1987, when wolves were reduced by 84%, the percentage of calves averaged 20.1 (a 105% increase).

The percentage of calves in fall was negatively correlated with late winter wolf densities ($r = -0.97$, $P < 0.01$) (Fig. 2). Wolf reduction, therefore, appears to have improved calf survival.

Caribou Adult Natural Mortality

In total, 20 radio-tracking flights were conducted, and they provided 479 contacts with radio-collared caribou. Sixteen radio-collared caribou died from various causes during this study. The calculated annual mortality rate for the sample of radio-collared caribou in 1982-83, prior

Table 1. Wolf population status in the range of the Finlayson Caribou Herd, 1983-87. (See also Hayes and Farnell 1984, 1985, and 1987).

Year	No. of wolves alive	No. of wolves dead	% wolves remaining	No. of wolves/1,000 km^2	Recovery rate (λ)
1983:					
before removals	215	--	--	11.3	--
after removals	110	105	51	5.5	--
1984:					
before removals	140	--	--	7.3	1.27
after removals	34	106	16	1.8	--
1985:					
before removals	83	--	--	4.4	2.44
after removals	34	49	16	1.8	--
1986:					
before removals	83	--	--	4.4	2.44
after removals	31	52	14	1.6	--
1987:					
before removals	83	--	--	4.3	2.64
after removals	37	45	17	1.9	--

Table 2. Fall sex and age composition of the Finlayson Caribou Herd, 1982-86.

	No. of caribou					
Year	Adult cows	Calves	Yearlings	Bulls	Total	% calves
Pre-Wolf Control:						
1982	719	121	56	335	1,231	9.7
Post-Wolf Control:						
1983	330	113	82	234	759	14.9
1984	611	226	90	305	1,272	20.9
1985	262	131	75	190	658	19.9
1986	464	205	132	256	1,047	19.6

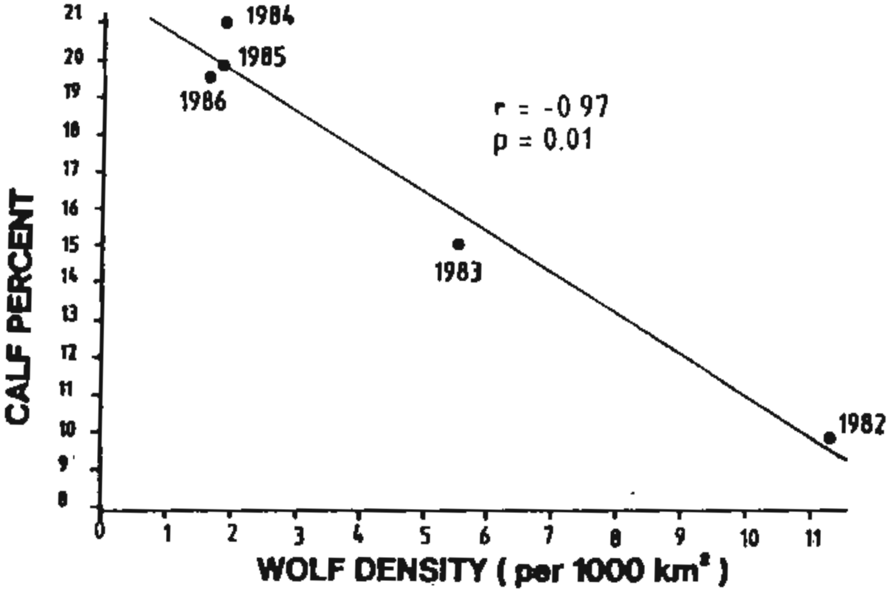

Fig. 2 : Relationship between percent calves in the fall and late winter wolf densities

to wolf reductions, was 27.7% (n = 5/18) (Fig. 3). This rate decreased slightly to 24.2% (n = 3/17) in 1983-84, after a 49% reduction in wolf numbers, and decreased further to a mean of 11.1% from 1984 through 1987 when wolf numbers were reduced further. Thus, the natural mortality of radio-collared caribou decreased by 60% after a substantial wolf reduction occurred in 1984. The adult natural mortality rate of radio-collared caribou decreased significantly ($P < 0.01$) and was positively correlated with the density of wolves in late winter ($r = 0.93$) (Fig. 4). Therefore, wolf reduction may have improved adult survival.

Predators were implicated in all mortalities of known causes (Fig. 3). Wolf predation was implicated in at least 8 (50%) cases, bear predation in 2 (13%) cases, and an unknown predator in 1 (6%) case. We were unable to determine the cause of death in 5 (31%) cases. More radio-collared caribou died between March and June (85%, n = 12/16) than in any other period. This seasonal peak in mortality suggests that woodland caribou may be vulnerable to predation and other natural causes of death following the hardships of winter. A seasonal peak in mortality at the beginning of the observation period likely caused adult natural mortality to be consistently overestimated in our study.

Winter Severity

Late winter snow depths in the study area were generally favorable for caribou. Between 1983 and 1986, the mean snow depth for 8 stations on the FCH winter range was 41.5 ± 11.3 cm, slightly deeper (+4.4 cm) than the 11-year average snow depth at Ross River (Fig. 5). The depth of snow on the FCH winter range was less than the critical depth for solitary animals to dig craters (50-60 cm) and far less than that for groups of caribou (80-90 cm) (Russell and Martell 1984).

Food Limitation

In general, the winter diet of the FCH, as determined from fecal analyses (Table 3), is similar to that reported for other caribou populations wintering in taiga habitat (Russell and Martell 1984). The diet was comprised predominantly of lichens (primarily *Cladonia* spp.). Graminoids (grass-sedge) were the second most abundant component of the diet,

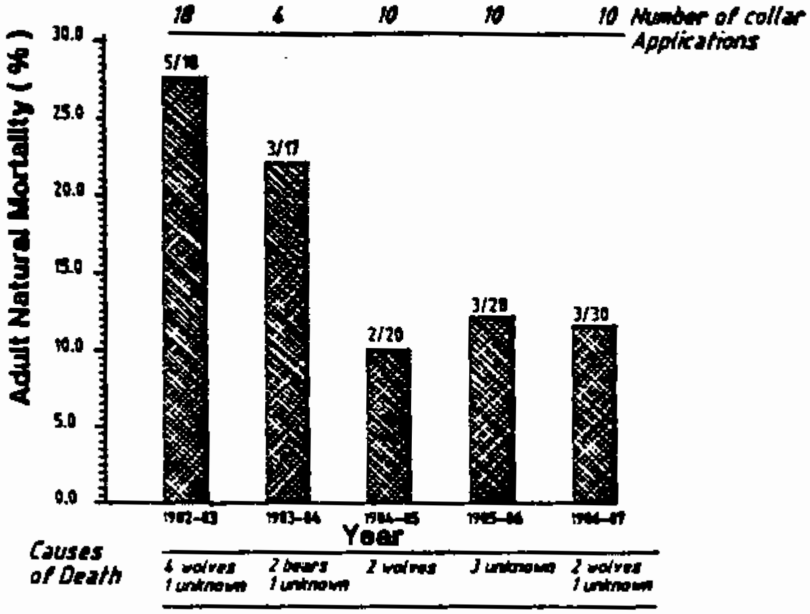

Fig. 3 : FCH Adult Natural Mortality Rate using radio-collar survivorship, March 1982 to March 1987.

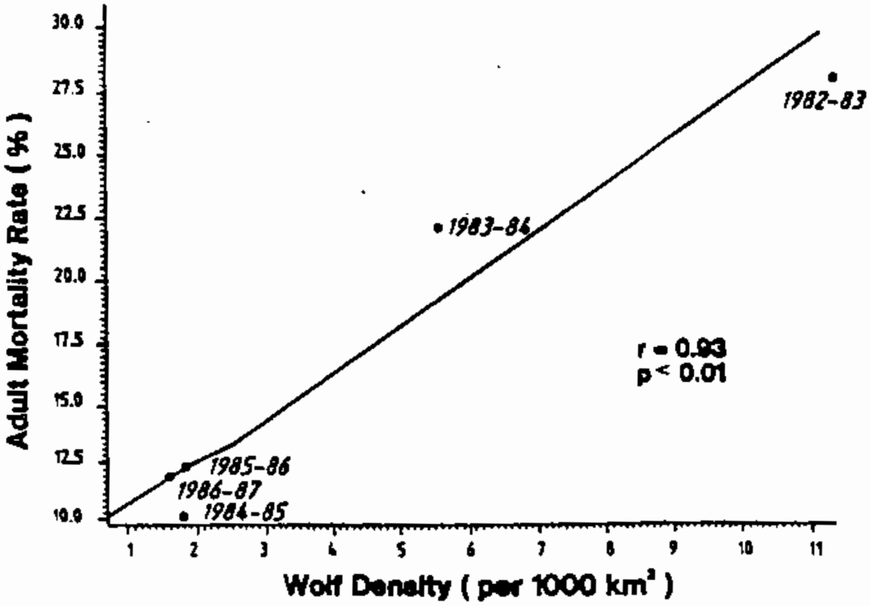

Fig. 4 : Relationship between the adult natural mortality-rate and late winter post-reduction wolf density.

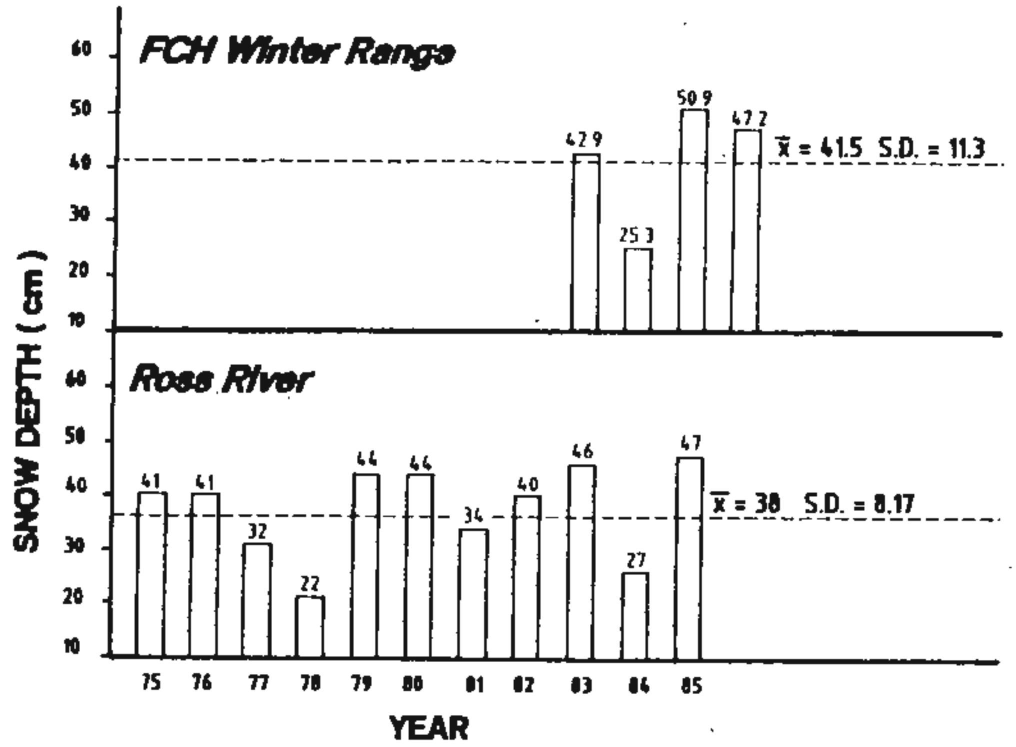

Fig. 5 : The mean snowdepth measurement on the FCH winter range during March, compared to snowdepth data measured at Ross River, Yukon by Water Resources of Canada.

Table 3. Average percentages (+SE) of identifiable plant fragments in fecal samples collected from the range of the Finlayson Caribou Herd, 1982-86, compared with those collected from the range of the Porcupine Herd, 1979-82, by Martell and Russell (1987).

Plant genus or group		Finlayson 1982-85 n = 8		Porçupine 1979-82 n = 15
Moss		0.83 ± 0.99		7.4 ± 1.50
Fruticose lichens		62.6 ± 12.3		66.3 ± 3.36
Cetraria - type	5.1 ± 2.53		12.1 ± 1.76	
Cladonia - type	54.6 ± 16.43		48.4 ± 3.72	
Stereocaulon	2.9 ± 3.74		5.8 ± 1.38	
Foliose lichens (*Peltigera*)		10.4 ± 9.35		6.2 ± 2.57
Mushrooms		1.0 ± 2.61		
Horsetails (*Equisetum*)		4.4 ± 3.91		2.8 ± 0.68
Graminoids		9.5 ± 6.79		2.4 ± 0.38
Carex	8.6 ± 6.7		1.3 ± 0.32	
Eriophorum	0.3 ± 0.42		0.4 ± 0.29	
Poa	0.6 ± 1.46		--	
Deciduous shrubs (*Salix*)		1.8 ± 2.99		2.3 ± 0.54
Evergreen shrubs		9.5 ± 4.07		12.4 ± 2.63
Dryas	--		0.6 ± 2.3	
Ledum	3.5 ± 2.26		1.1 ± 0.25	
Picea	2.2 ± 1.25		1.3 ± 0.41	
Vaccinium	3.4 ± 2.90		9.3 ± 2.31	
Forbs		0.2 ± 0.40		0.3 ± 0.10

followed by evergreen and deciduous shrubs. Herbs and moss were minor components of the late winter diet of the FCH.

The late winter diet of the FCH was probably better than that of the Porcupine Caribou Herd (Martell and Russell 1987) (Table 3), a highly productive and increasing population (Whitten 1986). While proportions of lichen in the diets of both herds were similar, the incidence of moss was much lower (0.8%) and the incidence of graminoids higher (13.8%) for the FCH. A high content of relatively indigestible moss in the diet is considered to be indicative of poor range (D. Russell, pers. commun.). In contrast, graminoids are highly digestible compared with other vascular plants, and are rich in protein and phosphorus (Klein 1982). High protein and mineral intake during late pregnancy and early lactation leads to a higher milk yield in cows and subsequent increased birth weight and growth of calves.

In summary, we believe that nutritional factors, based on the indices of snow depth (food availability) and diet quality, remained constant over the duration of the study and did not play a key role in the demography of the FCH.

CONCLUSION

Survival of FCH caribou increased immediately following wolf reductions and was likely due to decreased predation by wolves. If other factors have remained constant, then wolf predation was likely limiting this caribou population previously. Reduced severity of winters does not explain the dramatic increase in survival of caribou; however, favorable snow conditions and diet may have helped maximize survival.

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DEMOGRAPHY OF THE GEORGE RIVER CARIBOU HERD: EVIDENCE FOR REJECTING POPULATION REGULATION BY WOLF PREDATION

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Abstract: The George River Caribou (Rangifer tarandus) Herd in northern Quebec/Labrador increased from about 5,000 animals in 1954 to 472,200 (or 1.1 caribou/km^2) prior to the 1984 calving season. Range used by the herd expanded from 160,000 to 442,000 km^2 for the period 1971-84. The exponential rate of increase (r) was estimated at 0.11 in the 1970's, concomitant with a stable sex and age composition of the herd. Calf: female ratio in autumn was relatively constant ($\bar{x} = 0.52$) from 1973 to 1983, but decreased to about 0.39 in 1984-86. This decrease was induced by lower pregnancy rates and possibly by higher post-natal mortality rates. The harvest rate was relatively low in the 1970's (about 3%/yr), but likely increased in the 1980's because of more hunters and a greater impetus to exploit caribou for subsistence. The cumulative impact of the lower calf recruitment and the greater exploitation by humans in recent years may have appreciably decreased the growth rate of the herd. In addition, a greater year-round competition for food resources, and a greater energy expenditure associated with range expansion, are potential regulatory factors. We suggest that the nature of caribou-habitat interactions in continental regions may be conducive to long-term cycles in caribou numbers if the rate of human exploitation remains low. At present, wolf predation does not appear to be an important mortality factor capable of regulating the George River Herd. Possibly the virtual absence of an alternative ungulate species may preclude wolves from increasing in numbers. Controlled harvest may be used to reduce the growth rate of the herd in an effort to avoid severe habitat deterioration and a major decline in herd size.

Key Words: caribou, demography, population regulation, *Rangifer*, wolf predation

UTILIZATION OF CARCASSES OF NEWBORN CARIBOU KILLED BY WOLVES

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Abstract: Utilization of carcasses of newborn barren-ground caribou (*Rangifer tarandus groenlandicus*) calves killed by wolves (*Canis lupus*) was detailed for 2 years of a 3-year study of caribou calf mortality. The 131 carcasses of wolf-killed calves used in this evaluation were obtained by low-level helicopter searches on the calving grounds of the Beverly Caribou Herd in June 1982 and 1983, District of Keewatin, Northwest Territories, Canada. Utilization of those 131 carcasses by wolves was incomplete, suggesting that wolves were killing in excess of their short-term needs. Evidence was obtained for "surplus killing" (no utilization of carcass); "excessive killing" (only slight utilization of carcass); and "specialized feeding" (apparent preferences for milk curds and viscera over muscle tissue) by wolves. Herring and glaucous gulls (*Larus argentatus*, *L. hyperboreus*) heavily scavenged most of the carcasses, accounting for much, if not most, of the utilization, especially the consumption of tongues, eyes, and probably most of the deep muscle tissue. Grizzly bears (*Ursus arctos*), arctic foxes (*Alopex lagopus*), and rough-legged hawks (*Buteo lagopus*) were apparently lesser scavengers of dead caribou. No evidence was obtained for wolves scavenging dead calves (or adult caribou). Eagles (*Aquila chrysaetos*) and ravens (*Corvus corax*) were essentially absent, and we saw no evidence of wolverine (*Gulo gulo*) or lynx (*Lynx canadensis*).

Key Words: calves, Canada, *Canis lupus*, carcass, caribou, Northwest Territories, *Rangifer*, utilization, wolves

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One approach to estimating the extent of wolf predation on caribou (Rangifer tarandus) is to measure the food requirement of captive wolves and then extrapolate to the equivalent amount in caribou (e.g., Kuyt 1972). However, such an extrapolation would underestimate the effect of wolves on caribou. Management implications of such underestimates become particularly important if wolves kill more newborn caribou than needed for sustenance alone.

During June 1981, the first year of our 3-year study of caribou mortality on the calving grounds of the Beverly Herd, we rarely observed heavy utilization by wolves of newborn caribou that they had killed. Subsequently, we detailed the utilization of carcasses found in June 1982 and 1983. In a previous paper we discussed and classified the non-utilization and incomplete utilization of carcasses of newborn calves killed by wolves when more than 1 calf carcass was found at a given site (Miller et al. 1985). Feeding on wolf-killed calves by scavengers could increase the apparent utilization of the carcasses by wolves. In this paper we document the utilization by wolves and scavengers of all wolf-killed newborn caribou found in June 1982 and 1983.

This study was conducted under the Canada-Northwest Territories Wildlife Research Agreement. The Canadian Wildlife Service (CWS), Western and Northern Region, Environment Canada, and Polar Continental Shelf Project (PCSP), Energy, Mines and Resources Canada funded this research. We are especially grateful to G. D. Hobson, Director, PCSP, for his continued support of our research. We thank S. J. Barry, CWS, for statistical advice; and R. D. Cameron and J. L. Davis, Alaska Department of Fish and Game, G. L. Holroyd, CWS, and D. C. Heard, Wildlife Management Division, Department of Renewable Resources, Government of the Northwest Territories, for reviewing an earlier version of the material.

METHODS

Our study area was the northern portion of the tundra calving grounds of the Beverly Caribou Herd (Fleck and Gunn 1982). We flew nonsystematic searches for dead caribou in a Bell 206B turbo-helicopter at 10-30 m above ground level at 90-160 km/hr. We performed detailed field necropsies on all dead caribou found. We found carcasses of 131 newborn caribou calves (June 1982 and 1983) that had been killed by wolves and determined the degree of utilization of each by predators and scavengers. All but 2 of 69 wolf-killed calves found in June 1982 were estimated to be ≤7 days of age at death; of these, most (80%) were judged to be ≤3 days old. In June 1983 all of the 62 wolf-killed calves found were estimated to be ≤7 days of age; and again, most (73%) were judged to be ≤3 days old. Sex composition of the calves found in 1982 was 35% females, 46% males, and 19% indiscernible; and in 1983, 42% females, 45% males, and 13% indiscernible.

Intact calves or calves scavenged only slightly by gulls (i.e., those with eye(s) and/or anterior portions of the tongue removed) were used to calculate mean intact body weight on an annual basis. We weighed the carcasses with a straight spring scale to the nearest 0.25 kg. In 1982 we weighed 15 intact wolf-killed calves (≤7 days old): mean 6.42 ± 0.23 kg (SE), range 4.75-7.75 kg; and in 1983, 10 calves (≤7 days old): mean 5.35 ± 0.28 kg (SE), range 4.50-7.25 kg.

We used the type, size, and location of wound(s); occurrence of hemorrhage(s), or frank blood; and tissue trauma induced before death to differentiate predation (wound inflicted on living calf) from scavenging (post-mortem tissue damage). Type and size of entry into the body cavity also helped to distinguish between feeding by wolves and gulls.

Three approaches were used to estimate carcass utilization by wolves and gulls. First, we listed which of the following were missing from each carcass: deep muscle, viscera, tongue, and eye(s). The amounts of muscle and viscera missing were then visually rated as all, most, or some. The second approach was to calculate annual minimal-maximal estimates of mean annual percentage utilization of carcasses according to the following equation: Range in overall % utilization = $[(ax - c/ax) \cdot 100] - [(bx - c/bx) \cdot 100]$, where a = annual mean whole body weight; b = annual mean whole body weight + 2 SE; c = total weight of carcass remains on an annual basis; and x = number of calf carcasses found during that year. The third approach was to calculate percentage utilization (by weight) of individual carcasses relative to mean whole body weight for that year, and then classify each carcass descriptively as minimally used (1-9%), lightly used (10-34%), moderately used (35-49%), or heavily used (50-69% and 70-90%).

We recorded all sightings of wolves, grizzly bears, arctic foxes, herring gulls, glaucous gulls, rough-legged hawks, parasitic jaegers (Stercorarius parasiticus), long-tailed jaegers (S. longicaudus), pomarine jaegers (S. pomarinus), golden eagles, and ravens.

RESULTS

In 1982 we judged that 51 (74%) of the 69 carcasses of wolf-killed calves were both fed on by wolves and scavenged by gulls, 16 (23%) were only scavenged by gulls, 1 was only fed on by a wolf, and 1 was not used (Tables 1 and 2). Utilization of individual carcasses varied from <10% to about 90% (Tables 1 and 2). The range in total live weight of the 69 wolf-killed calves found in June 1982 should have been 443-475 kg, and the total weight of the remains of those 69 carcasses was 300 kg. Therefore, overall utilization by both wolves and gulls on an average weight basis was 32-37%.

In 1983 we judged that 35 (56%) of the 62 carcasses of wolf-killed calves were both fed on by wolves and scavenged by gulls, 24 (39%) were only scavenged by gulls, 1 was only fed on by a wolf, and the remaining 2 were not used (Tables 1 and 2). Utilization of individual carcasses varied from <10% to about 90% (Tables 1 and 2). The expected total body weight of the 62 wolf-killed calves was 336-356 kg, and the total weight of the 62 carcass remains was 245 kg, indicating 27-31% utilization by wolves and gulls.

Carcass Handling and Utilization by Both Wolves and Gulls

In 1982 we determined where wolves or gulls had entered the thoracic and/or abdominal cavities for 38 (75%) of the 51 wolf-killed calves that were both fed on by wolves and scavenged by gulls. Too little remained

Table 1. Percentage distributions of carcass utilization of 126[a] wolf-killed caribou calves ($\leq$1 week old) on an average weight basis, Beverly Herd calving grounds, Northwest Territories, June 1982 and 1983.

		% utilization class				
Year	*n*[b]	1-9	10-34	35-49	50-69	70-90
<u>Utilization by wolves and gulls</u>[c]						
1982	49	4	39	16	33	8
1983	35	--	43	26	20	11
<u>Utilization by gulls only</u>						
1982	16	88	12	--	--	--
1983	24	54	29	17	--	--
<u>Utilization by wolves only</u>						
1982	1	--	100	--	--	--
1983	1	--	100	--	--	--

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[a] Five of the 131 carcasses were not used in this consideration: see footnotes b and c.

[b] One and 2 of the wolf-killed calves in 1982 and 1983, respectively, were untouched by wolves or gulls and are not included in this table.

[c] Two of the 51 wolf-killed calves fed on by wolves and scavenged by gulls in 1982 were >7 days old at death and were not used in this table.

Table 2. Summary of carcass utilization of 128[a] wolf-killed caribou calves, Beverly Herd calving grounds, Northwest Territories, June 1982 and 1983.

		% with deep muscle missing	Utilization class			% with viscera missing	Utilization class			% with tongues missing	% with eye(s) missing
Year	*n*[a]		All	Most	Some		All	Most	Some		
Utilization by wolves and gulls											
1982	51	67	--	43	24	100	80	20	--	88	84
1983	35	89	26	43	20	100	89	11	--	86	83
Utilization by gulls only											
1982	16	--	--	--	--	13	--	--	13	75	81
1983	24	42	4	21	17	58	38	8	12	88	75
Utilization by wolves or gulls											
1982	68[b]	50	--	32	18	79	60	16	3	84	82
1983	60[b]	68	17	33	18	83	68	10	5	85	78

[a] One and 2 of the 69 and 62 wolf-killed caribou calves in 1982 and 1983, respectively, are not included in this table because they were neither fed on by wolves nor scavenged by gulls.

[b] In each year 1 calf carcass was apparently only fed on by a wolf and had most of the viscera removed only.

of the other 13 carcasses to determine the original points of entry. Thirty-three (87%) of the 38 carcasses were entered through the rib cage, 27 (71%) through the flank, and only 6 (16%) through the abdomen. Thirty-one (94%) of the 33 carcasses with rib cage entries had broken, severed, or separated ribs, suggesting that wolves were involved. In 6 cases where ribs were separated but not broken or missing, the wolf had apparently entered the posterior margin of the rib cage in the area of the floating ribs; 4 entries also involved the flanks, and 2 were restricted to the rib cage. Only 2 of the 33 carcasses had intact rib cages, suggesting that gulls had entered the thoracic cavity through a single intercostal hole and that wolves had entered through the flank.

The entries in 21 (68%) of the 31 carcasses with damaged rib cages were associated with large openings where a wolf had apparently entered the flank and/or abdomen. In those 21 carcasses, 15 (71%) of the body entries were through the rib cage and flank; 5 (24%) through the rib cage, abdomen, and flank; and 1 (5%) through the rib cage and abdomen. One additional rib cage entry by a wolf was associated with a gull entry in the anal area and some scavenging on the left shoulder. The remaining 9 wolf entries through the rib cage were restricted to the rib area.

Forty-five (88%) of the 51 calf carcasses utilized by both wolves and gulls had all or part of the tongues removed and 43 (96%) had the eye(s) removed. The tongue was totally removed from 42 carcasses and only partially gone from 3 carcasses. Both eyes were removed from 30 carcasses; only the left eye from 7 carcasses; and only the right eye from 6 carcasses. Apparently gulls always removed all or part of the tongue through the mouth and removed the eye(s) by pecking in the eye sockets.

The heads were partially removed from 10 (20%) of the 51 carcasses. The missing portion of the head was the cranium in 9 cases and the nasal and turbinate bones of the face in 1 case. Eight of those 10 heads had the tongues and eyes removed by gulls.

In 8 cases gulls had pecked holes in the anal area to enter the abdominal cavity. We have no evidence that wolves entered the abdominal cavity by biting into the anal area.

Overall utilization was highest on the 49 carcasses of calves ≤ 7 days old that were apparently both fed on by wolves and scavenged by gulls (39-43%). The viscera were completely removed, along with most ($\underline{n} = 22$), some ($\underline{n} = 8$), or no ($\underline{n} = 11$) deep muscle tissue, from 41 (80%) of the 51 carcasses. Most of the viscera were removed from the other 10 carcasses along with some ($\underline{n} = 4$) or no ($\underline{n} = 6$) deep muscle.

In 1983 we determined where wolves or gulls had entered the thoracic and/or abdominal cavities for 29 (83%) of the 35 wolf-killed calves that were both fed on by wolves and scavenged by gulls. Too little remained of the other 6 carcasses to determine the original points of entry. All 29 carcasses were entered through the rib cage, 23 (79%) were also entered through the flank, and 22 (76%) were also entered through the abdomen. Twenty-eight (97%) of those 29 carcasses had some broken, severed, or separated ribs, apparently caused by wolves in 26 cases. Separation of posterior ribs from the sternum in 2 of the remaining 3 carcasses may have occurred through dehydration. However, in those 2 carcasses a wolf had apparently also entered through the abdomen and flanks, possibly weakening the sternal articulations of the ribs. Only 1 carcass had an intact rib cage; a scavenging gull entered the thoracic cavity through an intercostal hole and a wolf entered through a hole in the abdomen and flank.

In all 28 carcasses with damaged rib cages, the entries were all associated with larger areas where a wolf had bitten into the flank and/or abdomen. In those 28 carcasses, 15 (54%) of the body entries were through the rib cage, abdomen, and flank; 7 (25%) through the rib cage and flank; and 6 (21%) through the rib cage and abdomen.

Thirty (86%) of the 35 calf carcasses utilized by both wolves and gulls had all or part of the tongues removed and 29 (83%) had the eye(s) removed. The tongue was totally removed from 15 carcasses and only partially gone from the other 15 carcasses. Both eyes were removed from 12 carcasses; only the right eye from 13 carcasses; and only the left eye from 4 carcasses. Gulls apparently removed all or part of the tongue through the mouth on 18 carcasses and removed the eye(s) by pecking in the eye sockets on 21 carcasses. In 2 of the 3 other cases, wolves had bitten into the base of the tongue and ripped it out ventrally between the mandibles; in the third case the wolf had bitten off the mandibles and tongue from the head.

Nine carcasses (26%) were missing all or major portions of the head, and we assume that wolves consumed the tongues on all 9 and the eye(s) on 8 carcasses. One partial skull from these 9 carcasses still included the eye sockets; the eyes had apparently been removed by gulls (this case is included in the 21 given above).

In 6 cases gulls had pecked holes in the anal area to enter the abdominal cavity. We have no evidence that wolves entered the abdominal cavity by tearing out muscle tissue in the anal area.

Overall utilization was highest on the 35 carcasses of calves that were apparently both fed on by wolves and scavenged by gulls (39-43%). The viscera were completely removed with all (*n* = 9), most (*n* = 14), some (*n* = 5), or no (*n* = 3) deep muscle from 31 (89%) of the 35 carcasses. Most of the viscera were removed from the other 4 carcasses along with most (*n* = 1), some (*n* = 2), or no (*n* = 1) deep muscle. Utilization of individual carcasses ranged from 10-34% to 70-90%; utilization of 11 carcasses (31%) exceeded 50%.

Carcass Handling and Utilization by Gulls Only

In 1982, 6 (37%) of the 16 carcasses only scavenged by gulls had single-hole body entries. Three of the holes were in the rib cage, 2 were through the flank, and 1 was in the anal area. No subsequent feeding was evident in 2 of the entries through the rib cage or in both flank entries. In 1 calf, part of the stomach and some of the intestinal tract had been removed through the rib cage. In a second calf, part of the intestinal tract had been removed through the anal area. The body cavities of the remaining 10 carcasses had not been entered but the tongue or eye(s) had been removed: 7, tongue and eye(s); 2, tongue only; and 1, eye(s) only.

The tongue had been totally removed from 8 and partially removed from 4 of the 16 carcasses. The eye(s) were taken from 13 of the 16 carcasses: both eyes in 3 cases, the right eye in 7 cases, and the left eye in 3 cases.

Clearly, overall utilization by gulls of these 16 carcasses was light. The range in total live weight of the 16 calves should have been 97.4-103.5 kg, and the total weight of the remains of those 16 carcasses was 99.5 kg, indicating that overall utilization on an average weight basis ranged between -2 and 4%. Carcass utilization by gulls only was markedly lower (1-9% to 10-34%) than that involving both wolves and gulls (Table 1).

There were 2 marked differences in the pattern of points of entry into the body cavity between carcasses only scavenged by gulls and those fed on by wolves and scavenged by gulls:

1. There were no abdominal entries when carcasses were only scavenged by gulls.

2. Gulls entered carcasses through separate holes in the rib cage and flank rather than through 1 continuous hole.

In 1983 we determined the points of body entry for all 24 calf carcasses that were only scavenged by gulls. Nineteen (79%) of the carcasses were entered through the thoracic and/or abdominal cavities: 12 times through the flank, 10 through the rib cage, and 6 in the anal area. In 9 of the 19 carcasses, entry was through 2 separate holes: 6 times in the rib cage and the adjacent flank, twice in the flank and the anal area, and once in the rib cage and the anal area. The body cavities of the remaining 5 carcasses had not been entered but the tongue or eye(s) had been removed: 8, tongue and eye(s); 1, tongue only; and 1, eye(s) only.

The tongue had been totally removed from 4 and partially removed from 17 of the 24 carcasses. The eye(s) were taken from 18 of the 24 carcasses: both eyes in 3 cases, the right eye in 9 cases, and the left eye in 6 cases.

Overall utilization of the 24 carcasses was 12-17%. All of the viscera were taken along with all (*n* = 1), most (*n* = 5), some (*n* = 1), or no (*n* = 2) deep muscle from 9 (38%) of the 24 carcasses. Most of the viscera were missing from 2 other carcasses along with some (*n* = 1) or no (*n* = 1) deep muscle, and in another 3 carcasses some viscera were gone but no deep muscle had been removed. Of the remaining 10 carcasses with no viscera taken, 8 had no deep muscle removed and 2 had some deep muscle missing. Individual carcass utilization (1-9% to 35-49%) was markedly lower for these 24 carcasses than for the 35 carcasses fed on by both wolves and gulls (Table 1).

The differences observed in 1982 between the pattern of points of entry into the body cavities of calf carcasses scavenged only by gulls and that of carcasses both fed on by wolves and scavenged by gulls persisted in 1983: no abdominal entries by gulls only; and no single entries by gulls involving more than 1 body area.

Carcass Handling and Utilization by a Wolf Only

In 1982 and 1983, respectively, overall carcass utilization averaged 10-15% and 22-26% for carcasses fed on only by a wolf. In contrast, individual carcass utilization for both years fell within the 10-34% class.

DISCUSSION

Wolves fed on only 75% and 58% of the wolf-killed calves that we found in June 1982 and 1983, respectively. However, gulls scavenged 97% and 95% of those carcasses, respectively. When wolves fed on a carcass, they consumed more than 50% of each carcass 30% of the time in 1982 and 18% of the time in 1983. Overall utilization of those carcasses by wolves and/or gulls was 42% lower in 1983 than in 1982. Evidence obtained during this study (including initial observations in 1981) for "surplus killing" (no utilization of the carcass) and "excessive killing" (slight utilization of the carcass) of newborn caribou by wolves, and for "specialized feeding" (apparent preferences for milk curds and viscera) by wolves has been reported in detail by Miller et al. (1985) and Miller and Gunn (1986).

No clear relationship was evident between the major parts removed (i.e., deep muscle or viscera) and the percentage utilization class for individual carcasses. In 1982 and 1983, 13% and 6%, respectively, of the carcasses with no deep muscle tissue missing were still classified at >50% utilized; whereas, in 1982 and 1983, 38% and 65%, respectively, of the carcasses with deep muscle taken were <50% utilized.

Wolves usually tore into the stomach behind the rib cage or through the lower part of the rib cage, often biting off some or all of the floating ribs. Gulls usually extracted viscera and stomach contents from unopened carcasses by making an intercostal hole in the central portion of the rib cage. If the carcass is already open, gulls will feed without making new entries. Sometimes gulls extract all the viscera and stomach contents through a small intercostal hole and never consume any deep muscle tissue. Gulls also select eyes and tongues, especially the tips.

Patterns of carcass utilization by wolves and gulls are seemingly stereotyped. Gulls removed eyes and portions of tongues first, then either abandoned the carcass (in areas of abundant carrion; Miller et al. 1985) or began extracting viscera and stomach contents. In contrast, wolves usually took the milk curds from the stomach first; then the viscera; and lastly, if at all, the deep muscle tissue.

Similarly, removal of the tongue by a wolf vs. a gull is usually easy to recognize. A wolf most often takes the tongue by biting in from the throat, frequently removing the mandible(s) and the entire tongue. Gulls remove the tongue through the mouth, often leaving the posterior portion in the carcass.

We are uncertain why wolves frequently made such little use of many calves they killed. The frequency of incomplete use is, in fact, unknown because our methods did not allow us to determine the numbers of calves that were totally consumed or the observability bias against heavily used carcasses. However, our data suggest that wolves killing newborn caribou calves may have become specialized feeders, taking only high-quality milk curds and selected viscera. Therefore, we suggest that much of the utilization of the wolf-killed calves was possibly by scavenging gulls, especially the consumption of eyes, tongues, and much of the deep muscle tissue. Access to easily killed newborn calves, the constant movement of postcalving groups of caribou, and no known attachment of the wolves to dens all argue against wolves returning to kills or scavenging carcasses on the calving grounds.

We have no evidence of active wolf dens on the calving grounds; thus, it is likely that the wolves preying on newborn calves are not associated with a den pack and do not occupy a specific territory. The principal wolf denning areas are to the south of the calving grounds.

A few grizzly bears were present on the calving grounds in 1983 during calving and early postcalving and could have accounted for some predation and scavenging of newborn (and adult) caribou. However, utilization of newborn caribou calves by grizzly bears, whether a result of predation or scavenging, is apparently nearly complete and, therefore, virtually undetectable (except through scat analysis). Usually only the odd limb is found, and it is assumed that the rest of the carcass was consumed by a bear.

During the 2 years of this study, scavenging of carcasses was mainly by gulls. Herring gulls, and to a lesser extent glaucous gulls, were persistent and voracious scavengers. They patrolled calving and postcalving groups of caribou, apparently searching for remnants of afterbirth and carcasses. Gulls worried maternal cows in attempts to feed on bloody afterbirth near freshly dropped calves. On occasion, gulls also tried to approach newborn caribou, not yet able to stand, but the maternal cows displaced the gulls by charging them. No gulls were seen to attack healthy calves, although the presence of some hemorrhaged wounds suggests that occasionally gulls feed on moribund calves. Gulls also followed cows with remnants of placental tissue protruding from their vaginas. Such cows often trotted short distances to evade gulls that hovered nearby in the strong ground winds. Sometimes, if the gull was flying within only a meter or so of the ground, the cow would turn, rush, and occasionally rear up at the gull, which would avoid the oncoming cow by drifting downwind.

Most of the carcasses only scavenged by gulls were lightly utilized compared with those fed on by wolves and scavenged by gulls. This difference is inexplicable, but it did allow us to observe and compare the handling and utilization patterns of gulls and wolves. An increased utilization of a carcass, even by gulls only, would have resulted in loss of most of the characteristic features that allowed us to make the distinction between scavenging by gulls and feeding by wolves.

Rough-legged hawks were likely minor scavengers in June 1982 and 1983. Jaegers were infrequently seen in both years, and only a few golden eagles and ravens were sighted on the calving grounds in 1982, and none were observed in 1983. Arctic foxes were rare and, at most, minor scavengers (no active fox dens were seen). The extent of scavenging by grizzly bears is unknown. We observed no evidence for the presence of wolverines or lynx. The role of caribou calf carcasses as a plentiful, but localized and only briefly available, food supply in the ecology of gulls, the principal scavengers, is conjectural. However, incomplete utilization of carcasses by gulls suggests that the food available exceeded the requirements of the gulls in the study area.

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CALF MORTALITY IN THE PORCUPINE CARIBOU HERD

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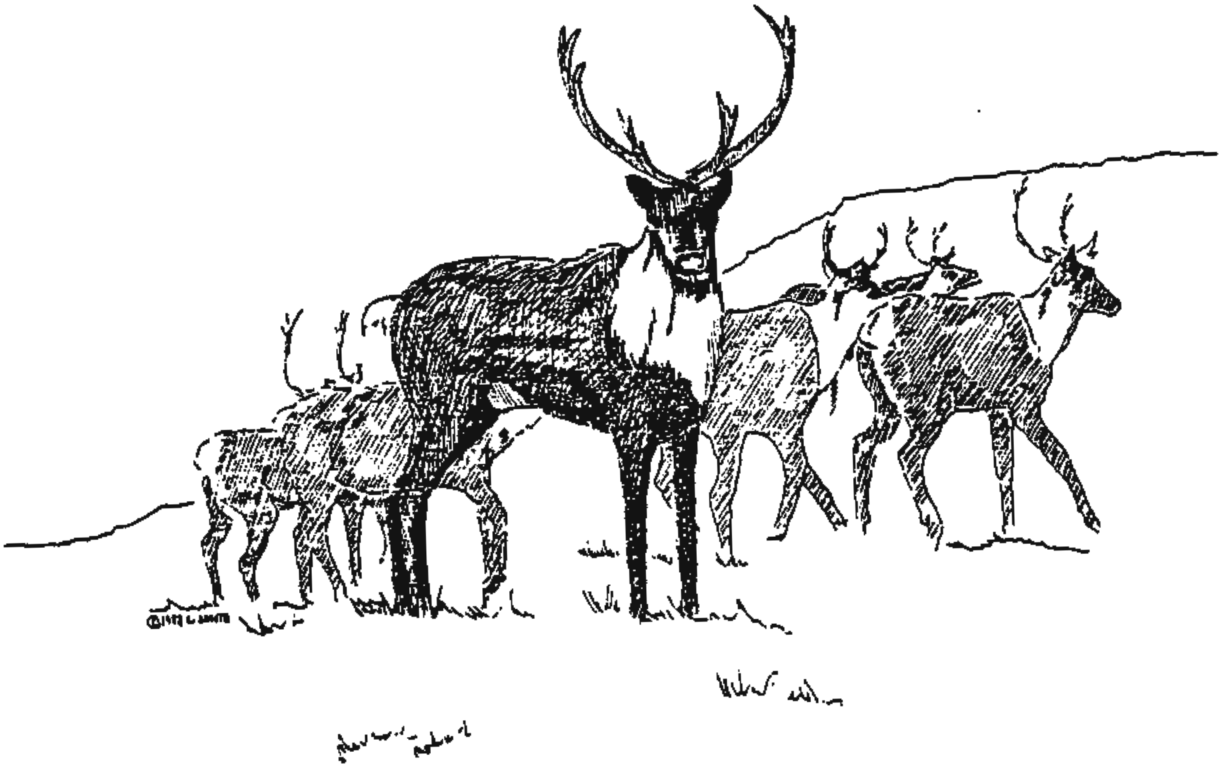
Abstract: From 1983 through 1985, the mortality of calves in the Porcupine Caribou (*Rangifer tarandus granti*) Herd was studied cooperatively by the Alaska Department of Fish and Game and the U.S. Fish and Wildlife Service. Mortality-sensing radiocollars were placed on 179 neonatal calves during early June. Eighty-seven radio-collared parturient females and their uncollared offspring provided additional data and functioned as a control. Mortality rates during June were higher for uncollared calves (30%) than for collared calves (10%). Many uncollared calves died within 48 hours of birth, whereas collared calves were likely older than this when captured. Eliminating mortalities occurring within 48 hours of birth from the uncollared calf sample yielded mortality rates (12%) that were similar to those of the collared calves. Most mortality among collared calves involved predators: wolves (*Canis lupus*), brown bears (*Ursus arctos*), and golden eagles (*Aquila chrysaetos*). Predation was heaviest in the foothills to the south and east of the highest density calving area.

Key Words: calf mortality, caribou, Porcupine Herd, radio-collared, *Rangifer*

PART III



ASSESSMENT TECHNIQUES AND MANAGEMENT APPLICATIONS

MULTIPLE REGRESSION METHODS FOR MODELING CARIBOU POPULATIONS

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Abstract: Multiple linear regression (MLR) offers a useful method to model the dynamics of caribou (Rangifer tarandus) populations where changes in population parameters are brought about by several factors. Assumptions of using this statistical procedure are delineated and techniques necessary to meet these assumptions are discussed. Use of compounded independent variables is discouraged because they may violate assumptions of independence and artificially inflate values for coefficients of determination. Recommendations for determining an adequate sample size are provided. Multiple regression may not be useful when severe multicollinearity occurs among independent variables. All possible regressions, true stepping, or backward stepwise procedures are advocated for model building, depending upon the power of the available computing system. Examination of residuals is necessary to test the aptness of MLR models, and particular patterns may indicate the absence of important independent variables or that some variables do not meet the prescribed assumptions of this technique. Methods to correct such problems are suggested. Final presentation of the model should include the unstandardized equation with an adjusted multiple coefficient of determination (R^2_a) and a prediction error. Standardized regression coefficients should be presented as well as partial coefficients of determination. Interpretation of these parameters are dealt with relative to their biological significance. Finally, problems in testing the validity of the model are discussed.

Key Words: caribou, model, multicollinearity, multiple regressions, *Rangifer*, statistics

Recent advances in computer technology and statistical software have made complex biometric models readily available to wildlife biologists. Such models have been used to examine animal-habitat relationships, population dynamics, and distributional patterns (Capen 1981, Verner et al. 1986, Wehausen et al. 1987). Unfortunately, increasing ease of operating modern computing systems has not been matched by an equivalent understanding of assumptions inherent in application of these procedures. The purpose of this paper is to: (1) describe one kind of biometric model--multiple linear regression (MLR); (2) show how MLR can aid in understanding the dynamics of caribou (*Rangifer tarandus*) populations; and (3) summarize selected procedures, outcomes, and assumptions of MLR.

We thank X. P. Quang for his advice on statistical procedures. M. P. Gillingham and S. Fleischman provided many useful comments.

Why Multiple Linear Regression?

Many types of models other than MLR might be employed to investigate ungulate population dynamics (Starfield and Bleloch 1986). Further, complex statistical procedures should not be used when simple ones will suffice. For instance, McCullough (1979) explained most (85%) of the variation in reproductive rate of white-tailed deer (*Odocoileus virginianus*) with a single independent variable, population density. In that case, simple linear regression (SLR) was sufficient to explain the dynamics of the population.

Often, however, complex systems cannot be reduced to a single, important variable. MLR offers a reasonable approach for studying the response of populations to interactions of several environmental factors. Another advantage of MLR is the incorporation of laws of probability in model building rather than just relying on a subjective opinion about how well the model functions.

Regression analysis is a procedure by which an understanding of the statistical relationship between 2 or more variables can be gained. Once this relationship is understood, information on some of the variables can be used to predict or model the magnitude of another. Thus, MLR predicts change in the dependent variable (Y) as linear functions of independent variables (X's).

MLR Parameters

This paper outlines the regression process from experimental design to final model (Fig. 1). In this section we present the components of regression models and provide interpretations necessary to understand what follows.

For purposes of this discussion, 35 years of data for a hypothetical caribou population will be considered (Table 1). During those 35 years, the following 6 variables were recorded: calf:cow ratio; number of caribou; female harvest; number of wolves in the area; percentage cows in the population; and depth of snow on the ground in March. Long-lived animals like caribou might be influenced by weather patterns occurring over several years. Therefore, an additional compounded variable, 3-year running average of March snow depth, also was included. We would like to know what factors control recruitment of young into the population, thus the variable of greatest interest is the calf:cow ratio. Specifically, biologists want to know whether any of the other variables help explain variation observed in calf:cow ratio. The calf:cow ratio, then, is the "Y" or dependent variable, and the other 6 variables are "X's" or independent variables. Using the method of least squares (described in most statistics texts) and modeling procedures we discuss later, the following equation was constructed:

$$\text{Calves:Cow} = 0.772 - 0.00005\ (\text{no. of Caribou}) - 0.001\ (\text{Female Harvest}).$$

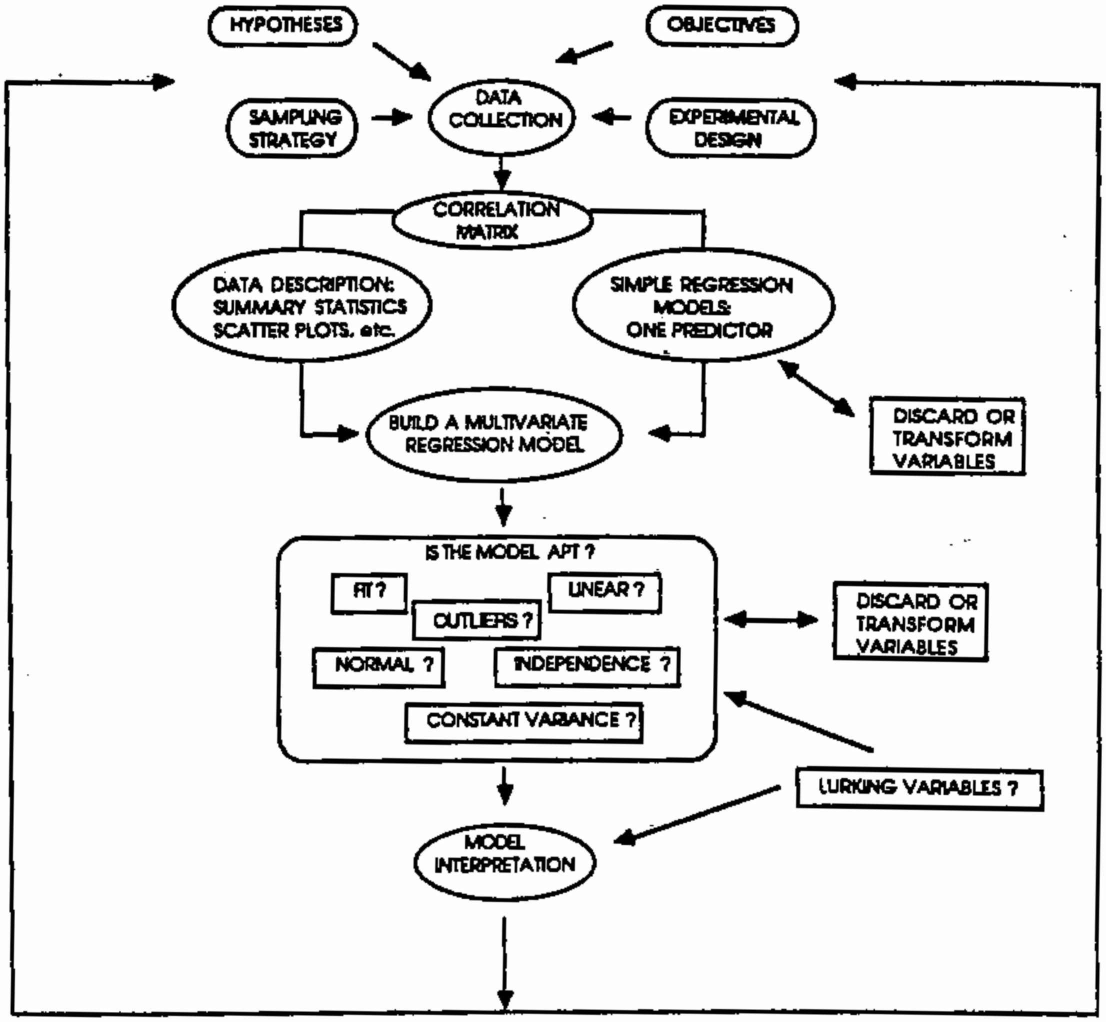


Fig. 1. A graphical summary of MLR model-building procedures described in this paper.

Table 1. Sample of raw data and resulting descriptive statistics for the hypothetical caribou population.

Year	No. of caribou	No. of females harvested	No. of wolves	No. of calves/ cow	% cows	March snow depth (in)	3-year average snow depth (in)
Raw Data							
1	5000	154	270	0.2829	52.0	5.00	
2	5000	168	270	0.3368	42.0	1.00	
3	4000	126	270	0.4477	34.0	18.0	8.00
4	3100	132	265	0.5069	27.0	13.0	10.667
5	2288	67	260	0.6034	30.0	7.00	12.667
-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-
35	5000	44	270	0.4429	36.0000	5.00	8.00
Descriptive Statistics							
N	35	35	35	35	35	35	33
Min.	2000	10	80	0.222	17	1	4
Max.	8083	168	270	0.669	66	22	13
Mean	4180.11	76.0	185.77	0.48	37.57	9.1	9.4
S. D.	1931.10	52.68	69.62	0.149	14.38	5.7	2.97
Coeff. var.(%)	46.2	69.3	37.5	31.0	38.3	62.6	31.6

This corresponds to the multiple regression equation: $Y = b_o + b_1X_1 + b_2X_2$. The b's in this equation are the parameters of the regression model, and commonly are called regression coefficients. The b_o term corresponds to the y-intercept, and b_1 indicates the degree of change that would be observed in Y if X_2 were held constant and X_1 varied. Likewise, b_2 indicates the change in Y expected if X_1 is held constant and X_2 varied. Such a model will estimate calf production rate for any year in which estimates of harvest and population size are available.

Associated with a regression model is the analysis of variance (ANOVA) table (Table 2). This table shows the partitioning of the deviations of the observed Y's around their mean value (SSTO for total sum of squares) into 2 components: (1) deviation of the fitted regression line about the mean value of Y (SSR for sum of squares explained by regression); and (2) deviation of the observed values of Y around the regression line (SSE for error sum of squares). The value of the regression model often is assessed by MSR/MSE, which is the ratio of the regression and error sums of squares divided by their respective degrees of freedom. If this ratio exceeds a tabled "F"-value at the specified level of probability (e.g., $\alpha = 0.05$), the regression is significant. Put another way, number of caribou and harvest of females explain a significant portion of the variability in the calf:cow ratio.

Another measure of the utility of a regression model is the coefficient of determination (r^2), which is the proportionate reduction in the total variation of Y that results from the information contained in the X variable (SSR/SSTO). The ratio SSR/SSTO ranges from $0 \leq r^2 \leq 1$. The closer r^2 is to 1, the greater the explanatory value of the regression model (e.g., more variation in Y is explained). R^2 (the coefficient of multiple determination) represents the proportionate reduction in the variability of Y when 2 or more X-values are considered. This value is equivalent in concept to r^2, and the 2 values are identical in simple linear regression (i.e., when there is a single independent variable).

Table 2. Analysis of variance table for multiple linear regression model predicting changes in Y (calves/cow) with values of X_1 (number of caribou) and X_2 (female harvest).[a]

Source of variation	Degrees of freedom (df)	Sum of squares (SS)	Mean square (SS/df)	$\underline{F}$-test	Probability of "F" as large or larger
Explained by	2	$\Sigma(\hat{Y}_i-Y)^2$	0.333	$\frac{MSR}{MSE}=121.6$	0.0001
Regression		0.665=SSR			
Error	32	$(Y_i-\hat{Y}_i)^2$	0.003		
Component		0.088=SSE			
TOTAL	34	$(Y_i-\hat{Y}_i)^2$ .753 - SSTO			
X_1	1	0.642	0.642	N/A	
X_2X_1	1	0.024	0.024	$\frac{MSR\ X_2X_1}{MSE}$ =8.672	0.01

[a] One degree of freedom is lost for each parameter entering the model (e.g. β_0, β_1, β_2). The contribution of X_2 given X_1 (X_2X_1) already in the model is assessed by the partial $\underline{F}$-ratio = (MSR X_2X_1)/MSE. A similar partial $\underline{F}$-test of (MSR X_1X_2)/MSE could be constructed in a second regression run in which X_2 is entered first. These partial $\underline{F}$-tests are equivalent to $\underline{F}$-to-enter tests performed by stepwise regression procedures. Thus, $\underline{F}$-to-enter of X_2 would be 8.672.

A significant F-test, or a high R^2, are often the only values considered by biologists using MLR, in part because most computer programs provide these statistics as basic output. Unfortunately, analyses often stop at that point without developing a further understanding of the assumptions and limitations of the model (Box 1966). The worth of a model cannot be assessed on the basis of these measures alone, and the utility of a model goes beyond those basic outcomes. In following sections, we discuss some of the broader ramifications of regression models.

Experimental Design

Selection of variables to be sampled and the manner in which data are collected will have a profound effect on the outcome and reliability of regression models. Thus, an adequate knowledge of the biology of the animal to be studied is the first (and most important) step in constructing a model. Although some required information may be available in the literature, it may be necessary to conduct a preliminary study to clarify some aspects of the animal's biology.

All too often data are collected without a particular method of analysis in mind. Such data may be difficult to analyze with MLR or, in some cases, with any statistical method. Remedial actions may be possible (Milliken and Johnson 1984), but it is better to collect data specifically for analysis by a particular method. Draper and Smith (1981:295) provide additional remarks about the use of such "unplanned" data. There is, however, no substitute for advanced planning.

Of course, the model selected will depend upon the hypotheses to be tested. A concise statement of the question(s) to be asked is usually necessary and always desirable for coherent and meaningful results (Green 1979).

Basic Assumptions of the Model

Five basic assumptions are necessary for the valid use of SLR or MLR: (1) for each value of X (independent variable) the associated values of Y (dependent variable) are distributed normally; (2) variances of Y-values are equal (homoscedastic) at all levels of X; (3) errors associated with Y-values sum to zero; (4) values of Y are independent of each other for all

X's; and (5) measurements of X-values are without error (Zar 1984:268). Fortunately, regression statistics are robust so long as violations of these basic assumptions are not too severe (Zar 1984:268, Neter et al. 1985:83).

Sample Size

Reliability of a model is reduced if sample sizes are too small for the number of variables included in the model (Noon 1986). As the number of independent variables (m) approaches the sample size (n), matrices used to calculate MLR statistics become singular (i.e., have a very large number of potential solutions). For this reason, it is recommended that sample sizes (n) be kept above a minimum of m + 10 (where none of the assumptions of MLR have been violated). For example, to predict a parameter for a caribou population such as "recruitment rate" with 4 independent variables (m), a minimum of 14 years (n) of observations is desirable. The confidence in predictions from MLR models increases with sample size. A sample size of at least n-m >50 is required for the valid use of MLR where the assumptions of this technique are violated substantially (Harris 1975:50). Few studies of caribou populations have lasted that many years! Nonetheless, we recommend about 10 samples (n) for each variable (m) in the final model (i.e., m X 10).

Preliminary Data Handling

Once data have been collected, the next step in building a regression model is a careful examination of the variables. Descriptive statistics ($\bar{x}$, SD, range) for each variable should be scrutinized and presented with the final model (Table 1). A complex biometric model without at least a summary description of data used to construct it may be difficult to interpret and certainly will be of limited value.

After examining summary statistics, SLR's should be performed to examine bivariate relationships between all combinations of variables. Such preliminary analyses can screen problems in data that might be difficult to tease from multivariate models. MLR assumes relationships between X's and Y are linear (although the resulting response surface for fitted values of Y in the final model need not be so). Variable pairs not exhibiting linearity require transformation. Nonlinear multiple regression techniques exist (Zar 1984:351) but are beyond the scope of this paper.

Independent variables (X's) also should be normally distributed and have equal variances to meet assumptions of MLR (Zar 1984:328). Unequal variances or "heteroscedasticity" may be detected by plots (Figs. 2 and 3) of residuals (differences between observed and fitted values). Heteroscedasticity also can be evaluated by comparisons of error mean squares in different ranges of the data set (Neter et al. 1985:123). Weighting of variables and or transformations may correct this problem. Histograms or plots of residuals against their expected values or normal scores may be used to detect deviation from linearity and normality (Fig. 4). A high coefficient of correlation (r) between residuals and normal scores suggests normality (Neter et al. 1985:120). Several other formal procedures are available for assessing normality of variables (Conover 1980:359, Neter et al. 1985). The graphic method of Shapiro and Wilk (1965) is effective and easily understood; also see Sokal and Rohlf (1969:119-126). A condition of multivariate normality (a requirement for multiple correlation) may be inferred from a series of bivariate comparisons. Multivariate normality is difficult to determine, but if pairs of variables are not normally distributed, multivariate normality is unlikely to occur (Dunn 1981, Johnson 1981). This is especially important if it is uncertain which variable is dependent upon the other (e.g., do wolves control caribou or vice versa?). In this case, the procedure becomes multiple correlation by definition (i.e., the dependent variable is uncertain), and multivariate normality is required.

Several transformations are available to normalize data (Zar 1984:236-242; Neter et al. 1985:134-141). It is important to test for normality again after the transformation has been completed. Some transformations used to alleviate problems with heteroscedasticity and additivity also may normalize distributions (Zar 1984:236-242, Neter et al. 1985:120).

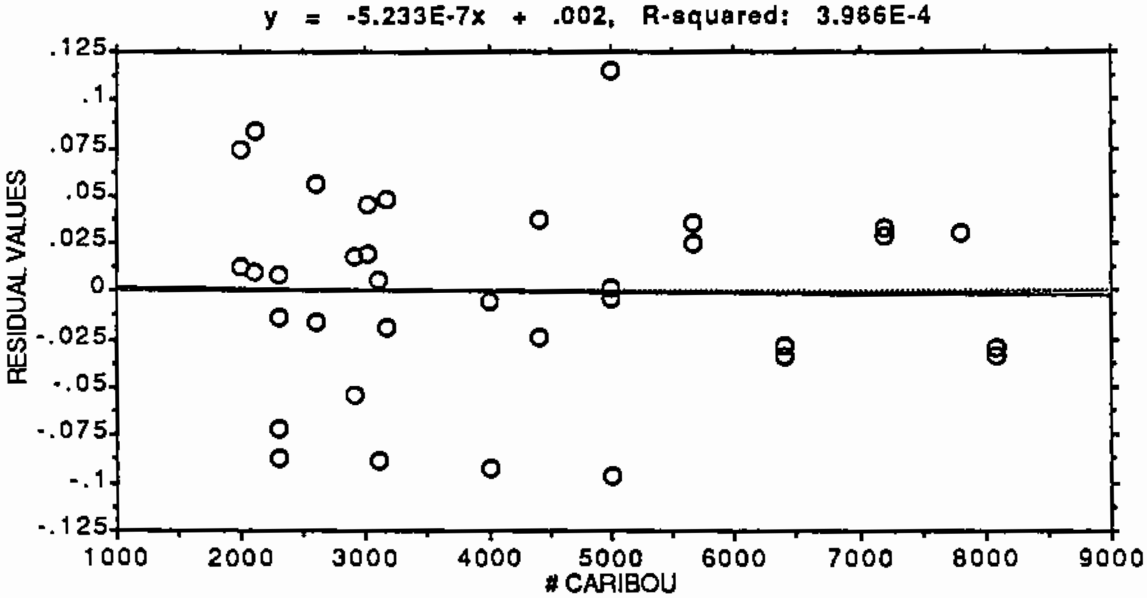


Fig. 2. Plot of residuals against X_1 showing that variances (error terms) tend to be greater when caribou numbers are smaller. Unequal variances (heteroscedasticity) must be corrected before proceeding with model building.

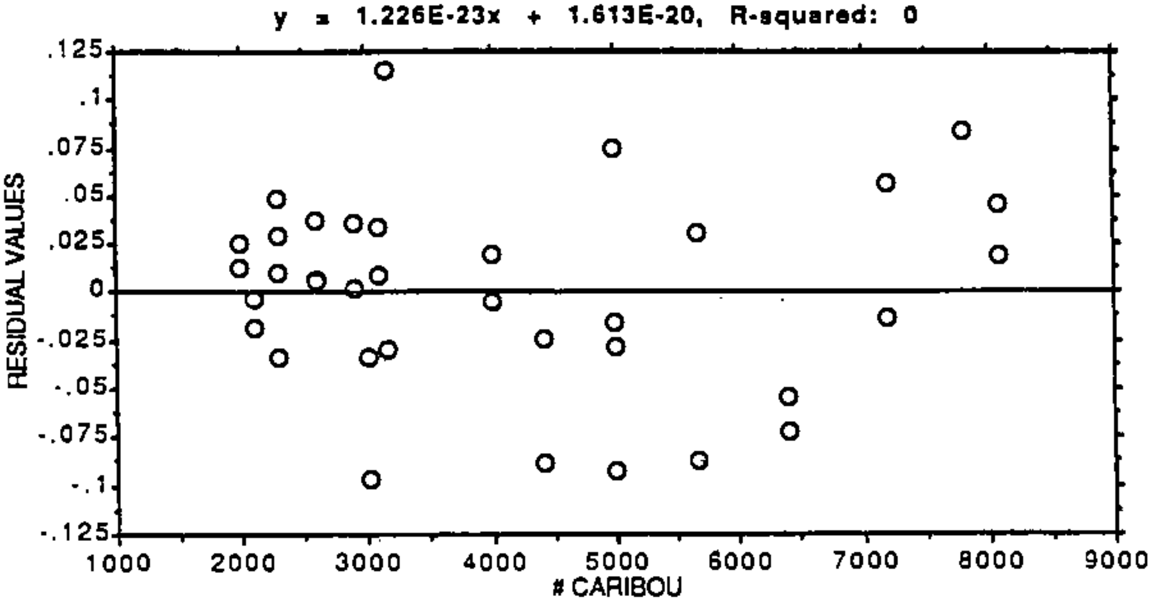


Fig. 3. Plot of residuals (Yi - $\bar{Y}$) against X_1 showing no trend in variances or error terms with population size.

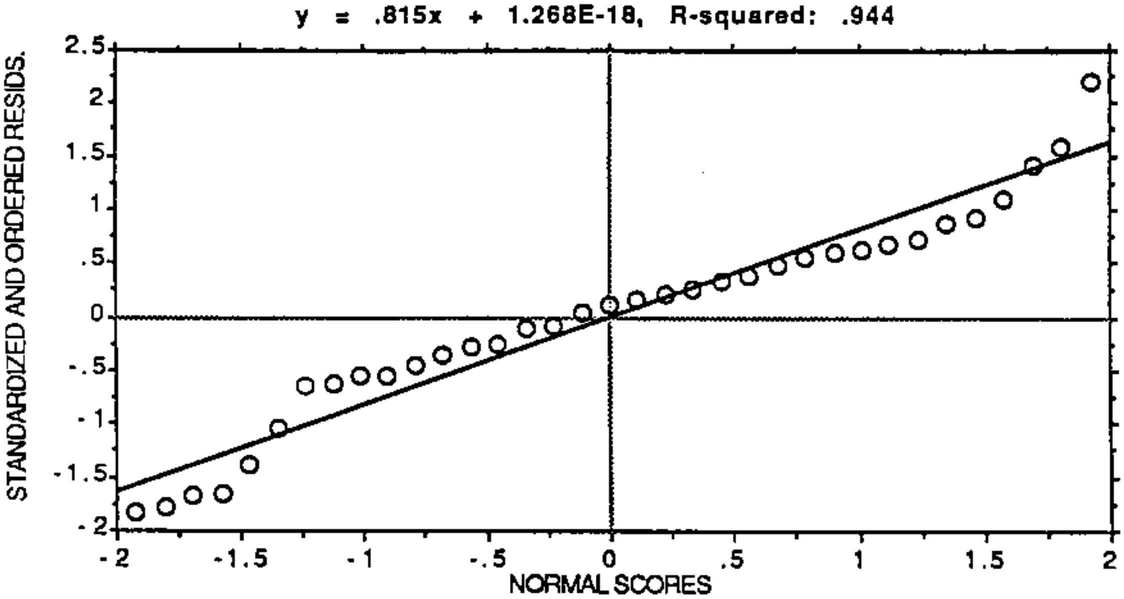


Fig. 4. Plot of standardized, ordered, residuals against normal scores. Points lying along a straight line suggest normality (this relationship may indicate a slight departure from normality typical of a logistic fit).

Preliminary examination and modification of data can be time consuming and frustrating, but is essential if a valid model is to be constructed.

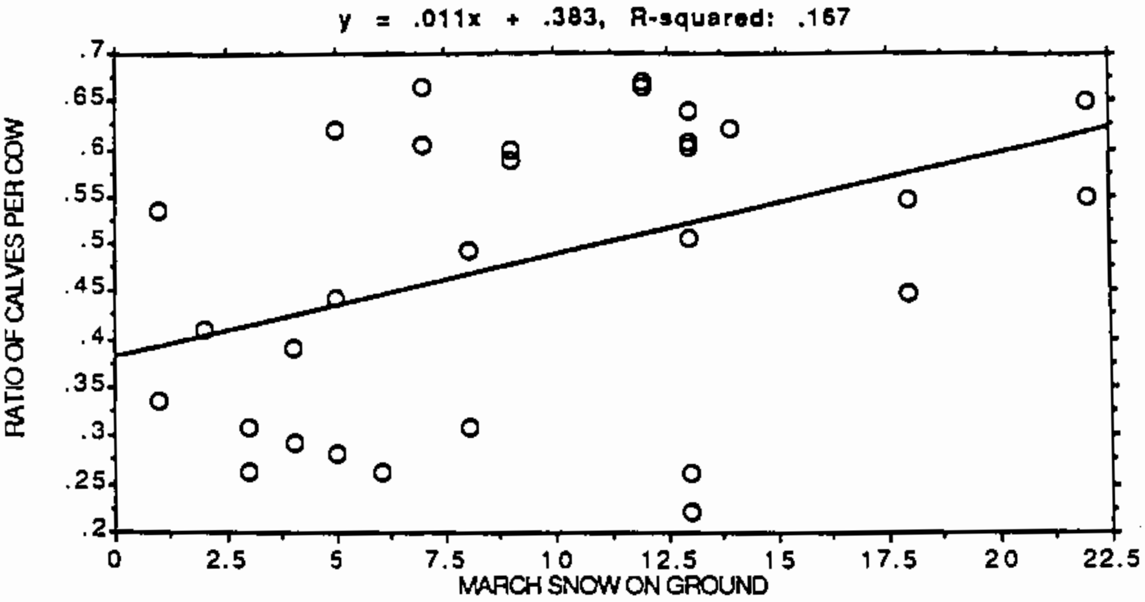
Compounded Independent Variables

Use of derived (or compounded) independent variables, such as running averages, should be avoided whenever possible (Green 1979:95). MLR requires that X-variables be known or measured without error. MLR also is applicable where X's are independent random variables (Neter et al. 1985:83). Because any level of X' (where X' denotes a compounded variable) is not independent of other values of X', this basic and important assumption of MLR is violated. Variables that are summed, averaged, or otherwise compounded across cases also may appear to provide more significant regression coefficients (e.g., coefficients differing significantly from zero) than the simple variables from which they were derived (Fig. 5) and should be avoided.

The importance of several years of snow might be assessed by assigning snowfall in the previous year (i.e., n-1) as a separate independent variable (e.g., X_1 = March snow in the same year as reproduction; X_2 = March snow in the previous year to reproduction; etc.). If some interaction in snowfall among years seems necessary to explain the biology, then, for example, $X_3 = X_1 X_2$ also might be examined as a separate variable (Neter et al. 1985:232-234).

Dealing with Multicollinearity

An important assumption of MLR is that independent variables are not substantially correlated. If multicollinearity among X variables exists, parameter estimates will have large variances (Neter et al. 1985:271-282, 382-390; Zar 1984:344). This problem is so severe that several authors (Green 1979:117, Pimentel 1979:45) have recommended against using a MLR approach. The removal of intercorrelated variables can be accomplished informally by examining a correlation matrix (Table 3) and eliminating 1 variable from each pair with $|r| \geq 0.70$. Selection of a variable from an intercorrelated pair to remove from consideration in model building can be based on the difficulty or cost of obtaining a particular measurement.



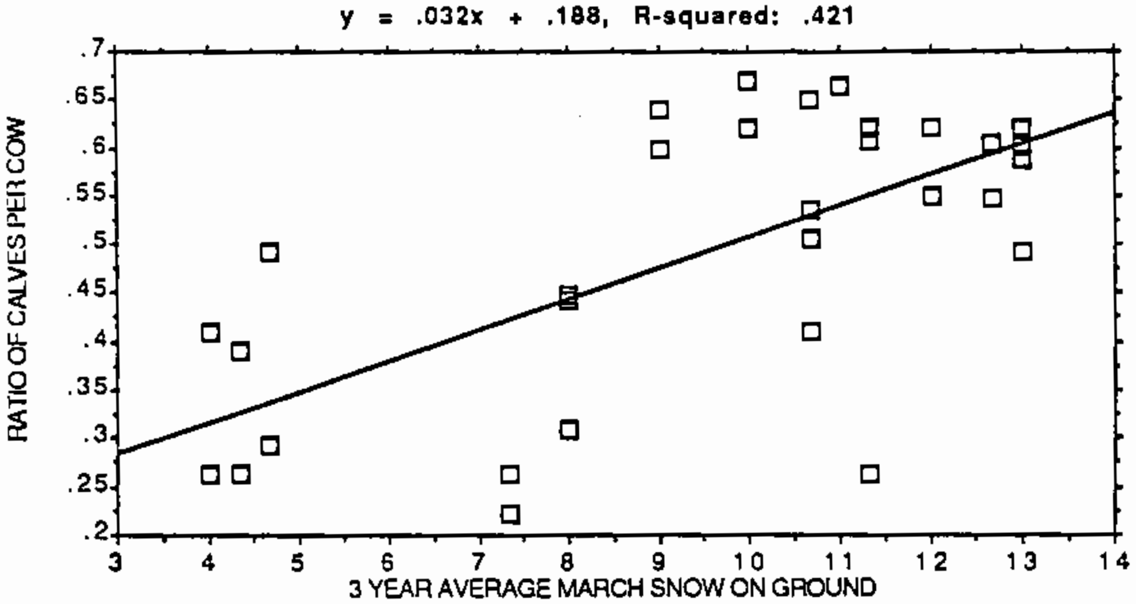


Fig. 5. Graphic representation of the effect of compounding variables. Compounded variables (below) often will have regression coefficients greater than simple variables (above) from which they were derived.

Table 3. Correlation matrix showing correlation coefficients (r) between all variable pairs considered in the caribou population.

Year	No. of caribou	No. of females harvested	No. of wolves	No. of calves/ cows	% cows	March snow depth (in)	3-year average snow depth (in)
	1	.769	.032	-.938	.776	-.319	-.557
		1	.024	-.788	.607	-.195	-.615
			1	.046	-.213	.116	.157
				1	-.758	.366	.649
					1	-.156	-.394
						1	.450
							1

Note: 2 cases deleted with missing values.

Construction of a correlation matrix is an essential step in building a valid regression model and should be presented with the final model.

After intercorrelated variables have been removed, and a model constructed with the remaining independent variables, further elimination of independent variables may be necessary. Another justification for removing one of a pair of similar variables is a change in sign of the regression coefficient associated with 1 independent variable when another independent variable enters the model. Reasons for this change in algebraic sign are discussed elsewhere (Mullet 1976). Large fluctuations in estimated variances of regression coefficients as other variables enter or leave the model also are indicative of multicollinearity among independent variables (Neter et al. 1985:390).

A protocol sometimes used to remedy multicollinearity is principal components analysis (PCA). PCA combines interrelated variables into a single independent variable (Draper and Smith 1981:258). We do not recommend this procedure because: (1) it is largely a descriptive technique in which statistical inference is not attempted; (2) the hodgepodge of variables loaded on a PCA axis often defies biological interpretation; and (3) this technique gives similar results from analyses of real and random data (Karr and Martin 1981). Mitchell-Olds and Shaw (1987) provide additional cautions about the use of PCA for regression analysis.

Several other methods have been suggested to remedy problems with multicollinearity after the model has been constructed (Belsley et al. 1980, Neter et al. 1985:390-400, Willan and Watts 1978). Whichever method is used, a final check of variance inflation factors (VIF's) is recommended (Table 4). A VIF >10 for any regression coefficient is thought to indicate problems with multicollinearity (Neter et al. 1985:391-393). This check is necessary because not all intercorrelated variables are readily apparent in the correlation matrix (i.e., X_1 may be strongly related to X_2 and X_3 together, but not singly) and may not have been removed from the model. If a computer package does not provide VIF, they may be calculated as the reciprocal of the tolerance value for each β-coefficient. Of course, VIF cannot be determined until a regression model is built; this topic is discussed in the following section.

Table 4. Multiple regression model predicting Y (calves/cow) with X-variables (number of caribou = X_1, female harvest = X_2).[a]

Parameter	Coefficient value	S.D.	Beta values	Partials	R^2	R^2_a	VIF
Intercept (b_o)	0.771	0.0215	-	-	-	-	
# Caribou (b_1)	-0.000056	0.000007	-0.727	0.671	-	-	2.2
Fem. Harvest (b_2)	-0.00074	0.00025	-0.265	0.213	0.884	0.876	2.2

[a] In addition to the basic model, adjusted (R_a^2) and unadjusted (R^2) coefficients of multiple determination, standardized regression coefficients (beta values), coefficients of partial determination (partials), variance inflation factors (VIF), and standard deviations of the regression coefficients are shown. Partial coefficients and β- values suggest the same relative importance of X_1 and X_2 (note that partial coefficients only may be positive values).

Selecting a MLR Procedure

Most statistical computing packages offer several multiple regression options. Opinions vary as to the "best" method for choosing a set of independent variables to be included in the model (Draper and Smith 1981:294-380, Neter et al. 1985:417-443). We recommend 1 of 3 general methods for building a MLR model: (1) backward elimination; (2) "true" stepping; or (3) all possible regressions (Draper and Smith 1981:294-380, Neter et al. 1985:417-443).

Backward elimination of independent variables starts with all variables in the model and eliminates them one at a time based on their partial *F*-values (often *F*-to-remove = 3.996). This procedure has advantages of requiring less computing time and of initially including all variables so that none are "missed." Once a variable exits the model, however, it cannot re-enter the analysis. Backward elimination (as well as the other search algorithms we recommend) does not require the arbitrary selection of the first independent variable to enter the model. Order of variable elimination and variables not re-entering the model may affect the final outcome. If variables are not free to enter or leave at all stages, the first variable removed or entered may predetermine whether other independent variables become part the final model (Draper and Smith 1981:307-308).

"True" stepping possesses the advantage of allowing independent variables to enter and exit the model based on their partial *F*-values (typically *F*-to-enter = 4.00, *F*-to-remove = 3.996). Other numeric values of partial *F* might be used based on degrees of freedom associated with the mean square error (MSE), but the *F*-to-enter value *must be larger* than that of the *F*-to-remove (Neter et al. 1985:435). If values of α are used, however, α-to-enter should always be *smaller* than α-to-remove (i.e., α decreases as *F* increases). True stepping requires less computing time than an "all possible regressions" approach, but does not show the researcher all the models that might be built.

True stepping should not be confused with "forward selection" of variables, in which the biologist is asked to specify the order in which variables enter the model and sometimes the number of steps to be taken. Forward selection will not allow removal of a variable that already has been added to the model, as will a true stepping procedure (Neter et al. 1985:435).

An "all possible regressions" procedure builds a series of models that includes all potential combinations and arrangements of independent variables. Clearly, the "best" model will be among those generated by this method, but if there are many independent variables (m), it may be overlooked by a biologist scanning pages of computer output. There will be 2^m regressions, so that 10 independent variables (m) will result in 1,024 regression equations. This is time-consuming and usually wasteful of computer time because many potential combinations of variables would have otherwise been rejected without subjecting them to MLR analysis (Draper and Smith 1981:302). Many statistical packages incorporate a procedure to search for the "best" subset of equations (Garside 1971, Hocking 1972, Furnival and Wilson 1974). Thus, several equations representing the "best" one-variable solution, two-variable solution, three-variable solution, and so forth, are presented. The investigator then chooses the "best" model (i.e., the one explaining the most variation with the fewest variables).

Several methods are available to aid in selecting the best model. For situations in which a large number of independent variables ($m > 10$) are incorporated, a plot of the residual mean square error against the number or parameters in the model may be helpful. The best model occurs at the point where variation in the residual mean square error stabilizes (Draper and Smith 1981:298-299).

Another method involves Mallows' Cp statistic. Here, Cp-values are plotted against the number of parameters (p) in each model (Kennard 1971, Draper and Smith 1981:302, Neter et al. 1985:427). The model with the fewest variables lying closest to the line $Cp = p$ is considered best.

A final method is to select the model with the highest adjusted multiple coefficient of determination ($\underline{R}^2_a$) (Table 4). $\underline{R}^2$ only can increase as new variables are added to the model, regardless of the contribution made by these new variables. Indeed, the value for $\underline{R}^2$ when none of the independent variables are related to the dependent variable is m/n-1 (Harris 1975:46). $\underline{R}^2_a$ adjusts the gain in explanatory power by the number of parameters in the model and will only increase if the new information is more important than the loss of degrees of freedom (Draper and Smith 1981:303, Neter et al. 1985:423-425).

These search procedures and their statistical outputs are related mathematically and should result in selection of a similar best model. In practice, it is worthwhile to combine procedures in selecting a final model. For instance, several equations with high $\underline{R}^2_a$ and few independent variables might be compared with Mallows' $\underline{Cp}$. Similarly, the use of different procedures for determining which X's to include (e.g., backwards, true, or all models) should result in selection of the same independent variables; great discrepancies in variables selected may indicate problems.

Testing for Aptness

Once a regression model with appropriate independent variables has been selected, it is necessary to judge whether the model is apt. This procedure involves further examination of residuals. Residuals are plotted against fitted values of the dependent variable ($\hat{Y}$) and inspected for a pattern (Fig. 6). Residuals should not be plotted against observed values of Y with which they often are correlated (Draper and Smith 1981:147, Framstad et al. 1985). A cloud of points around the line Y = zero on the residual axis would be indicative of an apt model, whereas a positive or negative slope, parabola, or trapazoidal pattern of points may indicate violations of assumptions (Draper and Smith 1981:145-146, Zar 1984:288, Neter et al. 1985:113). Again, departures from the model that may be detected by an analysis of residuals include: (1) nonlinearity; (2) lack of constant variance in error terms; (3) error terms not being normally distributed; (4) outliers; (5) lack of independence in error terms; and (6) omission of

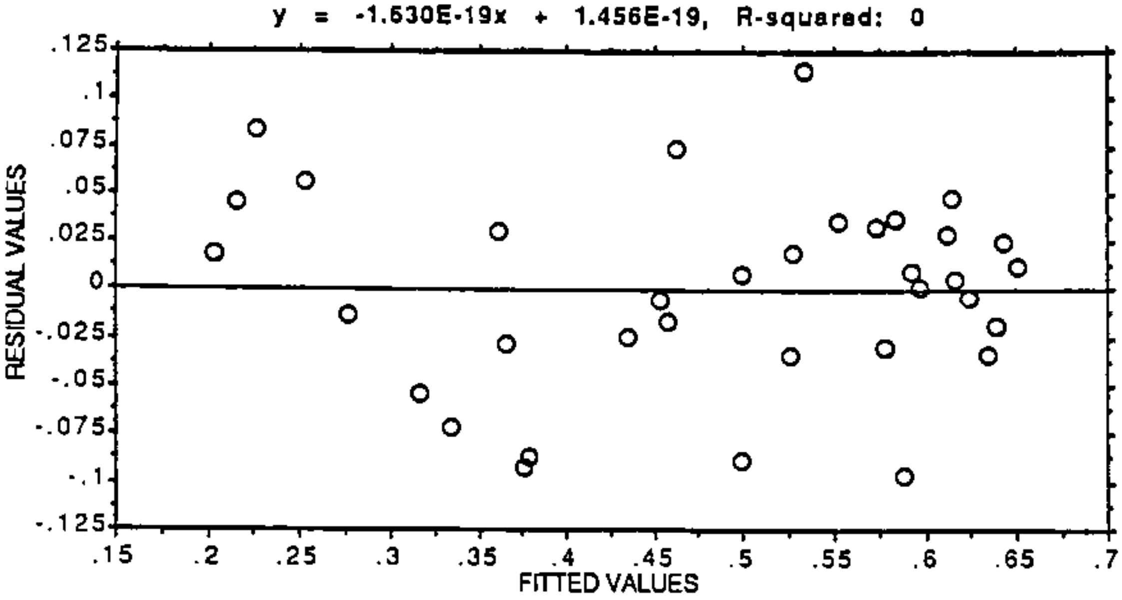


Fig. 6. Testing whether the final model is apt requires a plot of residual (Yi - $\bar{Y}$i) against the values fitted ($\bar{Y}$) by the multiple regression model.

important independent variables (Neter et al. 1985:111). Because of previous testing during the selection of independent variables, problems in 1-3 would not be expected at this time but are worth considering.

Outcomes from regression analyses may be strongly affected by outliers (observations that make extreme departures from expected values), especially when sample sizes are small (Draper and Smith 1981:152-153, Neter et al. 1985:114-115). In addition to the inspection of residual plots to locate outliers, a number of more formal procedures exist (Neter et al. 1985:400-411). Outliers should not be deleted unless measurement or recording errors are suspected. Outliers may add significant information to the model, such as when they result from interactions with variables omitted from the analysis (Neter et al. 1985:115).

Because studies of population dynamics typically require data collected over a number of years, it is worthwhile to plot residuals against time to ensure that no correlation exists among error terms (Fig. 7). Lack of independence sometimes may be corrected by incorporating time (years) as an independent variable in the model (Neter et al. 1985:115-118).

Searching for patterns in the residuals that result from a failure to include an important independent variable is essential to building a statistically sound and biologically meaningful model. Otherwise, controlling for multicollinearity through scrutiny of a correlation matrix or VIF's could result in elimination of the "wrong" variable in an intercorrelated pair. The Durbin-Watson test (Neter et al. 1985:450-460) offers a formal method by which temporal patterns in residuals may be detected. A significant outcome from this test will require re-examination of the correlation matrix, building a new model, and checking VIF's. If the problem is not thereby resolved, a search for another, and perhaps previously unconsidered, independent variable is in order. Failure to meet assumptions concerning residuals is evidence that the model is not apt, and reason to abandon a MLR approach. Conversely, a lack of pattern in the residuals and nonsignificant

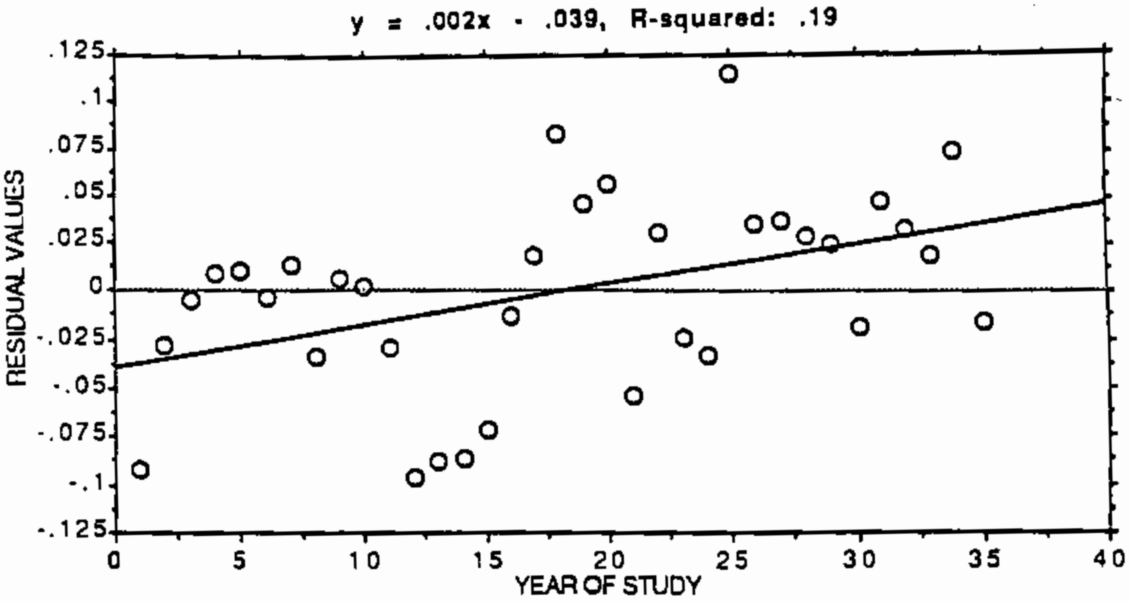


Fig. 7. Plot of residuals (Yi - $\bar{Y}$i) against time suggesting a possible relationship between year of study and size of variances (error terms).

outcome from a Durbin-Watson test suggest that selection of independent variables was reasonable, and modeling may proceed.

An important test for aptness of a regression model is the F-test for lack-of-fit (Marzluff 1986). This test is conducted after the MSE given by the regression analysis is partitioned into pure error and lack of fit components. Fit should be evaluated whenever possible. Partitioning of MSE, however, requires true, or at least closely approximate, replications (i.e., more than one observed Y for each value of the X's) (Draper and Smith 1981:42). For MLR applications to wildlife data, however, replicates are not likely because all X-values must be repeated. Thus, there may be little opportunity to test for lack-of-fit.

Model Interpretation and Validation

It is desirable to distinguish between models that are useful for prediction and those that are significant but lack predictive value. In general, a model is useful for prediction if the F-ratio is at least 4-5 times greater than that required for significance at the chosen level of α (e.g., $\alpha = 0.05$). Draper and Smith (1981:129-133) discuss and provide tables for determination of the F-ratio desired for prediction.

Great care should be taken in interpreting regression coefficients because their relative magnitudes are influenced by the units of measurement. For instance, if b_1 was millimeters of snowfall, and b_2 was number of wolves, they would not be directly comparable because of their different units. This problem may be resolved by calculating standardized regression coefficients or beta values (Zar 1984:338, Neter et al. 1985:261-263), which are unitless measures that may be compared directly so long as problems with multicollinearity have been rectified. Both unstandardized and standardized (which lacks b_o) regression equations should be presented for the final model.

The coefficient of multiple determination (R^2), mentioned earlier, also can be partitioned to evaluate the relative contribution of each independent variable to the regression. Coefficients of partial determination measure the contribution of each independent variable when all others have been included in the model (Neter et al. 1985:286). Coefficients of partial determination reveal information similar to that provided by standardized regression coefficients. These partial coefficients are less susceptible (but not immune) to problems with multicollinearity because they measure the contribution of each variable after adjustment for the degree of linear relationship with other variables (Neter et al. 1985:288). Nonetheless, coefficients of partial determination rely on output from the same matrices used for calculating other MLR statistics; thus rounding errors resulting from multicollinearity in these matrices also would affect coefficients of partial determination.

Both standardized beta-values and coefficients of partial determination suggest which variables are most influential in the final model. Keep in mind, however, that coefficients of partial determination will always have a positive algebraic sign, whereas standardized regression coefficients may be either positive or negative. Failure of both procedures to suggest the same order of influence (ignoring sign) for independent variables may be an indication of multicollinearity.

Just as the coefficient of multiple determination ($\underline{R}^2$) and $\underline{F}$-test reveal the predictive value of the total regression model, the significance of each independent variable also can be evaluated. Whether individual regression coefficients differ from zero (i.e., do they contribute significantly to the model?), from each other, or from some arbitrary value can be determined with partial $\underline{F}$-tests. Many computer programs present extra sums of squares that allow a variety of tests regarding the regression coefficients without additional computer runs or manual computations. Tests of significance for individual regression coefficients are performed in stepwise regression procedures as each variable is considered for entry into the model. These $\underline{F}$-to-enter tests are equivalent to partial $\underline{F}$-tests performed with derived extra sums of squares. Interval estimates for these regression coefficients can be derived from the standard deviations provided by most computer programs (Table 4).

Biologists often are interested in estimating the mean response (Y) at particular values of X-variables. Likewise, we sometimes wish to predict the response at some new level(s) of X's. Some computer programs will provide these values along with the other outcomes so long as the desired prediction levels of X's are provided. If these values are not generated automatically, confidence bands on predicted or estimated values of the dependent variables can be constructed from intermediate computer outputs. If the model is used for predictive purposes, it should be kept in mind that confidence intervals for predicted values of new observations (e.g., in future years) of $\hat{Y}$ are wider than those for expected (mean) values (Zar 1984:272-276, 344-346; Neter et al. 1985: Chs 3, 5, 7).

One question that should concern biologists using MLR is the applicability of the final model over the range of interest. This can be evaluated by examining stability of partial regression coefficients (β's). For instance, the entire data set might be subdivided into 5 periods, and β's recalculated for each time-interval (provided there are not too many independent variables in the model). If these β's varied greatly among periods, as in a step function, or exhibited a trend, it would be unwise to use all the data points to build 1 model for predictive purposes (Draper and Smith 1981:419); in this case it may be necessary to construct more than 1 model from these data. "Jacknife" and other resampling procedures also are available to examine the stability of β's (Wu 1986); another option is to use the "PRESS" statistic. Likewise, it is hazardous to attempt to use a model to predict the dependent variable when values of important independent variables lie outside the range used to construct the original model (i.e., be careful not to extrapolate too far beyond the range of observed values).

Another validation method is to randomly subdivide the data set and test the model derived from 1 subset against the remainder (e.g., percentage of observations predicted correctly) (Snee 1977, Draper and Smith 1981:419). Studies of caribou populations seldom will include a sufficient number of cases (years) to permit this procedure, or an opportunity to collect additional years of data.

It may be unwise to apply the results from modeling 1 caribou population to another, especially if variables fall outside previously measured ranges. Further, new and unmeasured conditions affecting dependent variables may be operating in the second population. If a second population model is built with the same variables contained in the first, however, it is possible to test it against the first model (Zar 1984:347-349).

A cautious approach to interpreting the final model is advisable. Even a valid and highly predictive equation may lack biologically important variables. For instance, "number of adult males" might not enter a model designed to predict recruitment rate (perhaps because sexual segregation reduces competition of adult males with young), but a population without these males certainly would fail to increase at the expected rate!

Certain variables that are highly intercorrelated with other variables included in the model may be overlooked even though they are directly responsible for the observed changes in the dependent variable. Such "lurking" variables are the reason that a MLR approach cannot be used to infer cause and effect.

We believe it unlikely that the dynamics of caribou populations will be understood fully by relying on an inductive approach that searches for past examples that "fit" existing hypotheses. Likewise, MLR analysis of unplanned data collected for other purposes has limited usefulness. The need for experimental (manipulative) studies of wildlife is well-documented (McCullough 1979, James and McCulloch 1985, Noon 1986). Certainly, a hypothetico-deductive approach to test factors regulating caribou populations will require such manipulations. Nonetheless, MLR offers a reasonable approach to identify important variables for such experiments, especially where complex interactions occur among many potential factors.

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UTILITY OF THE STRATIFIED RANDOM QUADRAT SAMPLING CENSUS TECHNIQUE FOR WOODLAND CARIBOU IN YUKON

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Abstract: Using past techniques, it has proven notoriously difficult to obtain demographic data on woodland caribou (*Rangifer tarandus caribou*) populations occupying forested environments. We report on an adaptation of a stratified random quadrat aerial census technique originally developed by Gasaway et al. (1986) to census moose (*Alces alces*) in Alaska. The adapted technique was applied to 2 caribou herds (the Wolf Lake and Finlayson Herds) in southcentral and eastcentral Yukon in winter 1986 and 1987. We compare the population size estimates derived from the stratified random technique with earlier attempts to census the herds using total count census techniques, and conclude that estimates based on the stratification technique are more reliable than those of the total census approach. In addition, we assess the sightability bias inherent in surveying caribou in forested environments and compare population estimates using a sightability correction factor with those in which the sightability correction factor is not used. We conclude that population estimates that fail to include a correction for sightability bias consistently and significantly underestimate population size. Finally, we assess the relationship between the number of quadrats sampled in the stratification technique and the associated precision estimates. We conclude that it is not always necessary for managers to survey all quadrats in the high-density stratum.

Key Words: caribou, census technique, Finlayson Herd, *Rangifer*, Wolf Lake Herd

At the 2nd North American Caribou Workshop in Montreal, October 1984, an open session was held on caribou (*Rangifer tarandus*) census techniques

(Meredith and Martell 1985). Participants identified the need for techniques to reliably estimate caribou population sizes, particularly for woodland caribou (*R. t. caribou*) populations occupying forested habitat. General problems associated with woodland caribou population estimates are: (1) poor sightability in forest environments; (2) the failure of observers to see all caribou; (3) caribou movements between areas sampled; (4) broad extrapolations resulting from highly variable population densities; (5) poorly based assumptions on population distribution and behavior; and (6) financial limitations.

The most common method used to census woodland caribou has been the "total count" (i.e., known minimum) during various seasons (Bergerud 1983). In summer, total counts have consisted of enumerating caribou on mountain snowfields during July (Ritcey 1976); aerial photography has been used to improve accuracy (Farnell and Russell 1984). Total counts have been used extensively to census breeding aggregations on alpine plateaus (Bergerud 1978; Edmonds and Bloomfield 1984; Hatler 1986; Farnell and McDonald 1987a,b). Both summer and fall total counts assume that the entire population is distributed in upland areas, which is rarely true (Hatler 1986). Total counts during winter (Fuller and Keith 1981) have been higher than those in fall (Edmonds and Bloomfield 1984) but remain inadequate for management or research purposes. Reliable total counts have, to our knowledge, only been obtained through intensive study of Yukon's Burwash caribou herd (Gauthier and Theberge 1985); these counts were reliable primarily because the Burwash herd ranges wholly in a tundra environment.

Population estimates derived from samples using capture-recapture methods have been satisfactory for caribou in tundra environments (Gauthier 1984), but the technique is inefficient because it requires impractically large samples. In recent years, spray paint marking has been used in British Columbia and Newfoundland to provide large samples for woodland caribou capture-recapture estimates. This technique has the potential to provide useful data in certain types of forested environments (J. Elliot, pers. commun.; S. Mahoney, pers. commun.). Population estimates derived from strip-transect samples have been improved when stratified (Siniff and Skoog 1964). Quadrat sampling methods have produced higher population estimates than the strip-transect method, but neither method has proven satisfactory for purposes of woodland caribou management (Fong et al. 1985). We suggest that reliable estimates for woodland caribou populations inhabiting forested environments may best be achieved during winter with an intensive sampling method.

Radiotelemetry-assisted studies of woodland caribou in Yukon have consistently documented confined distributions of animals during late winter (Farnell and Russell 1984; Farnell and McDonald 1987a,b). These distributions are considered "traditional" and are the result of an obligatory response to increasing snow depths over winter combined with habitat preference (Farnell and Russell 1984; Farnell and McDonald 1987a). Studies have further shown that Yukon's woodland caribou populations are discrete and should be managed individually. Based on the above findings, we believe that stratified quadrat sampling of caribou on winter ranges can provide reliable estimates of the size of distinct populations.

We report on an adaptation of a stratified random quadrat sampling aerial census technique (SRQT) originally developed by Gasaway et al. (1986) to census moose (*Alces alces*) in Alaska. The adapted SRQT was applied to 2 woodland caribou populations (the Finlayson and Wolf Lake Herds) in east-central and southcentral Yukon in winters 1986 and 1987, respectively. We compare the SRQT population estimates with earlier estimates based on total count techniques. In addition, we assess caribou sightability in forested environments and compare population estimates using or lacking a sightability correction factor (SCF). Finally, we assess the relationship of the number of quadrats sampled in the SRQT to the associated precision estimates.

The authors thank E. J. McDonald, R. Markel, J. Carey, A. Baer, B. Gilroy, and H. Slama, Wildlife Technicians, whose many long hours of aerial surveys made possible these caribou population estimates.

STUDY AREAS

The Wolf Lake and Finlayson Caribou Herds occupy areas of similar physiography and climate. The Wolf Lake Caribou Herd ranges in the southcentral Yukon and is bounded by the Nisutlin River to the west, the upper Liard River to the north, the eastern flank of the Cassiar Mountains to the east, and the Alaska Highway to the south (Fig. 1). The survey area selected for censusing the Wolf Lake Herd corresponds to the herd's winter distribution in 1987, and occurred wholly within the Wolf Lake lowlands. This area is dissected by plateaus and rolling hills ranging from 600 to 1,500 m in elevation; treeline is at 1,200 to 1,350 m. The area is extensively forested. Vegetation was described by Oswald and Senyk (1977).

The Finlayson Caribou Herd ranges in the eastcentral Yukon and is bordered by the Ross River drainage to the west, the Logan Range of the Selwyn Mountains to the north and east, and the St. Cyr Range of the Pelly Mountains to the southern boundary (Fig. 1). The winter distribution and subsequent survey area selected for the Finlayson Herd in 1986 occurred in the Ross River-Pelly River lowlands. Terrain in this area consists of deeply cut broad valleys, with occasional rolling hills and plateaus. Elevations are above 1,000 m, except for the 2 major river valleys which lie below 600 m. The Finlayson study area is also extensively forest-covered and described by Oswald and Senyk (1977).

METHODS

The SRQT first requires delineating a survey area, which in our case was the winter distribution of the study populations. The survey area is then divided into quadrats using, to the extent possible, natural features to define boundaries. Quadrats may vary in size but should be large enough such that movement of animals among quadrats over a 24-hour period is unlikely. Once quadrats have been defined, a low-level survey of the survey area is flown by fixed-wing aircraft to stratify the entire area based on the relative density of the caribou present. The strata categories are ranked in gross classifications, such as high, medium,

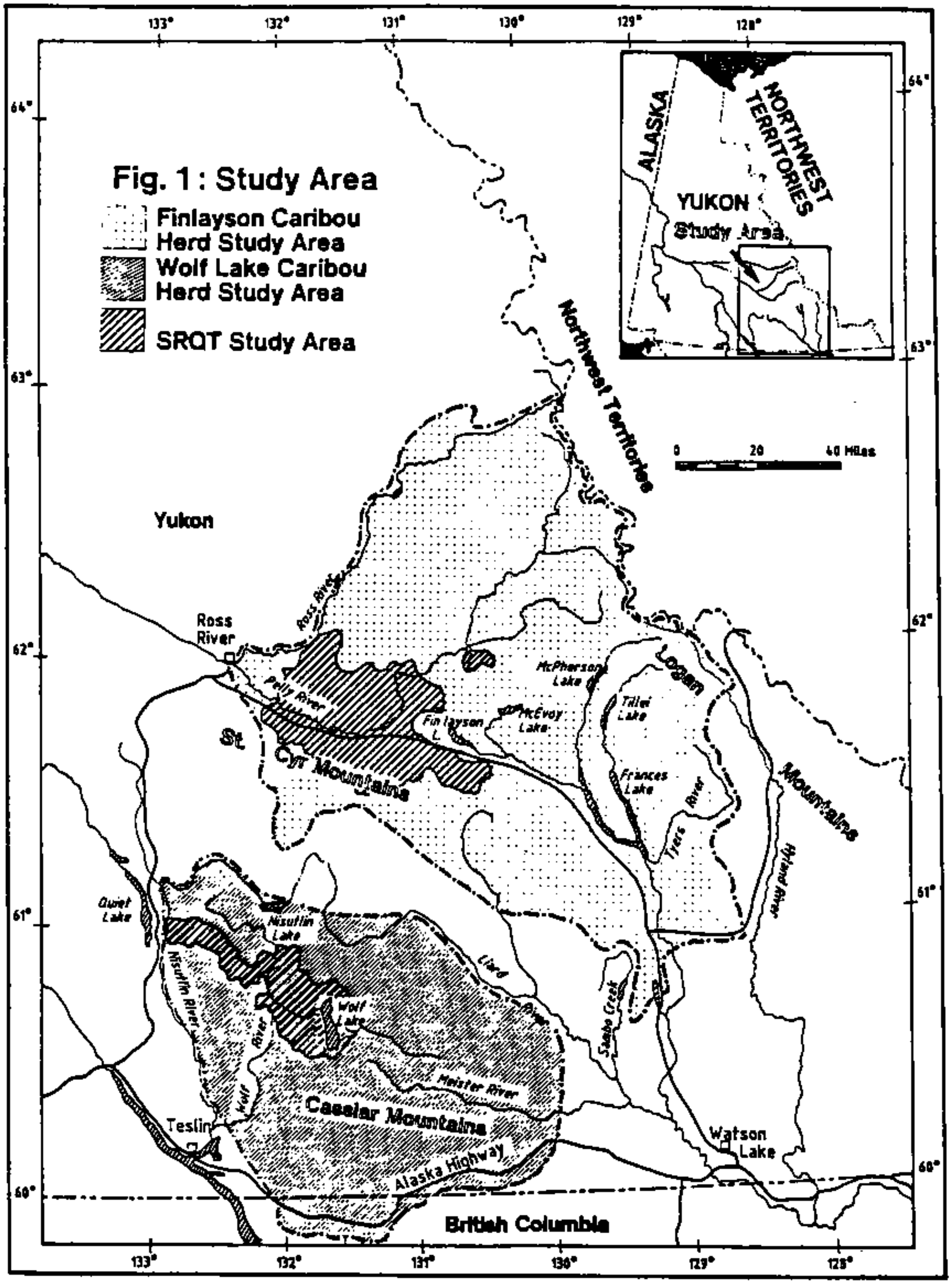


Fig. 1 : Study Area

low, or very low. Not all such categories may be present in a given survey area. The survey flight line must transect all quadrats, and each quadrat is subjectively assigned to a stratum based on number of animals and/or amount of sign seen.

A random sample of quadrats is chosen from each stratum for more intensive sampling. Of the total number of quadrats chosen, the proportion from each stratum should be proportional to the variation in the stratum.

Once quadrats have been chosen for more intensive sampling, they are searched in the order in which they were randomly drawn for each stratum. Intensive sampling should immediately follow the stratification flight to reduce the possibility of animal movement among quadrats. In Yukon, intensive surveying has been conducted by helicopter, using a search intensity of at least 4 min/mi^2. Number of animals and age and sex composition are recorded for each sighting.

To assess sightability biases, a number of quadrats are re-surveyed at a survey intensity of approximately 12 min/mi^2. These more intensive surveys are conducted to establish a sightability correction factor for population estimates (Gasaway et al. 1985).

Gasaway et al. (1986) provided a computer program for the Hewlett-Packard 41C and 41CV hand-held calculator that provides stratum and total population estimates with associated confidence limits. We have adapted that program for mainframe and micro-computers using the SAS (Statistical Analysis System) programming package (Version 5). The program is available on request from the authors.

In applying the SRQT to our study populations, we established 44 quadrats for the Wolf Lake area and 85 for the Finlayson area. Based on stratification flights, quadrats in each area were classified according to 2 density categories--high density (primary stratum) and low-to-moderate density (secondary stratum). Table 1 shows the total number of sample units within each stratum for each study area, the number selected for intensive sampling, the number used to establish a SCF for each area, and the size of each study area.

Table 1. Summary of survey data for the Wolf Lake and Finlayson Caribou Herds.

	Wolf Lake		Finlayson	
	High stratum	Low stratum	High stratum	Low stratum
Total number of quadrats	15	29	39	46
Number of quadrats in intensive survey	15	11	39	19
Number of quadrats surveyed for the sightability correction factor	8	0	8	0
Total area per stratum (sq km)	486.6	540.43	519.5	662.8

Earlier attempts to census these herds consisted of total counts during the breeding season in October. A helicopter was used to enumerate and classify caribou, both on alpine plateaus and across the herd distribution as determined by radiocollar relocations. These total counts were carried out on the Finlayson Herd in 1982, 1984, 1986, and on the Wolf Lake Herd in 1985 and 1986.

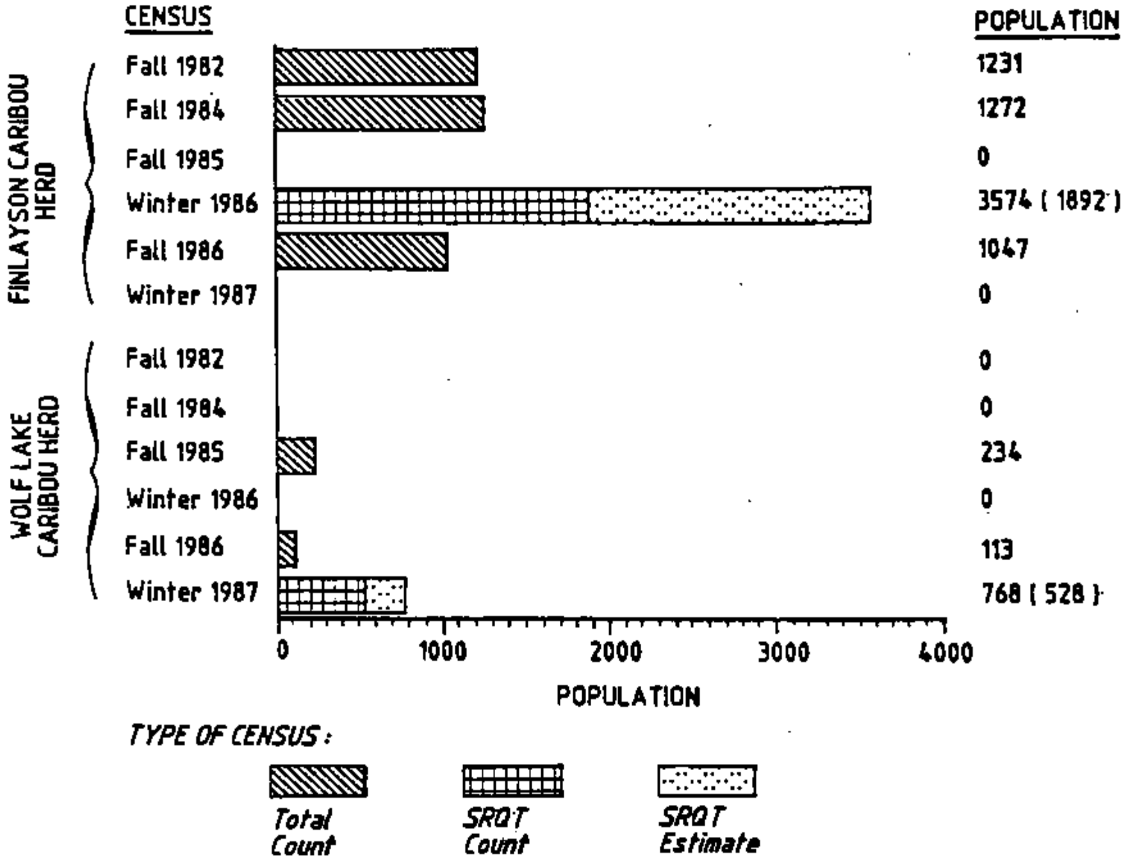
In addition to deriving population estimates for management purposes, objectives of this project were to: (1) compare the SRQT with the earlier total count technique; (2) assess the need for sightability correction factors; and (3) determine if acceptable estimates could be achieved by sampling less than the full number of quadrats within the primary stratum. To address the second objective, population estimates were calculated using the SCF and compared with estimates derived without using the SCF. The third objective was addressed by calculating a population estimate and confidence limits based on all quadrats that were sampled, and then recalculating population estimates by progressively removing information for additional quadrats from the calculations. For example, 15 quadrats were sampled in the primary stratum of the Wolf Lake Herd and 8 of those were resampled at a higher intensity to derive a SCF. We first calculated a population estimate based on all 15 quadrats, and then removed the information for the last quadrat that was randomly selected and recalculated the population estimate based on 14 quadrats. We repeated this procedure for the Wolf Lake Herd until information for only 3 quadrats in the primary stratum remained. At that point, only 2 of the original 8 sets of intensive search data were left to establish the SCF. As population estimates based on the SCF cannot be calculated with information on less than 2 quadrats, the iterative procedure stopped at that point. Therefore, there were 13 population estimates for the Wolf Lake Herd based on information from 15 through 3 primary stratum quadrats. For the Finlayson Herd, 23 population estimates were calculated based on information from 39 through 17 primary stratum quadrats; data on <17 quadrats yielded confidence limits on the population estimates that were too wide to provide usable information.

RESULTS AND DISCUSSION

Figure 2 compares earlier total counts of the 2 study herds with estimates derived from the SRQT. The number of caribou estimated and observed during SRQT surveys greatly exceeded the number observed during total counts. For the Finlayson Herd, 49% more caribou ($\underline{n}$ = 1,892) were observed on the SRQT survey (March 1986) than determined from the previous highest total count of animals in October 1984 ($\underline{n}$ = 1,272). Similarly, a total count of caribou (October 1986) after the SRQT survey was 45% lower ($\underline{n}$ = 1,047). The estimated population size (3,574) derived by SRQT was 181% higher than the highest total count (1,272).

For the Wolf Lake Herd, 126% more caribou ($\underline{n}$ = 528) were observed on the SRQT survey than on the previous highest total count ($\underline{n}$ = 234) in October 1985. The estimated population size (768) derived by SRQT was 228% higher than the highest total count (234).

Fig. 2 : Total census counts and expanded population estimates (SRQT method) for the Wolf Lake and Finlayson caribou herds.



In both cases the disparity between the total counts and SRQT results are likely due to greater accuracy in the SRQT method rather than population flux. The problems with total counts during fall seem to be: (1) the inaccurate assumption that all animals are distributed entirely in open habitats; (2) no correction for animals not observed; and (3) no estimate of precision.

Our population estimates for the 2 study herds derived from the SRQT, including the SCF (the expanded total) and excluding it (the observed total), are shown in Table 2. Confidence limits are given for the estimates derived using the SCF. The observed population estimate for the Wolf Lake Herd falls within the 95% confidence interval of the expanded population estimate, but the same is not true for the Finlayson Herd. The SCF was 1.3 for the Wolf Lake Herd vs. 1.7 for the Finlayson Herd, and the 95% confidence interval was ±28.0% of the mean for the Wolf Lake Herd vs. ±17.6% for the Finlayson Herd (Appendix A). These results suggest that incorporating a SCF is a significant improvement in census techniques. Applying a SCF accounts for much of the increase in the population estimates for the 2 study herds when comparing results from the SRQT and the total count censuses.

Table 2. Observed and expanded population estimates with 90% and 95% confidence intervals for the Wolf Lake and Finlayson Caribou Herds.

	Wolf Lake Herd	Finlayson Herd
Observed[a] population estimate	578	2,052
Expanded[b] population estimate	768	3,574
90% confidence interval	569-940	3,071-4,077
95% confidence interval	553-992	2,947-4,202

[a] Estimate without a SCF.
[b] Estimate with a SCF.

Figure 3 shows population estimates for the Wolf Lake and Finlayson Herds that incorporate the SCF (expanded totals), with their associated 90% and 95% confidence limits, and population estimates that do not incorporate a SCF (observed totals). Appendix A (pp. 223-227) provides a detailed summary of all calculated values. Figure 3a indicates that the precision estimate for the Wolf Lake Herd widens above ±30% of the mean at the 90% confidence level; attaining 90% precision required sampling 11 of 15 quadrats (73% sampling effort) in the high-density stratum (assumes 11 quadrats were sampled in the low-density stratum) (Appendix A). With sampling effort >73% in the primary stratum, precision estimates fall between ±22 and ±29%.

For this analysis, we have arbitrarily decided that population estimates with >±30% precision at the 90% confidence level are of limited utility, and that estimates with >±40% precision are of little practical value. At the 95% confidence level, surveying all 15 quadrats in the Wolf Lake Herd was required to obtain a precision <±30% (Fig. 3c). In contrast, Figure 3b shows that, for the Finlayson Herd, the precision estimate at the 90% confidence level exceeds ±30% when only 23 of the 39 quadrats (59% sampling effort) in the high-density stratum are sampled (assumes 11 sample units surveyed in the low-density stratum) (Appendix A). Above this 59% sampling effort, precision estimates fall between ±14 and ±26%. Acceptable precision at the 95% confidence level for the Finlayson Herd (Fig. 3d) required that 27 (69%) of the 39 quadrats be sampled. These results suggest that calculations of variance, and not rules of thumb, should guide managers in deciding the number of quadrats to be sampled within high-density strata. In Yukon, managers have learned through experience that most or all quadrats within the high-density stratum, and ≥40% of the quadrats within the medium stratum, need to be sampled. Less emphasis is placed on sampling within the low or very low strata because of the reduced probability of encountering substantial numbers of animals there.

In conclusion, the unrealistically low population estimates derived from total count censuses of the 2 study herds contributed to the concern of those responsible for managing them. In addition, the unknown accuracy

Fig. 3 : Observed and expanded population estimates with 90% and 95% confidence intervals for the Wolf Lake and Finlayson Caribou herds according to the number of plots sampled.

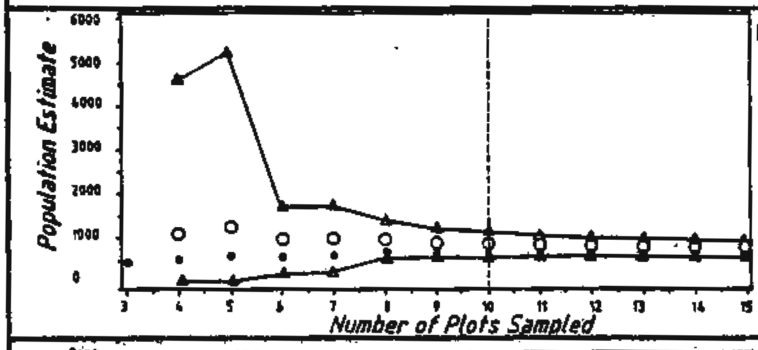


Fig. 3a : Wolf Lake Herd with 90% confidence intervals

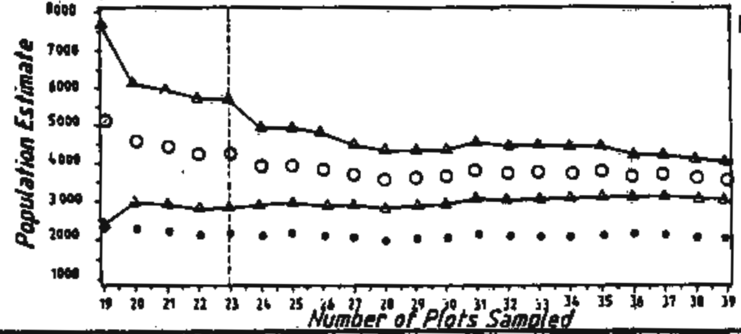


Fig. 3b : Finlayson Herd with 90% confidence intervals

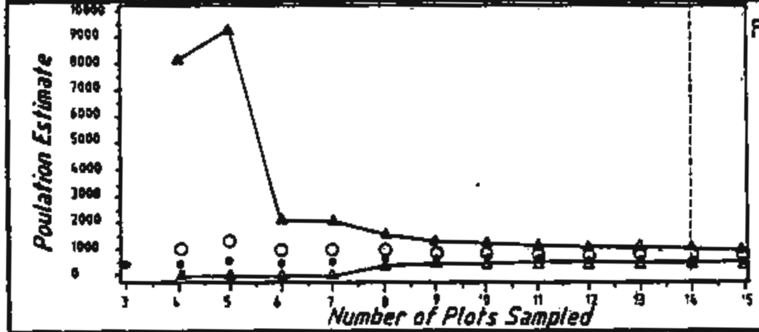


Fig. 3c : Wolf Lake Herd with 95% confidence intervals

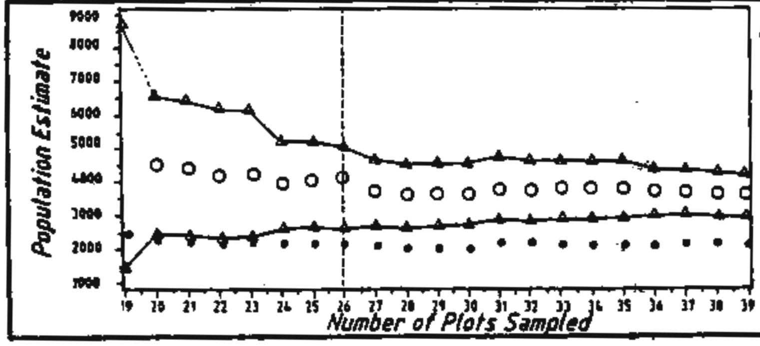


Fig. 3d : Finlayson Herd with 95% confidence intervals

LEGEND :

○ Expanded population estimate

• Observed population estimate

△ 95% confidence intervals

Note : All estimates at and to the left of the vertical reference line have precision estimates >30%

of the total count estimates and no associated measure of precision concerned those studying the population dynamics of the herds. In particular, the low estimates for the Wolf Lake Herd elicited concern about the population's viability and suggested the need for more restrictive harvest levels. In the case of the Finlayson Herd, intensive management practices required accurate population estimates to interpret the results. The higher population estimates resulting from the SRQT method have been important in addressing many management concerns for these herds. Clearly, precise (and ideally, accurate) population estimates are essential to interpret population dynamics and for effective management of populations. We hope that the results of this paper will be of value to other woodland caribou managers.

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THE USE OF AERIAL PHOTOGRAPHY TO CONDUCT CARIBOU SHORT-YEARLING COUNTS

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Abstract: In March and April 1986, we evaluated the use of 35 mm aerial photography for short-yearling (9.5-11 months old) counts in the Western Arctic Caribou (*Rangifer tarandus granti*) Herd (WAH) of Alaska. Two pilot and observer teams used PA-18 Super Cubs for the counts. Each observer photographed groups of caribou with a hand-held 35 mm single lens reflex camera. Photos were taken at 9-30 m above ground level, 20-90 m from the caribou and at an airspeed of approximately 110 km/hr. The 2 observers simultaneously reviewed the slides and, by mutual agreement, classified each caribou as a short-yearling or adult ($\geq$21.5 months old). Criteria for identification included body size, face length, antler length and configuration, presence of antler velvet, pelage color, and presence of neck mane.

The 2 survey teams exposed 1,541 frames in 4 days ($\bar{x}$ = 385 frames/survey team/day, range = 250-500). A total of 6,599 caribou were photographed on 1,159 slides ($\bar{x}$ = 5.7 caribou/slide, SD = 3.9, range = 1-34). We identified 1,227 short-yearlings (18.6% of the sample). Observer variability was evaluated from a subsample of 109 slides containing 512 caribou images. We and 3 caribou specialists independently classified the caribou on the slides. We counted 110 short yearlings (21.5%), and the 3 specialists' counts were 122 (23.8%), 121 (23.6%), and 114 (22.3%). The difference between our count and that of each specialist was not significant (t-test; $P > 0.05$), nor were differences among counts by the 3 specialists ($P > 0.2$).

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Twenty-five percent of the slides were unusable for any combination of the following reasons: (1) caribou image too small (i.e., distance >30 m for the 55 mm lens and >40 m for the 70 mm lens; (2) vertical angle to caribou >40-50°; (3) caribou >20-30° from perpendicular side-view; (4) improper exposure; and (5) obstructed view of caribou. Experienced personnel should be able to attain a usability rate of ≥90% for slides.

Review of the slides required 27.5 hours, about 30 minutes for each box of 34-38. The average number of caribou per slide could be increased in future surveys if the distance between the airplane and caribou was monitored more closely. An average of 10 caribou per slide may be attainable. This would substantially improve efficiency because of (1) increased sample size, (2) less time and film needed to photograph each group of caribou, and (3) broader distribution of survey effort (as a result of the reduced time per group).

While most short-yearlings can be recognized at a single glance, others are more difficult to identify. Our ability to identify some short-yearlings was seriously compromised because the slide images represented only 1/1000 second in time. Video-filming with slow-motion and stop-motion capabilities may be a solution to this problem and should be tested.

Our survey approach did not achieve an overwhelming improvement in efficiency compared with the conventional, nonphotographic technique. However, we believe that efficiency would be enhanced if faster airplanes (e.g., Cessna 185) and motor-driven cameras were used. The slides of caribou from this project can be used to: (1) train future observers, (2) refresh the memories of experienced observers, and (3) standardize and calibrate the identification technique among observers working in different geographic areas.

Key Words: aerial photography, caribou, northwest Alaska, _Rangifer_, short-yearling, Western Arctic Herd

OPTIMUM POPULATION SIZE FOR THE NELCHINA CARIBOU HERD?

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Abstract: The Nelchina Caribou (*Rangifer tarandus granti*) Herd, located in southcentral Alaska, has been a particularly important wildlife resource because of its proximity to the majority of the state's human population. During recent years, the herd has undergone major population fluctuations, ranging from a high of 60,000-90,000 animals in the mid-1960's to less than 10,000 in 1972. The herd now numbers about 31,000. Between 1977 and 1987 the herd increased at an average annual rate of 8%. During the same period, about 4% of the herd (>80% males) was harvested each year. Lichen biomass is again decreasing on heavily used portions of the range after a recovery during the 1970's. Currently, the management goal for the herd is to attain 30,000 animals older than calves (38,000-40,000 total caribou). We are uncertain about the appropriateness of this figure and are soliciting suggestions on how best to determine an optimum size for the herd.

Key Words: caribou, management strategy, Nelchina Caribou Herd, population dynamics, range condition, *Rangifer*

In this paper, we present historical and current information on the Nelchina Caribou Herd (NCH) to elicit suggestions for future herd management, particularly regarding optimum population size. The NCH is managed by the Alaska Department of Fish and Game (ADF&G). The general management objective is to maintain herd size and productivity at levels compatible with acceptable range condition, while allowing a substantial human harvest.

The NCH ranges the upper Susitna and Copper River drainages in south-central Alaska, which form a large basin surrounded by 4 mountain ranges (Fig. 1). Historically, the herd occupied a range of about 52,000 km^2 (20,000 mi^2). This herd has been particularly important to Alaska residents because of its proximity to the majority of the state's population and because access is provided by several highways. During the past 30 years, more than 110,000 caribou have been harvested from the NCH. The popularity of hunting caribou from this herd was shown in 1984 when 12,500 people applied ($5.00 fee) for 1,900 available permits. Obviously, interest in harvesting animals far exceeds the opportunity.

The NCH has been studied extensively and served as the major study population for Skoog's (1968) classic treatise on caribou ecology. No reliable estimates of herd size were available prior to 1955. However, based on fragmentary reports by early explorers, Skoog (1968) concluded that the NCH was relatively large in the mid-1800's. He believed that the herd had declined to fairly low numbers by 1900 but had begun to grow again during the 1940's. The herd was probably never below about 10,000 animals (Skoog 1968).

Since 1955, the NCH has been censused several times (Fig. 2). The census methods used did not always produce reliable estimates; in retrospect, certain estimates were likely in considerable error. However, when the entire set of results is examined, some trends emerge. The herd apparently increased from about 40,000 animals in the mid-1950's (Watson and Scott 1956) to a peak of about 70,000 in the early to mid-1960's (Siniff and Skoog 1964). Some authors (Lentfer 1965, Van Ballenberghe 1985) believed that the herd may have numbered 90,000 in 1964. By 1967, the NCH had apparently declined to about 61,000 (Hemming and Glenn 1968). The decline continued into the early 1970's, to a low of 8,000-10,000 animals (Bos 1973, 1974, 1975).

Speculation about the cause of this decline has implicated a number of possible factors, but the relative importance of each is unknown. Bos (1975) suggested that egress of caribou to other areas could have played a role based on Glenn's (1967) observations of caribou moving from the

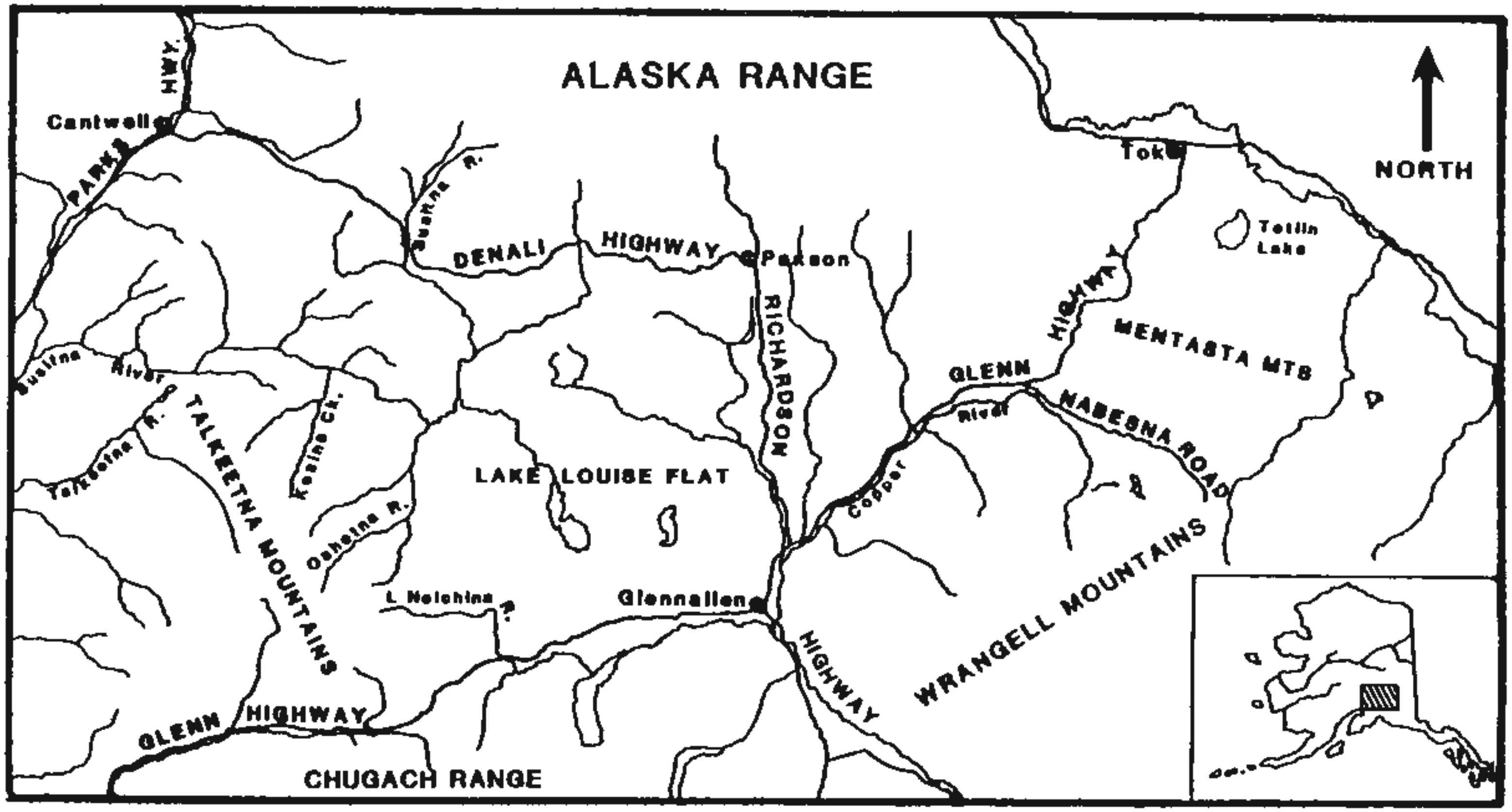

Fig. 1. Nelchina caribou range with basic geographic features.

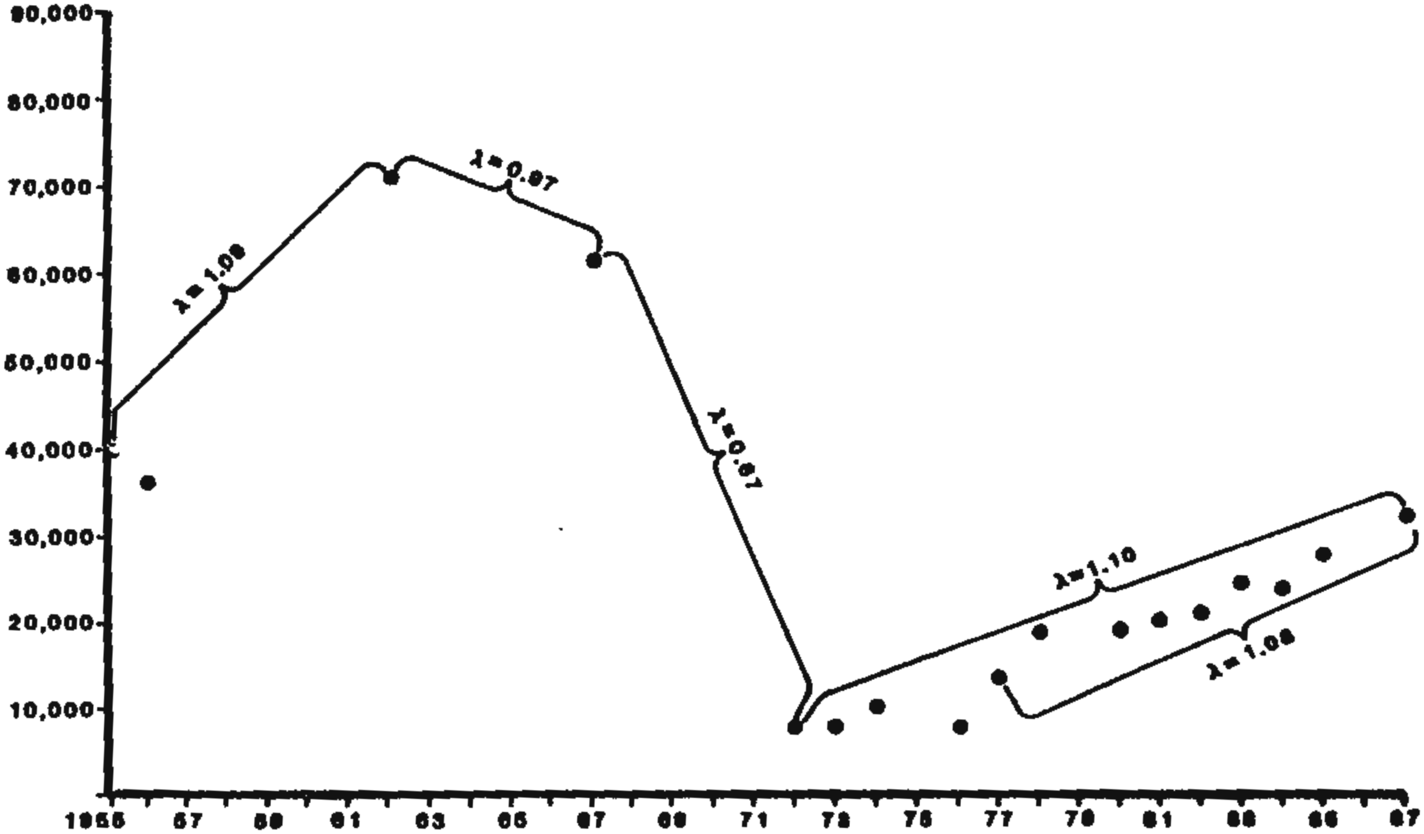

Fig. 2. Population estimates and finite rates of increase (λ) for the Nelchina caribou herd, 1955-87.

normal range of the NCH. Since 1980, when NCH caribou were first radio-collared, similar movements by collared caribou have been seen, but all such caribou subsequently returned to the NCH range. Additional reports of NCH caribou outside their normal range and in areas of apparently less suitable habitat were also received during the 1960's (S. Eide, pers. commun.). Doerr (1979) and Van Ballenberghe (1985) did not believe that egress was of major importance in the decline.

A high harvest is generally acknowledged as a factor in the decline of the NCH. Between 1964 and 1972, nearly 56,000 caribou were reported taken. If unreported illegal kills and crippling losses are also considered, the total would be much higher. Excessive harvest late in the decline was particularly devastating. In 1971, about 10,000 caribou were killed by hunters, a figure similar to the total population estimate for the following year.

Unfavorable winter weather may also have contributed to the decline. Four relatively severe winters (i.e., deep snow) occurred shortly before and during the decline (Van Ballenberghe 1985). Low spring calf:cow ratios were observed following these winters. Van Ballenberghe (1985) concluded that calf survival correlated well with winter severity.

Wolf (Canis lupus) numbers on the NCH range, low during the 1950's because of wolf control, increased during the 1960's. There is considerable disagreement on exact wolf abundance during this period (Rausch 1967, Van Ballenberghe 1981, Ballard and Bergerud 1988), but it is clear that many more were present during the decline than during the previous growth phase of the NCH. Bergerud (1978, 1980) showed a strong correlation between wolf abundance and calf recruitment to the NCH, based primarily on the relative frequency of various cohorts in the caribou harvest. However, because there is little evidence for selective predation on Nelchina caribou calves, the validity of the correlation is questionable (Pitcher 1987); it is possible that increased predation on caribou of all ages contributed to the decline.

It is also possible that density-dependent food limitation played a role in the decline of the NCH. When the herd was at its peak, caribou density was high (perhaps 1.5-2.0/km^2) relative to other North American herds. Studies in 1970 indicated that the lichen flora had diminished substantially over the previous 10 years (Pegau and Hemming 1972), and concern was expressed that the range could not continue to support high numbers of caribou. Hemming (1975) concluded that the NCH exceeded carrying capacity during the 1960's. In contrast, Skoog (1968) believed that food was not limiting and concluded that "the Nelchina herd has remained particularly healthy during the early 1960's." At the time, he observed "only what might be considered normal incidence of disease and parasite infestations." However, there were some reports of a high incidence of disease among hunter-killed animals examined at check stations when the herd was large (S. Eide, pers. commun.). Bergerud (1980) argues that mainland caribou herds are not normally food-limited, at least from a density-dependent standpoint, because they are able to move about and utilize a wide variety of plant species.

In retrospect, the NCH may have declined because of a combination of factors, including excessive human harvest, increased predation by wolves, and several winters severe enough to reduce calf survival. It is also possible that social strife and range deterioration associated with high population density were implicated. Any 1 or 2 of these factors might have caused some decrease in the population, but perhaps the cumulative impact of all of the above factors over an 8-year period resulted in the major decline.

After the magnitude of the decline was recognized, conservative management practices were implemented, including restricted harvests, comprised primarily of males. Since 1973, winters have been generally mild, and since the late 1970's, wolf numbers have been relatively low. Results of censuses conducted since the mid-1970's indicate fairly rapid growth of the NCH. From 1977 through 1987, the finite rate of increase for the herd averaged 1.08 (i.e., 8%/yr), but may have decreased somewhat over this period.

In 1976, a management guideline was established to restrict the harvest to ≤5% of the herd until it reached 20,000; thereafter, the annual increment could be harvested (ADF&G 1976). This guideline was based on the belief that the previous decline was brought about by emigration and reduced recruitment initiated largely by a density-dependent response resulting from overuse of lichen ranges (Bos 1975, ADF&G 1976). The results of range studies in 1970 suggested that the lichen flora had been badly abused and would require many years to recover (Pegau and Hemming 1972).

In 1981, recognizing that the herd size goal of 20,000 was imminent, ADF&G began re-evaluating that goal. The decision to allow the herd to increase to 30,000 adults (ca. 38,00-40,000 total caribou) was based on several considerations. Studies conducted in 1977 (Lieb et al. 1986) indicated that lichen biomass on the range of the NCH had increased substantially since 1970. Also, current literature suggested that free-ranging mainland caribou herds are not normally limited by absolute shortages of food (Bergerud 1980). Further, analyses by Doerr (1979) and Bergerud (1978) suggested that human harvest, predation, and severe winter weather may have been the major causes of the 1965-72 decline. This evidence convinced managers that the herd could safely be allowed to increase.

CURRENT STATUS

If the current rate of increase continues, the herd will number the desired 30,000 adults within the next 3-5 years. ADF&G is re-evaluating the appropriateness of that management goal, and we hope that future discussions among caribou biologists will aid that process.

Certainly, range carrying capacity must be considered when adopting a herd size goal. Studies of Nelchina caribou-range relationships, focusing on the lichen flora, have been in progress for more than 35 years. Between 1955 and 1962, 39 range stations, including exclosures, were established at various sites throughout much of the NCH range. These range stations were examined at approximately 5-year intervals from 1957 through 1983. As mentioned above, lichen biomass declined sharply during the 1960's (Pegau and Hemming 1972), corresponding to the period of peak caribou abundance, and then began to increase in the early 1970's when the herd was at its low (Lieb et al. 1986). By 1983, with the herd continuing to grow, increases in lichen abundance had generally halted in areas of substantial caribou use. In areas of light caribou use, however, lichen biomass continued to increase. Excluding calving and summer range in the eastern Talkeetna Mountains, percentage lichen cover in 1983 was about twice that in 1970 and about the same as that in 1977. Calving and summer range, having a documented history of nearly continuous, heavy caribou use for over 35 years, was characterized by low lichen abundance, a situation which has changed little since range studies were initiated. The core of the winter range, which has been moderately utilized in recent years, was rated fair-to-poor in lichen biomass in 1983. In contrast, many peripheral areas of the Nelchina range that had received little caribou use during the 1970's provided good-to-very good lichen range.

Productivity, survival, and general condition of NCH caribou have been good in recent years, but it is clear that a population of 20,000-30,000 has had a substantial negative effect on the lichen flora--even on moderately utilized seasonal ranges. Lichen standing crops are expected to continue decreasing with either increased or stable herd size. Managers are concerned that even current numbers of caribou have dramatically affected lichens and that only limited areas of lichens in good condition remain within the traditional range of the NCH. A larger herd and the resultant range deterioration could reduce body condition, increase the incidence of disease, reduce productivity and survival, increase the use of less suitable habitats, and/or trigger egress.

While lichens are a highly preferred winter food of caribou, certain herds (e.g., Alaska Peninsula herds) apparently do reasonably well on lichen-poor ranges during much of the year. The NCH has been moderately productive in recent years, despite calving and summer ranges with little lichen biomass. Of course, lichens are not normally considered a preferred summer forage, but rather are important to caribou because they are one of the few highly digestible sources of energy available during winter.

We are facing a dilemma. ADF&G must satisfy the diverse desires of the hunting and nonhunting public while maintaining habitat quality to standards that remain ill-defined. For example, a management strategy aimed at maintaining lichen stands on traditional winter ranges will require a modest herd size, possibly smaller than now exists; but on the other hand, there is considerable public interest in a harvest far greater than current herd size can sustain. Thus, management decisions must strike a balance between satisfying public demands and enhancing the long-term well-being of the NCH.

Most resource users are well aware of the potential benefits associated with a larger NCH population. However, managers must carefully consider the potential adverse consequences of continued herd growth. In general, costs of a management program will increase as herd size increases. Censusing a larger herd will be more difficult and may require a census technique that is more accurate than the direct count-extrapolation procedure currently in use. Assuming that productivity remains at current levels, an annual harvest of about 10% would be required to stabilize the herd. However, a harvest of this magnitude could increase the difficulty of maintaining high-quality hunting experiences. Anticipated problems include crowding, keener hunter competition, a proliferation of all-terrain vehicle (ATV) use and associated habitat damage, and possible overharvest of subherds of caribou and of local moose populations. In addition, multiple bag limits will increase the likelihood of crippling losses. Land owners and managers may become intolerant of increased numbers of hunters and habitat damage caused by ATV use. Winter hunting might also increase. Although winter hunts are attractive to many potential users, they may create additional management problems. Crippling losses may increase, and hunters may tend to concentrate along the road system, posing a safety hazard and inviting criticism from the nonhunting public. Also, winter hunts could increase the likelihood of overharvesting the nearby Mentasta Herd, which often mixes with the NCH during winter in portions of the winter range.

Reaching an appropriate compromise on management of the NCH will require informed input from both wildlife users and professionals. Comments and suggestions are welcome.

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SPRING COMPOSITION AS AN INDEX OF RECRUITMENT IN BARREN-GROUND CARIBOU

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Abstract: In the Northwest Territories, estimates of caribou (Rangifer tarandus) population size are expensive and are obtained only every 2-3 years. The calf:cow ratio in March and April is an index of recruitment that can be obtained every year to help interpret population trends. Although spring calf:cow ratios are commonly calculated for caribou, the biases and sampling errors of the field methods have not been measured.

Our objectives were to: (1) determine the best way to define a sample unit and the best method for estimating the precision of calf:cow ratios, and (2) test for sampling biases by comparing calf:cow ratios based on sample units located arbitrarily with sample units located near radio-collared cows. Calf:cow ratios were calculated based on field classifications of caribou in the Bluenose Herd during March 1986 and 1987. About 30 sample units (n = 29, 1986; n = 31, 1987), which were groups of caribou, were chosen by their association with a radio-collared individual (mostly cows) or were chosen arbitrarily, as is normally done for spring classification counts. Classification was done either from the ground where landing by fixed-wing or helicopter was possible, or directly from the helicopter. Caribou were classified as calves (9 months old), male or female yearlings, adult females, young bulls, or mature bulls. Estimates of calf:cow ratios and their standard deviations were compared using cluster analysis procedures and the jacknife technique (Cochran 1977).

Groups of caribou were classified during the period 7-17 March 1986 and during 3-14 March 1987. In 1986 our estimate of the calf:cow ratio in groups associated with radio-collared cows was significantly lower than

our estimate in groups selected arbitrarily (Table 1). In 1987 the opposite was true.

Table 1. Number of calves/100 cows, Bluenose Herd, 1986 and 1987.

Year	Collared groups Mean	Collared groups SD	Arbitrary groups Mean	Arbitrary groups SD	Analysis
1986	52	2.9	64	4.8	Cluster
	52	3.0	64	4.9	Jacknife
1987	55	4.7	42	3.0	Cluster
	55	4.8	42	3.1	Jacknife

In 1986 we were not able to attribute the difference between estimates to observer bias, or the effects of group size, location, or the proportion of males in the group. In 1987, however, location and percentage of males in the group had a significant effect on the calf:cow ratio.

We concluded that about 30 sample units, where sample units were representative groups of about 100 caribou, provided an acceptable estimate of the mean and standard deviation of the calf:cow ratio. Because the jacknife technique does not require data to be normally distributed, it is more appropriate than cluster analysis. We were unable to fully explain the significant differences between the ratios from the 2 methods of group selection. The radiocollars led us to locations that would not have been sampled by arbitrary group selection. Our data suggest that groups sampled farther from their winter range and groups with fewer bulls had lower calf:cow ratios, probably because some calves stayed behind with the bulls when their mothers began migrating to the calving ground. We recommend, therefore, that spring composition counts be conducted before spring migration begins.

Further data on the timing of the breakdown of the cow-calf bond and the subsequent segregation of calves from cows (particularly male calves), as

well as the calf mortality rate through winter, would assist in interpretation of the calf:cow ratios as indices of recruitment. Data collected from the Bluenose Herd in 1986 and 1987 suggest good calf survival and potential growth for the Bluenose Herd.

Key Words: caribou, *Rangifer*, recruitment, sex and age composition

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STATUS OF THE RAY MOUNTAINS CARIBOU HERD

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Abstract: A resident herd of caribou (*Rangifer tarandus granti*) inhabits the Ray Mountains, located on the north side of the Yukon River between the Alaskan villages of Tanana and Rampart. U.S. Bureau of Land Management personnel conducted 12 aerial surveys of caribou in early winter, late winter, and spring 1983-87. The highest caribou count was 511 obtained in early winter 1987. In spring 1983 and 1984, 22% and 23%, respectively, of the total caribou observed were calves, while in spring 1985-87 only 5-12% of the total were calves. Apparent mortality between birth and 11 months of age for the 1983 and 1984 cohorts was 41% and 56%, respectively. Caribou inhabit 2 distinct areas, one north and the other south of the Tozitna River. Caribou ranged throughout ca. 214,000 ha in spring, but occupied only ca. 20,000 ha in late winter. Two major routes of seasonal movement were identified. Management concerns for the herd are discussed.

Key Words: caribou, minerals, population status, *Rangifer*, Ray Mountains

A small herd (500+) of caribou inhabits the Ray Mountains, located north of the Yukon River between the Alaskan villages of Tanana and Rampart. These caribou were once believed to be part of the much larger Western Arctic Herd (WAH). Between 1950 and 1975, some WAH caribou migrated across the central Brooks Range into the Koyukuk River valley. Caribou were noted in the Ray Mountains during winters 1963-64 and 1973-74. Caribou migration into the Koyukuk River drainage ceased when the WAH declined from 242,000 to 75,000 animals during the early 1970's (Davis and Valkenburg 1978). However, Davis and Valkenburg (1978) did not discount the possible existence of a resident Ray Mountains Herd (RMH). Subsequent investigators located caribou on summer range, winter range, and calving areas in the Ray Mountains, thus confirming presence of a herd (Davis 1978, Farquhar and Schubert 1980, Robinson 1985).

Objectives of this project were to: (1) determine population status and trend of the RMH, and (2) delineate herd distribution, seasonal use areas, and migration routes on land managed by the U.S. Bureau of Land Management (BLM). This information was necessary to determine potential impacts from conflicting land uses. In addition, caribou survey data obtained by BLM personnel could be used by the Alaska Department of Fish and Game (ADF&G) to set hunting seasons and bag limits. This report summarizes data collected on the RMH from April 1983 to October 1987.

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STUDY AREA

The northern boundary of the 596,000-ha study area was set at 66°N latitude, the approximate northern boundary of contiguous land administered by BLM in the vicinity of the Ray Mountains (Fig. 1). The other boundaries were based upon professional judgment of what constitutes caribou habitat in the Ray Mountains. The eastern boundary excluded much of the forested area along the Big Salt and Ray Rivers. The southern boundary was marked by the 300-m contour line along the north bank of the Yukon River. The western boundary was the 300-m contour line east of the Tozitna River and Dagislakhna Creek.

The diverse terrain of the Ray Mountains ranges from 122 m elevation at the Yukon River to 1,682 m atop Mt. Tozi. The southern exposures are relatively steep and dissected by deep canyons, whereas the northern exposures are generally flatter with rounded ridge tops. The Tozitna River, flowing from east to west in a broad valley, separates the mountain range into 2 sections. Vegetative cover includes graminoid tussocks, black spruce (Picea mariana), shrubland, and alpine tundra. In

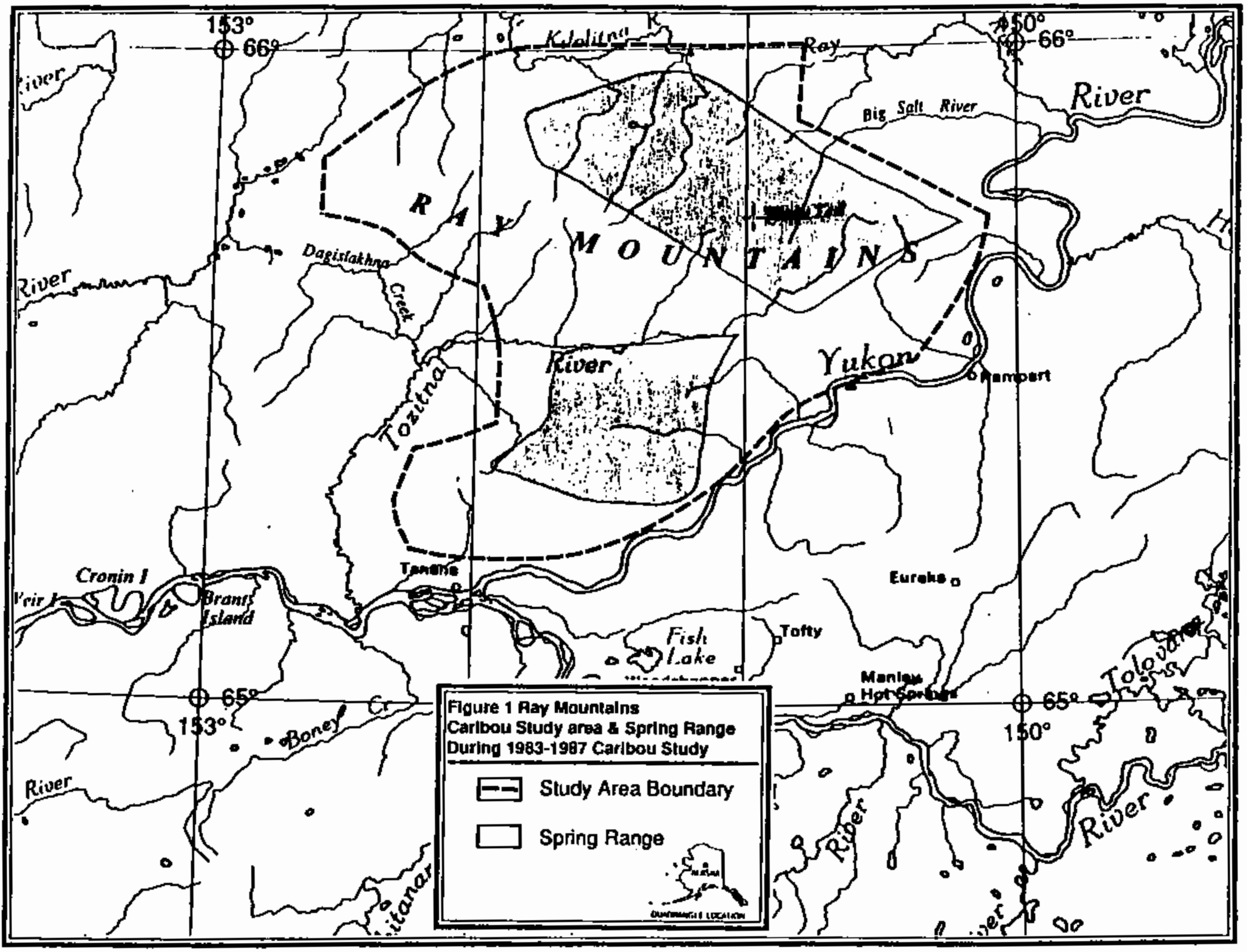

Figure 1 Ray Mountains Caribou Study area & Spring Range During 1983-1987 Caribou Study

addition to caribou, moose (Alces alces), grizzly bears (Ursus arctos), wolves (Canis lupus), various furbearers, rock ptarmigan (Lagopus mutus), and numerous non-game species inhabit the study area. Detailed information on the region can be found in Farquhar and Schubert (1980) and BLM (1986).

METHODS

BLM personnel conducted 12 aerial surveys of caribou in the Ray Mountains between 6 April 1983 and 21 October 1987 (Table 1). Surveys were flown during early winter (Oct-Nov), late winter (Mar-Apr), and spring (May) using either a Piper Super Cub or Cessna 185. A standard 2-day aerial survey was established in May 1984. The survey covered primarily treeless habitat; forested habitat was avoided due to poor sightability of caribou. A typical flight began at an altitude of ca. 1,500 m at cruise airspeed. Once caribou tracks were located, the aircraft descended to ca. 150 m above ground level, speed was reduced, and the tracks were followed until the caribou were observed. Total numbers of caribou, sex and age composition (adults and calves), and locations were recorded and later transferred to a computer database file.

Polygons representing each seasonal use area were mapped manually by connecting the outermost locations of caribou observed. Movement routes were inferred from trails in the snow.

RESULTS AND DISCUSSION

Population Status and Trend

Surveys conducted during early winter were designed to describe rutting distribution and ascertain minimum herd size. The highest caribou count was 511 in 1987 (Table 1), which is comparable to the total of 507 in 1984, but considerably higher than the 400 caribou observed in 1983.

Table 1. Age composition of Alaska's Ray Mountains Caribou Herd, 1983-87.

Season	Total caribou observed	No. of calves	% calves	Survey conditions cloud cover	Survey conditions snow cover
Late winter 1983[a] (Apr 6 and 22)	164	--	--	Clear/fog	50%
Spring 1983[a] (May 19 and 26)	37	8	22	Clear/broken	<20%
Early winter 1983[a] (Nov 1)	400	67	17	Clear	>80%
Late winter 1984[a] (Apr 24)	387	49	13	Clear	50%
Spring 1984[a] (May 21 and 22)	168	38	23	Scattered	20%
Early winter 1984 (Oct 25 and 26)	507	63	12	Clear/fog	>80%
Late winter 1985 (Apr 19 and 21)	323	31	10	Clear	50%
Spring 1985 (May 21 and 22)	98	5	5	Clear	50%
Spring 1986 (May 28 and 29)	76	5	7	Clear	<20%
Early winter 1986[b] (Nov 17)	167	19	11	Scattered	50%
Spring 1987 (May 28 and 29)	69	8	12	Broken	20%
Early winter 1987[b] (Oct 21)	511	54	11	Broken	>80%

[a] Data from Robinson (1985).
[b] Incomplete survey.

The purpose of surveys conducted during the spring calving period was to locate and count newborn calves. In 1983 and 1984, 22% and 23%, respectively, of the total caribou were calves, while from 1985 to 1987 only 5-12% of the total were calves (Table 1). All of these percentages are less than the normal 27-30% reported by Bergerud (1980).

Relative calf abundance in November 1986 was 58% higher than that recorded in May 1986. This is likely attributable in part to sampling error resulting from small sample sizes and segregation; also, some calving may have occurred following the 1986 spring survey. Survey data for the Galena Mountain Herd (located immediately west of the RMH) show a similar pattern: 4% calves in May 1986 vs. 16% calves in October 1986, and 16% calves in May 1987 vs. 19% calves in June.

Among-year variation in the rate of predation during the first few days of life, as documented in other interior Alaska herds, may also have contributed to the variable percentage of calves in spring. Between 1974 and 1983, newborn calves in the Fortymile Caribou Herd suffered 56% mortality during the first 2-3 weeks of life. This mortality rate decreased to 42% between 1984 and 1986, which probably reflected the effects of ADF&G's wolf control program in 1982 and 1983 (Valkenburg and Davis 1987). If the peak of calving had occurred near 21-22 May in the RMH during the 5 study years, predators would have had 1 week to kill calves before the 28-29 May surveys were conducted in 1986 and 1987.

Only in 1983 and 1984 were data sufficient to assess calf survival from birth to late winter (based on changes in calf percentage and not calf:cow ratios). By early winter 1983 and 1984, the loss of calves was 23% and 48%, respectively. By April of the following year, the loss of calves increased to 41% and 56%, respectively. These percentages compare favorably with the average 50% survival to 12 months of age reported by Bergerud (1980).

The present data are insufficient to confidently establish a population trend. However, the total counts in early winter 1984 and 1987 suggest stability. Counts during late winter 1984 and 1985 yielded 13% and 10%

calves, respectively, also suggesting a stable population (Bergerud 1980).

Herd Distribution and Migration Routes

Caribou inhabited 2 distinct areas, 1 north and the other south of the Tozitna River (Figs. 1 and 2). During the calving period, caribou appeared to be most scattered, occupying ca. 214,000 ha (36% of the study area) (Table 2). As caribou gathered for the rut, their distribution decreased to ca. 97,000 ha (16% of the study area). By late winter, observed distribution of caribou was compressed to ca. 20,000 ha (3% of the study area).

Table 2. Size (ha) of seasonal use areas for Alaska's Ray Mountains caribou herd, 1983-87.

Season	North of Tozitna R	South of Tozitna R	Total	% of study area[a]
Spring	130,313	83,773	214,086	36
Early winter	81,345	15,378	96,723	16
Late winter	9,713	10,522	20,235	3

[a] Total size, 595,718 ha.

Two major movement routes were identified (Fig. 3). One route links Kilo Hot Spring with VABM Salt, and the other crosses the Tozitna River, linking the 2 major distribution areas. Several other caribou trails follow ridge tops.

Distribution and movement of caribou in the Ray Mountains do not follow the pattern exhibited by large, migratory herds. Larger herds aggregate annually on traditional calving areas, then disperse to summer and winter ranges (Lent 1964, Skoog 1968). Large aggregations of caribou are better able to detect and avoid predators, but require constant moving to prevent overgrazing of forage (Bergerud 1980). Small, scattered groups can seek isolation from predators while not depleting the available forage supply.

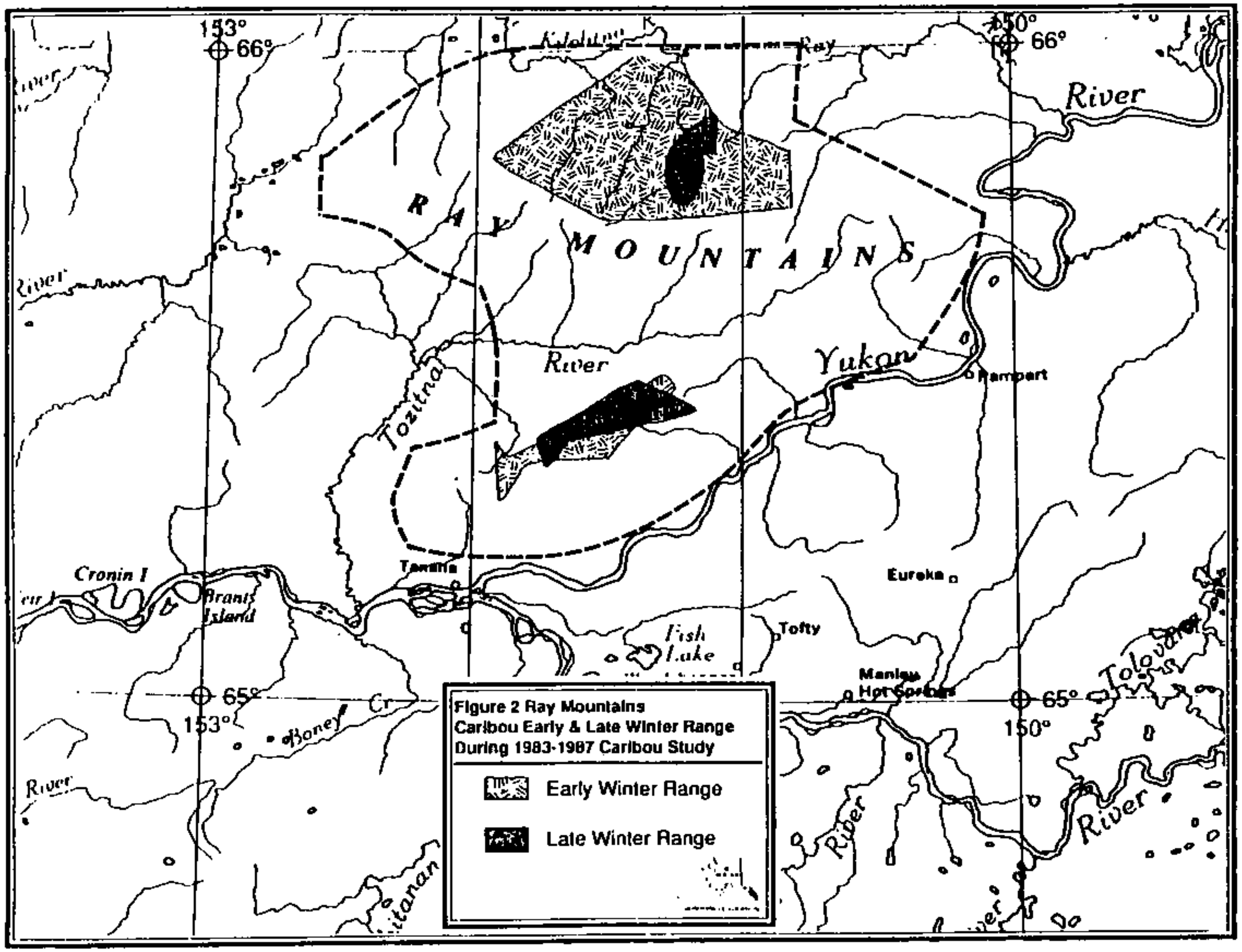

Figure 2 Ray Mountains Caribou Early & Late Winter Range During 1983-1987 Caribou Study

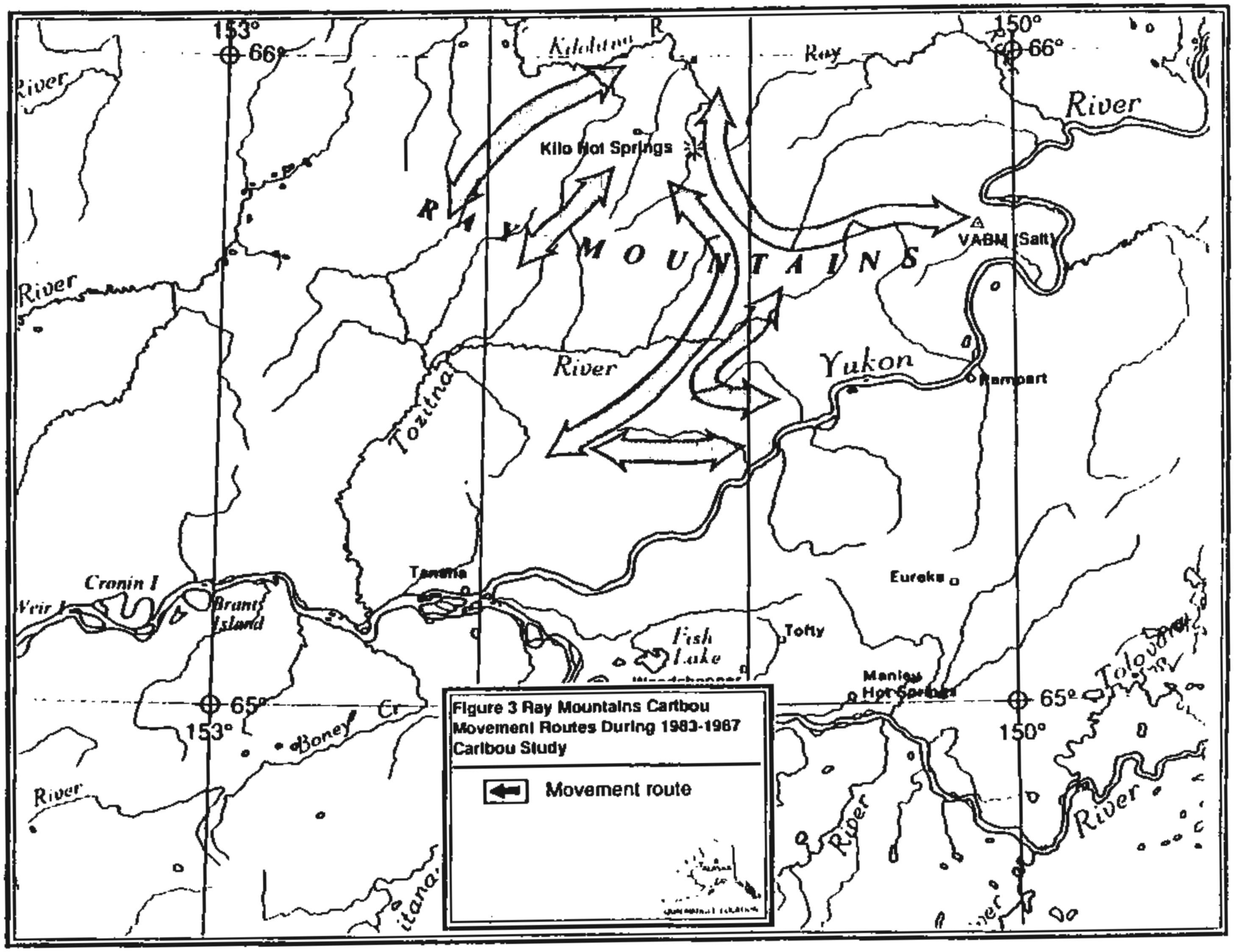

Figure 3 Ray Mountains Caribou Movement Routes During 1983-1987 Caribou Study

MANAGEMENT CONCERNS

Ray Mountains caribou are harvested by subsistence and sport hunters. Based on BLM data, ADF&G recommended that the season of 1 July-30 April, with a bag limit of 5 caribou, be changed to 10 August-30 September with a bag limit of 1 bull. The Alaska Board of Game approved this change in 1984 and also adopted a 1985 recommendation from the Tanana Fish and Game Advisory Council to allow an additional 2-week hunting season in March. Tanana residents hunted caribou in March 1986 and March 1987. Using the Dalton Highway for access, sport hunters take additional caribou each year near Caribou Mountain and Old Man.

Of all the BLM lands in the Central Yukon Planning Area, the Ray Mountains have the best potential for large-scale development of metalliferous minerals. Consequently, BLM's wildlife inventories (Robinson 1985) also included an identification of crucial caribou habitats. The Environmental Impact Statement (EIS) for the Central Yukon Resource Management Plan examined conflicts between caribou and potential development of mineral resources in the Ray Mountains (BLM 1986). The EIS preferred alternative was to open 90% of the caribou habitat to mineral entry and location, and 97% to noncompetitive leasing for oil and gas. All crucial habitats were included in these openings but were designated as Areas of Critical Environmental Concern (ACEC).

When the EIS was written, 741 federal mining claims totaling 5,998 ha were located throughout the Ray Mountains; of these, 680 were located for tungsten but are no longer active. The mineralized zone appears to be suitable caribou habitat, but our observations do not reveal significant use of the area by caribou.

In 1987, the following mining claims, covering 486 ha in the Ray Mountains, were recorded on BLM files: 47 gold, 7 asbestos, 5 chromite, and 1 unknown mineral. Current activity on these claims is exploratory in nature, so no immediate significant impacts on caribou are anticipated.

Coal and geothermal sources are leasable resources present in submarginal quantities. Profitable development would require a substantial price increase for the resources or a major cost-reducing advance in technology.

Kilo Hot Spring lies within the northern distribution area and has been leased for development as a medicinal hot springs. An airport lease application, a homesite, and a trade and manufacturing site are all affiliated with this hot springs lease. Human habitation, however, was not observed there during the caribou survey flights.

In 1986 and 1987, the Alaska Army National Guard applied to BLM for a land use permit in the Ray Mountains. The National Guard wished to conduct troop maneuvers, long- and short-range foot patrols, snow machine patrols, helicopter operations, and bivouac area training on 65,157 ha of land. The selected area covered 45% of the spring range, 84% of early winter range, and 74% of late winter range of the RMH south of the Tozitna River. The application included a request to use blank ammunition, but alluded to future use of live ammunition. A small arms firing range was proposed within the spring range, with a down-range safety zone in the winter range. BLM issued a permit for use of 12,950 ha from 1 October 1987 to 30 September 1988, but prohibited the use of live ammunition and pyrotechnics.

SUMMARY

The RMH resides in the southeastern portion of the greater range of the WAH. It exists as a discrete herd of more than 500 caribou, but the population appears to be stable. Observed distribution of the RMH is confined to 36% of the study area. The current low level of exploration for, and development of, mineral resources in the Ray Mountains does not conflict with the RMH. Authorized use of BLM lands by the Alaska Army National Guard should not cause significant impacts to caribou.

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QUANTIFICATION OF WOODLAND CARIBOU EARLY WINTER HABITAT, SELKIRK MOUNTAINS, BRITISH COLUMBIA

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Abstract: In winter 1986-87, there were 25-30 woodland caribou (*Rangifer tarandus caribou*) in the endangered population inhabiting the Selkirk Mountains in the Pacific Northwest. These caribou ranged primarily in southeastern British Columbia (B.C.) but also frequented northern Idaho and northeastern Washington. In March 1987, 24 woodland caribou from 2 B.C. populations were transplanted to northern Idaho to improve the Selkirk population's chances of long-term survival.

In 1985, the National Ecology Center, U.S. Fish and Wildlife Service, began studying early winter habitat of the Selkirk population, specifically during the period from first snowfall until snow conditions permit/cause caribou to move upslope to forest communities at 1,500 m-1,800 m elevation. Early winter use occurs primarily in mature/old-growth stands of economically important timber in both the Engelmann spruce/subalpine fir (*Picea engelmannii*/*Abies lasiocarpa*) and the western red-cedar/western hemlock (*Thuja plicata*/*Tsuga heterophylla*) communities; the ecotone between the 2 communities is also used extensively. The lower elevation, more densely canopied cedar/hemlock community is particularly important because snow is shallower there, which reduces energy costs to caribou and extends the availability of green vascular forage. In the higher elevation, more open-canopied spruce/fir community, the increased costs of locomotion through deeper snow are apparently offset by increased availability of highly digestible arboreal lichens (*Alectoria* spp./*Bryoria* spp.).

Compared with randomly selected locations, actual caribou use sites had significantly ($\underline{P} < 0.05$) more lichen-bearing, recently windthrown trees;

were at higher elevation; and had lower slope angles, canopy cover, and tree basal area. Arboreal lichen on windthrown trees was apparently important forage because vascular plants were buried by snow.

Because Selkirk caribou use spruce/fir and cedar/hemlock communities extensively during early winter, we recommend that mature old-growth stands of both forest types be maintained. Special considerations should be given to stands on less steep slopes where available arboreal lichen biomass is relatively high and is replenished by trees which are commonly blown down.

Key Words: caribou, early winter habitat, *Rangifer*, Selkirk

SCHAEFER

FIRE AND WOODLAND CARIBOU HABITAT IN SOUTHEASTERN MANITOBA

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Abstract: The effects of fire on the Aikens Lake population of woodland caribou (*Rangifer tarandus caribou*) were studied over a 2-year period. The population had been studied intensively (Stardom 1975, Darby and Pruitt 1984) prior to a 1980 fire which essentially consumed its entire pre-fire range. Appraisal of habitat was the primary objective of this study: quantity, quality, and accessibility of forages were estimated in recently burned (5-year) stands, and compared with those in intermediate (37-year), and old-growth (>90-year) condition. Appraisal measurements were correlated with patterns of habitat utilization by caribou over 2 winters.

Comparative range evaluation was based on a vegetation map depicting 4 strata of upland plant communities. Productivity of forage was determined in each community by harvesting and weighing the current growth of vascular plants and the standing crop of arboreal and terrestrial lichens. Relative quality of forages in summer and winter was inferred from (1) published digestibility studies of *Rangifer*, and (2) the relationship between digestibility and content of acid detergent fiber.

Estimating the relative accessibility of forage consisted of 2 aspects: snow conditions and the density of windfallen trees (deadfalls). Standard snow profiles were obtained over 2 winters to calculate values of the Värriö Snow Index (VSI); straightline transects were established to tally the intersection rate and stacking height of windfallen trees.

Results indicate that burned habitats have undergone a decline in the quality and accessibility of winter forages due to the combustion of

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Cladina lichens, an increase in snow thickness and hardness, and the accumulation of deadfalls. These alterations imply increased energetic costs for caribou to obtain the more scattered and less accessible forage after fire.

Overwintering Aikens caribou exploited the remnant lichen supply, but abandoned their burned range in late winter. Five and one-half years after fire, the population occupied an area entirely exclusive of its pre-fire range and essentially outside the 1980 burn. A synergistic effect of snow accumulation and windfallen trees is implicated. The effects on caribou distribution can be modeled with an evaluative index that combines VSI and deadfall frequency.

In the oldest growth stands (160 years), lichen and vascular plant abundance was diminished. Yet these habitats exhibited the most favorable nival conditions and may be important refuges during late winter.

This study underscores earlier contentions that both short- and long-term effects should be considered when evaluating the impacts of fire on caribou habitat. Taiga range is unsuitable for woodland caribou in its early and intermediate successional stages (up to 50 years following fire); yet periodic fire may be necessary to maintain optimal lichen resources. Moreover, the eventual effects of burning may not be immediately evident. Fires frequently leave unburned or partially burned inclusions which provide some remnant lichen forage, and because deadfalls will not accumulate for a few years, the detrimental effects of fire may not be fully realized for at least 5 years after a burn.

For woodland caribou, abandonment of range appears to be the fundamental adaptation to burning of their taiga habitats; thus, local fire history must be considered in the development of a management strategy. Current knowledge suggests that an average of 4 km^2 of sufficiently mature (>50 years old) winter habitat is required for each woodland caribou. Protection of range from fire may be necessary if alternative, lichen-dominated stands are unavailable.

The author wishes to thank the Canadian Committee of the 4th International Reindeer/Caribou Symposium whose travel grant made possible the presentation of this paper.

Key Words: Aikens Lake Herd, caribou, fire, forage, lichens, range, *Rangifer*, snow

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RECRUITMENT IN THE NELCHINA CARIBOU HERD 1952-70: LIMITATIONS OF THE DATA

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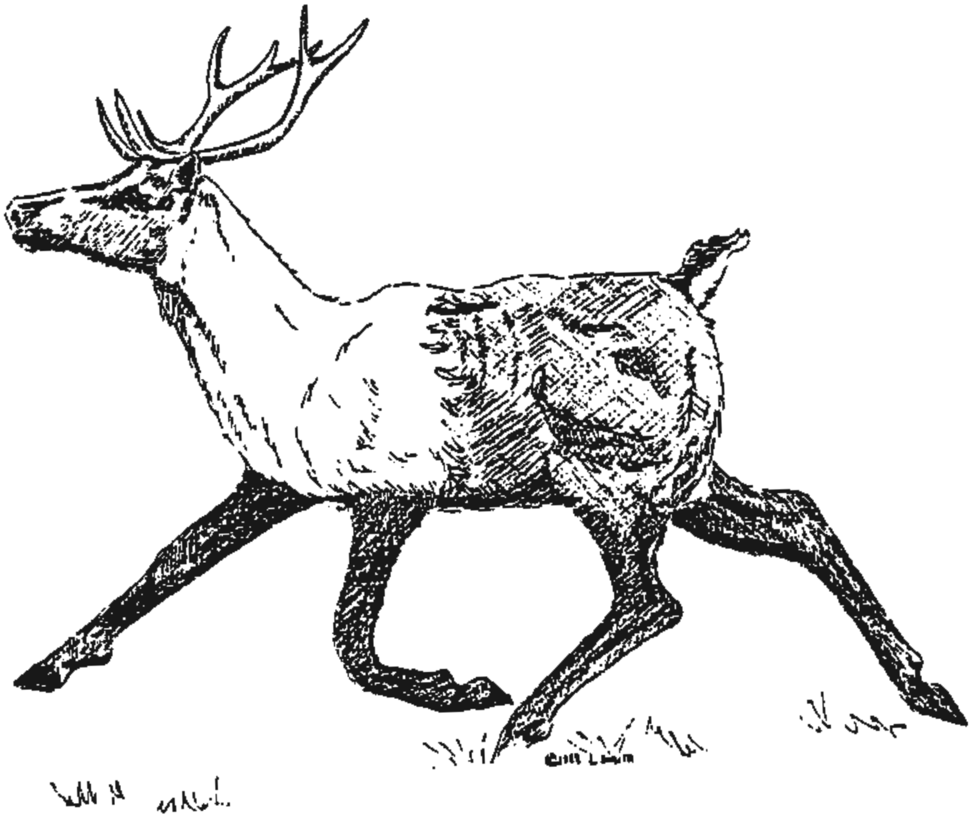
Abstract: A recruitment index for the Nelchina Caribou (*Rangifer tarandus granti*) Herd using the occurrence of 2.5-year-old males and females in the harvest of animals $\geq$2.5 years of age is critically evaluated. During the period 1952 through 1970, when the herd erupted and declined, ages of 3,314 males and 2,262 females killed by hunters were determined. Sample sizes for certain years, for example 1965, the first year of the decline, were small (n = 12 males and 27 females). From 1952 through 1959, when the herd was increasing rapidly, recruitment index trends of males and females were not consistent, nor were they in 1967 through 1970 when the herd was declining. During the entire interval 1952-70, recruitment indices for males and females were not significantly correlated, even when years of small sample sizes were deleted from the analyses. Because sample sizes for males generally exceeded those for females each year, use of an overall recruitment index based on the unweighted total of harvested animals of both sexes is unwarranted. Use of recruitment indices in correlation and regression analyses designed to explain various factors responsible for the increase and decline of the Nelchina Herd is discussed.

Key Words: caribou, Nelchina Herd, *Rangifer*, recruitment indices

PART IV



OTHER SUBJECTS

EFFICACY OF CARFENTANIL CITRATE AND NALOXONE FOR FIELD IMMOBILIZATION OF ALASKAN CARIBOU

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Abstract: Previously, M-99 (used with adjunct tranquilizers and reversed with M50-50) was the drug of choice for field immobilization of caribou (*Rangifer tarandus granti*) in Alaska that required darting from a helicopter. However, M-99 in a concentrated form has never been widely available in the United States, and large-bodied adult caribou could not be efficiently immobilized using the drug in 1 mg/ml concentration.

To overcome this problem, we began using Carfentanil Citrate (with adjunct tranquilizers and reversed with Naloxone), which is more potent than M-99 and available in 3 mg/ml concentration. Carfentanil delivered in 3-ml dart syringes has proven effective for immobilization of adult caribou.

In Denali National Park and Preserve, Alaska, 41 adult (>1 year old) and 11 10-month-old female caribou were immobilized with 3.9-4.5 mg Carfentanil and 5.0 mg Acepromazine. When ambient temperatures were <-20°C, 1 ml propylene glycol was added as antifreeze.

Of the 41 adult caribou, 35 were immobilized with 1 dart of Carfentanil (0.029-0.045 mg/kg body weight); induction time averaged 6.8 minutes. All caribou survived initial immobilization, and 100-150 mg Naloxone/mg Carfentanil was administered. Two animals died within 24 hours following capture, apparently from recycling narcosis. The remaining 6 females required 2 darts for immobilization (total Carfentanil doses, 0.057-0.082 mg/kg body weight). All 6 survived immobilization, and the effects were

reversed with 77-100 mg Naloxone/mg Carfentanil. Two animals died within 24 hours, presumably from recycling narcosis. A second dart was required for 3 of 36 females immobilized in late fall/early winter compared with 3 of 5 captured in late winter.

The 10-month-old females were immobilized with 1 dart of Carfentanil (0.057-0.075 mg/kg body weight); induction time averaged 4.2 minutes. Drug reversal for all was successful with 100 mg Naloxone/mg Carfentanil, and all 11 survived.

Elsewhere in Alaska, adult caribou have been immobilized using similar doses of Carfentanil in combination with Acepromazine and M-99, or with Xylazine. M-99 is marketed in propylene glycol solution which functions as an antifreeze and eliminates the need to dilute the other drugs. Twenty-eight adult females were immobilized with 3.0 mg Carfentanil (estimated mean dose, 0.026 mg/kg body weight), 5.0 mg Acepromazine, and 1.5 mg M-99; induction time averaged 7.0 minutes, and all caribou recovered following injection of 133-150 mg Naloxone/mg Carfentanil. Thirteen other females were immobilized with 4.0 mg Carfentanil (mean dose, 0.036 mg/kg body weight) and 100 mg Xylazine; induction time averaged 8.2 minutes, and these animals were revived with 125 mg Naloxone/mg Carfentanil.

Carfentanil, in these various combinations and doses, has proven effective in immobilizing caribou in Arctic and sub-Arctic Alaska. Known mortalities related to capture and handling have apparently resulted from recycling narcosis, suggesting that the antagonist, Naloxone, is too short-lived to counteract Carfentanil during its active life in the animal. Naloxone has a relatively wide margin of safety, however, and can be used in higher doses until a better antagonist becomes available. Intramuscular, rather than intravenous, injection of the antagonist is recommended.

Key Words: Carfentanil, caribou, immobilization, Naloxone, Rangifer

BODY COMPOSITION OF ADULT FEMALES FROM THE PORCUPINE CARIBOU HERD - A PROGRESS REPORT

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Abstract: A body composition study of female caribou (Rangifer tarandus granti) from the Porcupine Herd commenced March 1987. Objectives of this continuing study are to: (1) develop a technique for monitoring body condition based on indicator bones, muscles, and fat measurements from hunter-killed animals; (2) determine the minimum sample size required to ascertain significant changes in herd condition; (3) determine seasonal, migrational, and reproductive effects on body composition; and (4) evaluate the effects of body composition on female reproductive performance. Adult females are collected 4 times annually in a schedule designed to isolate the effects of summer and winter and of spring and fall migration. Both reproductive and nonreproductive females are collected each season. Indicator muscle (M. gastrocnemius, M. peroneustertius complex) and bone (femur, tibia-fibula, metatarsus) weights are regressed against total and ingesta-free body weight, while indicator muscle protein is regressed against total body protein estimated from Kjeldahl nitrogen. Kidney fat weight; back fat depth; indicator muscle fat content; and marrow fat content from the femur, tibia-fibula, and metatarsus are regressed against total body fat, which is estimated by chloroform-methanol extraction of samples from the carcass, ingesta-free viscera, and hide.

Preliminary results are available for 23 females collected during March, June, and September 1987. Among reproductive females, mean body weight was significantly higher in September (97.6 kg) than in March (87.5 kg) or June (81.7 kg). In contrast to mean body weight, fat deposits were consistently highest in March, even though seasonal differences were generally not statistically significant. In September, lactating females were consistently leaner than nonlactating females, with mean back fat depth equalling 0 and 6 mm, respectively. Similarly, mean femur marrow fat and mean kidney fat were 23% and 18% lower, respectively, in reproductive than nonreproductive females; these differences were not statistically significant, however. Among reproductive females, carcass fat-free dry weight remained relatively constant between March (23.7%) and June (24.7%). Carcass fat varies inversely with carcass water, averaging 11.0% and 65.4%, respectively, in March, and 6.0% and 69.2%, respectively, in June. Strong linear correlations were apparent between body weight and the weight of each indicator muscle and bone. However, correlation coefficients were higher for the regressions for indicator muscles than for indicator bones, and higher for the proximal than for the distal bones. Carcass fat, which ranged from 3% to 15%, was not well correlated with indicator muscle fat, which varied between 2% and 6%. Kidney fat weight was the best single predictor of carcass fat content; however, prediction of carcass fat was considerably improved by the combination of independent variables in multiple regression analysis. Of the variables examined, body weight was by far the strongest determinant of March fetal weight, accounting for 59.5% of the measured variation. The best predictive model for fetal weight suggests that the largest fetuses are produced by females that are characteristically lean in March, with low bone mass but high protein reserves.

This study is funded by the Northern Oil and Gas Action Program of the Department of Indian and Northern Affairs, and Environment Canada. Supplemental support has been provided by the Natural Sciences and Engineering Research Council of Canada, and a University of Alaska Fairbanks Graduate Resource Fellowship. Logistics and field support were given by the U.S. Fish and Wildlife Service (Alaska Fish and Wildlife Research Center and Arctic National Wildlife Refuge), Alaska Department of Fish and Game, Yukon Territory Game Branch, and Northwest Territories Game Branch.

Key Words: body composition, caribou, condition indices, Porcupine Herd, *Rangifer*

WOLF POPULATION FLUCTUATIONS IN THE NELCHINA BASIN OF SOUTHCENTRAL ALASKA: ARE REVISIONS OF PREVIOUS POPULATION ESTIMATES JUSTIFIED?

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Abstract: Between 1953 and 1978, 6 investigators independently estimated wolf (*Canis lupus*) abundance in the Nelchina Basin wolf study area. Their estimates indicated that the population was quite low in 1953 following wolf control. From 1957 until 1968, wolves were protected from legal hunting and trapping, and the population gradually increased, reaching peak numbers in 1965. Published maximum estimates of peak numbers ranged from 400 to 450. The reported rate of population growth from 1953 through 1965 was similar to the average for 7 other North American wolf populations (Keith 1983).

Large-scale illegal hunting apparently reduced the wolf population in 1966 and 1967, but it rebounded and reached a second peak of abundance in 1975 (Ballard et al. 1987). After 1975 increased legal hunting and trapping and wolf control by the State of Alaska caused the population to decline to 2.6 wolves/1,000 km^2 by spring 1982. From 1982 through 1986, the population recovered to 1980-81 levels.

After reevaluating available data, Van Ballenberghe (1981) revised the population estimates for 1953-78 and concluded that wolves did not reach peak numbers until 1975. The population growth rate implicit in Van Ballenberghe's (1981) revised estimates is much lower than that exhibited by other North American wolf populations with access to abundant prey. Based upon his revised wolf population estimates, Van Ballenberghe (1985) then reassessed the historical impact of wolf predation on the Nelchina caribou (*Rangifer tarandus granti*) herd--after also revising herd size estimates. He concluded that wolf predation had

a minor influence on population dynamics of the herd from 1948 through 1982.

Because of controversy about the Nelchina wolf population estimates and their importance in analyzing the population dynamics of the Nelchina Caribou Herd, we reviewed historical wolf census data. Van Ballenberghe (1981) was correct in that the area to which wolf census data were extrapolated varied by year; however, this alone does not justify the magnitude of his revised population estimates. Historical wolf population estimates included no measure of precision, and like current-day wolf censuses, their accuracy was largely a function of the experience and expertise of the individual interpreting the data. Large errors could result if original estimates are revised without original data or the input of the individuals who conducted the surveys. To illustrate the point, we show where Van Ballenberghe misinterpreted data for the 1965 wolf population estimate, an important year for evaluating impacts of wolves on Nelchina caribou. We conclude that, despite imprecision of historical wolf population estimates, the original estimates are better than Van Ballenberghe's revised estimates. Furthermore, the original estimates appear to be more consistent with expected growth rates than the revised estimates.

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COMPATIBILITY BETWEEN RESERVOIR DOWNSTREAM FLOW REGIME AND CARIBOU ECOLOGY IN NORTHERN QUEBEC

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Abstract: The management of downstream flow regimes of hydroelectric reservoirs constitutes a potential source of impact on caribou (*Rangifer tarandus*) but does not represent a driving force in regional caribou ecology. The predicted impact of the Caniapiscau Reservoir on caribou was based on data from the Caniapiscau Herd which, at the time, was very small compared with the George River Herd. In the early 1980's the George River Herd was expanding rapidly, apparently resulting in a merging of the 2 herds and modification of range occupancy. The impact of the Reservoir appears to have been light, as caribou have moved to adjacent areas for calving. No impacts on caribou were anticipated in the downstream portion of the Caniapiscau River because reduced water levels were expected. A sensational event such as the drowning of caribou downstream of a dam promotes speculation as to cause/effect. This paper presents a retrospective analysis of data on the flow regime at the site of the drowning of ca. 10,000 caribou in the Caniapiscau River in 1984. These data show that river sections naturally dangerous to migrating caribou were not necessarily attenuated by the reduced downstream flow from the reservoir. The 3 main conclusions are that: (1) downstream flow management has little effect on caribou ecology, (2) the responsibility for losses of caribou in downstream zones is difficult to determine without an adequate historical data base, and (3) cause/

effect relationships should only be considered after adequate studies are done.

Development of the La Grande Complex was initiated to exploit the hydroelectric potential of a series of Quebec's northern rivers. The project included the construction of 3 generating stations on the La Grande River and the diversion of the Eastmain and Opinaca Rivers to the north and the Caniapiscau River to the west (Fig. 1). Construction of the 10,000-megawatt complex began in 1973 and the last of the 3 generating stations was inaugurated in May 1984.

Impoundments in northern areas represent a potential source of impact to caribou. Although historical data on Quebec's caribou herds are not very comprehensive (Goudreault 1985), population surveys were conducted in the 1960's (DesMeules and Brassard 1963); more intensive studies were performed in the 1970's and 1980's, partly because of the interest in possible impacts of hydroelectric development (Hayeur 1982; Goudreault 1985; Paré and Huot 1985a,b). It was feared that construction of large reservoirs, especially in the Caniapiscau River, could lead to loss of critical terrestrial habitat, higher caribou mortality, or abandonment of the area by caribou. The possible consequences of diverting the lower Caniapiscau River, which flows toward Ungava Bay, were considered by the Caniapiscau-Koksoak Joint Committee. No negative impacts on caribou ecology were predicted to occur in the residual basins of the Caniapiscau and Koksoak Rivers.

When studies of the Caniapiscau Herd were in progress (Paré and Huot 1985b), the George River Herd was increasing rapidly. The accidental drowning of ca. 10,000 caribou in the Caniapiscau River elicited several questions concerning the expanding George River Herd. It also led to a reassessment of caribou habitat utilization and distribution within northern Québec and promoted an intensification of research on northern vertebrates, especially caribou.

The objective of this paper is to review the impacts of the Caniapiscau Reservoir on caribou. The evaluation focuses on the massive drowning of

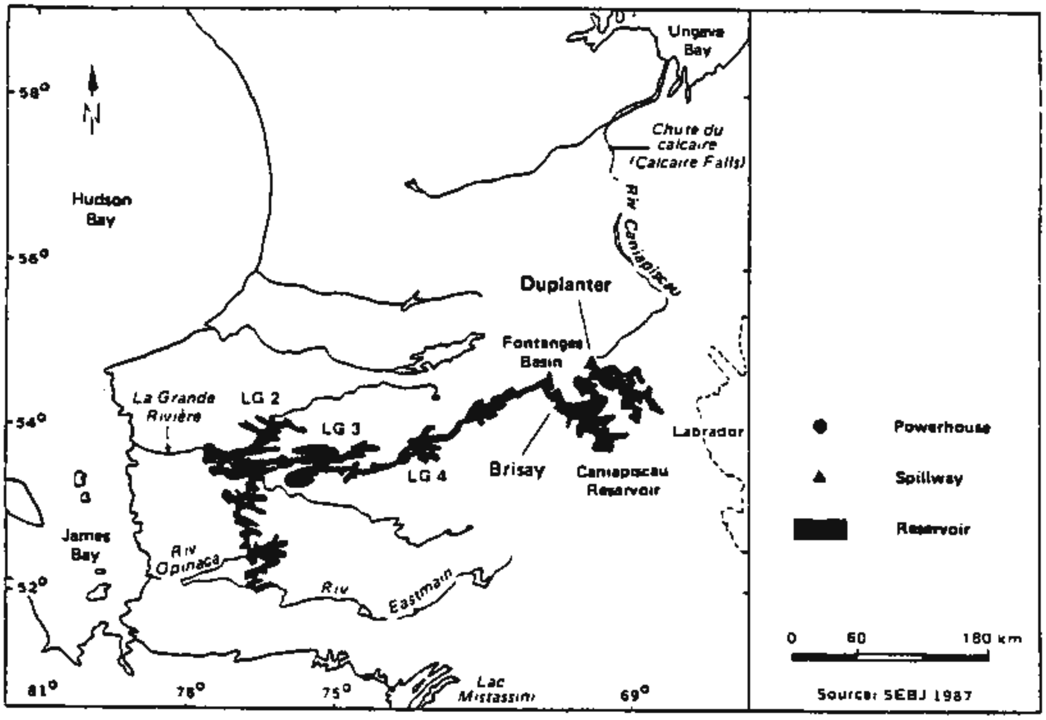


Fig. 1. The La Grande Complex.

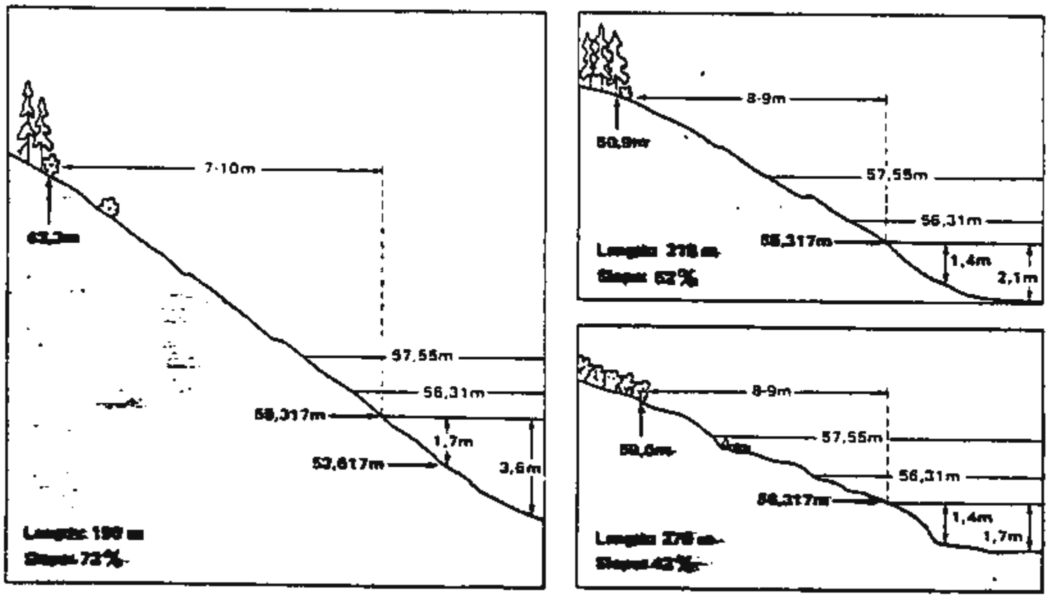


Fig. 2. Profiles of the rock facade on representative sections of the east shore of the main island.

caribou downstream of a retention dam and demonstrates that natural phenomena, rather than reservoir management, may have been responsible. The discussion also addresses the compatibility between reservoir operation and caribou ecology.

CANIAPISCAU RESERVOIR

The Caniapiscau River, which flows north to the Koksoak River, was cut off at Duplanter to create the 4,273 km^2 Caniapiscau Reservoir, located some 600 km upstream from Ungava Bay (Fig. 1). The lower Caniapiscau Basin still receives inflow from its tributaries, but the flow from the upper watershed has been reduced by an average of 776 m^3/sec.

The Caniapiscau Reservoir serves 2 functions: (1) it raises the water level to enable the flow to proceed southwest toward the La Grande River, and (2) its large volume is used to regulate the La Grande complex interannual flow via the Brisay Spillway at the west end of the Reservoir. At the north end of the Reservoir is the Duplanter Dam Spillway, a head structure with a maximum flow capacity of 3,340 m^3/sec. It is located in a remote area; the structures and operating mechanisms are not heated and the site has no electricity. This spillway was designed to be used only under exceptional circumstances and can be opened only according to an established protocol which includes the following 3 conditions: (1) downstream inhabitants must be notified, (2) gates must be opened slowly, and (3) the flow must not exceed the natural capacity of the river. From 1979 to 1985, the La Grande Complex was in a transitory phase of reservoir filling and testing, including testing of the operating structures. The Caniapiscau Reservoir was filled between October 1981 and June 1984. The Duplanter Spillway remained open between 4 June and 31 October 1984, due to technical and environmental constraints (Société d' énergie de la Baie James [SEBJ] 1984).

CARIBOU POPULATION

When development of the La Grande Complex was initiated in the early 1970's the Caniapiscau Herd numbered approximately 600 individuals (Audet

1979). The Caniapiscau Herd does not aggregate for migration, as do many northern herds, and caribou usually travel alone or in small groups. From 1981 to 1985, caribou from the north gradually invaded the area; the total winter population in 1984 was estimated at 13,000 individuals (Paré and Huot 1985a,b).

During the same period, the George River Herd was growing rapidly, and its distribution increased from an average of 160,000 km^2 during 1971 through 1975 to 442,000 km^2 for the period between 1981 and 1984. The 1984 population was estimated at 600,000, representing a mean annual increase of 14% between 1955 and 1982. The expanding George River Herd overlapped with the Caniapiscau Herd in winter, and it became difficult to differentiate between the 2 herds and monitor the movements of individuals from the Caniapiscau Herd (Paré and Huot 1985a).

IMPACT

The predicted impact of the Caniapiscau Reservoir itself on caribou was based on available data, principally the studies of Banfield and Tener (1958). Overall, the historical data base for the population was very limited, but at the time the Caniapiscau Herd was relatively small and did not form large migratory groups. The main anticipated impact of the project was flooding of the calving grounds, but the impact was mitigated somewhat naturally, as calving females moved to available areas on the periphery of the Reservoir. Those movements were facilitated by ice on the Reservoir. No major impacts were predicted on caribou downstream of the Reservoir because of the resultant reduced flow. It is probable that the Caniapiscau Herd was affected much more by the ingress of the George River Herd than by the creation of the Caniapiscau Reservoir (Paré and Huot 1985a, Nault and Le Henaff 1987).

The drowning of numerous caribou in the Caniapiscau River downstream of the Reservoir sent shock waves through conservation circles and fueled speculation concerning: (1) the impact of reservoir operation and (2) the effect of the loss of a large number of caribou on the overall population. A review of the drowning event follows. On or about

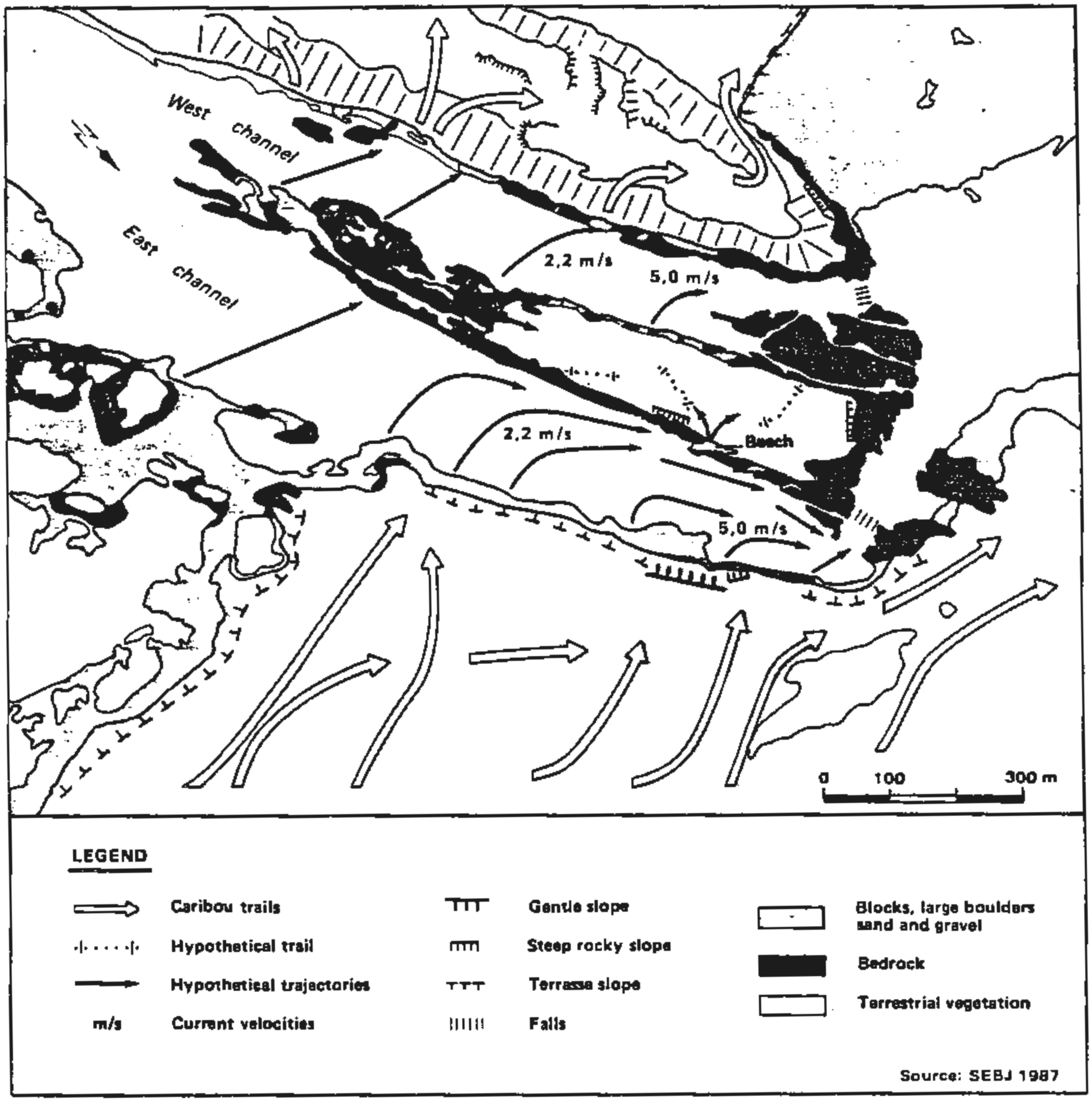
30 September 1984, ca. 10,000 migrating caribou drowned in the Caniapiscau River at Calcaire Falls, located 400 km below Duplanter Dam (Fig. 1). This occurred after a period of heavy precipitation in the watershed at a time when the upstream spillway was partially open. Because of the latter, operation of the Reservoir was suspected to be responsible for the hydrological conditions which led to the drownings.

The massive drowning made national and international news, and several public organizations and various articles alleged a cause/effect relationship between the drownings and operation of the Caniapiscau Reservoir. These allegations are difficult to refute or support without adequate data. Any valid analysis of the event requires consideration of more variables than the simple presence of a reservoir and a partially open spillway upstream from the drowning site.

To assess the hydrological conditions that prevailed during the event, studies were done by the SEBJ (1984) to compare the hydrological characteristics of the drowning site with natural conditions and the influence of Reservoir operation immediately prior to the drownings. Another study provided a detailed description of the physical features of Calcaire Falls and immediate upstream morphometry (Fig. 2) (Boudreault 1987). A detailed discussion of the probable causes of the drowning is available in a report prepared by SEBJ (1987). The main conclusions of that study are presented in this paper.

What Happened?

No one witnessed the drownings, and the circumstances can only be surmised from observations made thereafter or estimated from hydrological data. Observations of caribou trails immediately after the drownings (Ministère du Loisir, de la Chasse et de la Pêche [MLCP] 1985) and an analysis of aerial photographs taken on 27 August 1985 indicate that a number of caribou had entered the river at the head of Calcaire Falls from the east bank. Three of the trails were within 300 m upstream of the Falls, and 7 were ca. 500 m upstream; 3 additional trails were located farther upstream (Fig. 3).



Source: SEBJ 1987

Fig. 3. General features, current velocities, and hypothetical trajectories followed by caribou to enter the falls.

Evidently, caribou entering the river within 400 or 500 m upstream from the Falls were entrained by the current which averaged 2.2 m/sec, 2.5 m/sec at the surface (Fig. 3). Conceivably, the first caribou entering the river were followed by the rest of the group in a mass movement, being unaware of the dangerous current and the proximity of a 22-m falls. Thus, it appears that the majority of caribou attempting to cross the Caniapiscau River immediately upstream of Calcaire Falls perished in the east channel (SEBJ 1984).

Calcaire Falls constitutes a risky situation for crossing caribou. The upstream section consists of 3 channels separated by 2 islands. Most of the eastern shore of the main island is inaccessible under any flow conditions due to deep water and rock facades with 42-72% inclines (Fig. 2). The downstream section of the island is accessible by a small beach, but it is located in an area where current velocities exceed 4 m/sec (Fig. 3). The west bank of the Caniapiscau River appears to be accessible at several points under most flow conditions.

To summarize, the majority of caribou which entered the river on the east bank above Calcaire Falls in late September 1984 probably drowned in the east channel of the falls. The current velocity at that time, the disorderly crossings by large numbers of caribou, and especially the general inaccessibility of the east shore of the main island support this hypothesis. Observations of tracks indicate that a few caribou reached the island before crossing the remainder of the river (west channel), but no tracks were found on the west bank of the Caniapiscau River, indicating that few, if any, caribou had made the entire crossing (MLCP 1985).

Water levels and current velocities were determined by a hydrology study (SEBJ 1984) and from measurements taken on 2 August 1985. The data indicate that the 3,145 m^3/sec flow on 30 September 1984 produced a 5.0 m/sec current velocity at a point 100 m above the falls, 2.2 m/sec at at point 500 m upstream, and 1.1 m/sec at a point 3.1 km upstream. The data also show that, in a zone of critical current velocity, a change of flow does not significantly change the velocity. Thus, even a substantial change in flow would have only changed the current velocity from

5 m/sec to 4 m/sec immediately above the Falls. This raises 2 important points: (1) without the Caniapiscau Reservoir, flow conditions would have been ca. 3,500 m^3/sec, which is 12% higher than that calculated with the Reservoir in place (Table 1); and (2) in the critical section near the Falls, the flow would have been similar to that without the reservoir, while upstream the flow would have increased by up to 10%. Without an upstream spillway, conditions would have been worse, as the flow would have been augmented by approximately 12%, causing a slight increase in current velocity (Table 1).

Table 1. Representative water levels and flows at the Calcaire Falls.

Flow (m^3/sec)	Level (m)	Conditions (date)
635	55.04	Minimum level (Sep 1984)
1,140	55.32	Measured level (2 Aug 1985)
1,670	56.31	If spillway closed (30 Sep 1984)
3,145	57.55	Estimated level (30 Sep 1984)
3,500	57.80	Without the reservoir (30 Sep 1984)

It is estimated that closing the spillway at Duplanter would have had an insignificant influence on the outcome. The majority of drownings took place in the east channel; reducing the flow and lowering the level by 1.2 m would not have improved access to the island because the current velocity would not have been reduced significantly and the rock facades would have presented essentially the same constraints (Fig. 2). Crossings of the west channel, however, would have been facilitated by a reduction in current velocity in the upstream section, and access to the western shore would have been easier. If the Spillway had been closed, it is possible that the number of drownings would have declined slightly. However, for a large group of caribou negotiating the falls, the constraints associated with crossing the east channel would have been essentially the same whether or not the Spillway had been open.

CONCLUSION

The Caniapiscau Reservoir had little impact on the caribou population, and individual caribou seemed to adjust well to the new conditions. The drowning of caribou was not considered a major issue in the impact analysis. Closing the spillway would not have significantly reduced the dangers presented by some downstream sites to crossing caribou. Even a specific management effort to integrate the reservoir system with caribou movements would not eliminate those naturally dangerous sites. A total of at least 686 caribou have drowned at such sites between 1978 and 1983 (MLCP 1985). Analysis of the event at Calcaire Falls has shown that the site remains very dangerous for crossing caribou and cannot be improved by adopting different reservoir operating procedures.

On 30 September 1984, the downstream flow was well below the natural seasonal average, and closing the spillway gate at Duplanter would not have modified hydrological conditions significantly. However, an important drowning draws attention to the presence of hydroelectric production facilities and related structures, and there is a tendency to conclude a cause/effect relationship. News media, wildlife management agencies, and nature conservation groups are all under public pressure to explain such an accident. It is of utmost importance that such events be analyzed and explained in terms of available data and that care be taken not to draw premature conclusions as to cause/effect. The latter position puts the reservoir operator on the defensive, and it may take several months or years to clarify the situation retrospectively. Also, one must not forget that the true cause of such an event may never be clearly demonstrated.

Events such as drownings should be viewed from an ecological perspective and analyzed with proper data such as caribou movements, river hydrology, and site geomorphology. The data base should also include population trends and records of past drownings. Otherwise, it is unreasonable to offer cause/effect explanations. Finally, it is notable that early fears of an impact of the drownings on the overall caribou population have been shown to be largely unfounded (Struzik 1987).

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SEASONAL MOVEMENTS AND ACTIVITY OF THE PORCUPINE AND CENTRAL ARCTIC HERDS DETERMINED BY SATELLITE TELEMETRY

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Abstract: Daily movements and activities of up to 21 caribou (*Rangifer tarandus granti*) from the Porcupine and Central Arctic Herds were monitored by satellite telemetry from April 1985 through August 1987. Caribou from the 2 herds followed similar seasonal patterns. Mean daily distances traveled each year were greatest (up to 26 km/d) in July and lowest (4-6 km/d) in February. Extensive movements by some individuals continued into November, but between December and March only minor shifts in distribution occurred. Individuals monitored daily for 29 months displayed little fidelity to specific wintering areas, migration corridors, or calving sites. Short-term (1-min) and long-term (24-hr) activity sensors were used to monitor caribou activity patterns. The short-term index accurately differentiated among lying, feeding, walking, and running activities of captive caribou. However, we suspect that activity budgets calibrated from captive animals underestimated feeding time and overestimated lying time of wild caribou. For both herds, the seasonal pattern determined from long-term sensor data followed that of daily distances traveled. The long-term activity index appears to be useful for determining the calving date of satellite-collared cows. Analyses are ongoing to identify apparent biases in the short-term activity sensor data.

Key Words: activity, caribou, movements, *Rangifer*, satellite, telemetry

A MODEL OF THE ENERGY REQUIRED BY CARIBOU TO DIG A FEEDING CRATER

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Abstract: A theoretical model of the mechanical energy expended by caribou (Rangifer tarandus) while excavating a feeding crater is being developed to help quantify the effect of snow on forage availability. Model input variables are snow depth, density, and hardness; crater area; and angle of repose. Model output is mechanical energy per unit crater area (kJ/m^2). Mechanical energy required to dig a crater is conceptualized as consisting of 3 components: (1) energy required to penetrate the snow with the hoof and break it into moveable pieces, (2) energy required to plow the snow to the back of the crater, and (3) energy required to lift the snow from the crater. Estimates of metabolic energy expended per unit crater area were derived using data from other studies and plotted against model predictions of mechanical energy. The relationship between metabolic and mechanical energy was roughly linear and indicates a 20-25% efficiency in converting metabolic to mechanical energy. Thus, an estimate of metabolic energy per unit crater area can be derived from the model output and compared with the metabolizable energy available from the forage. Preliminary predictions of the model follow. First, angle of repose greatly influences crater volume and therefore energy expenditure, although the effect diminishes with increasing crater area. Under certain situations (e.g., deep snow, small crater area), soft granular snow with a low angle of repose may present a greater impediment than hard snow, which does not slough into the crater. Second, even under adverse snow conditions, the energy cost of digging a crater is low compared with the metabolizable energy available from the forage present on all but the most unproductive or heavily grazed ranges. However, the foraging time lost while cratering may be more important than the increase in energy expenditure associated with cratering itself.

Key Words: activity budgets, caribou, energetics, modeling, Rangifer, snow

AUDITORY AND VISUAL STIMULATION OF HEART RATE AND OXYGEN CONSUMPTION OF CARIBOU

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Abstract: Reaction of caribou (Rangifer tarandus) to harassment is usually assessed in terms of a behavioral response to certain stimuli. However, it is unknown if caribou react to natural and human-induced disturbance by increasing heart rate (HR) and energy expenditure (EE) without displaying overt (behavioral) responses. In this study we examined HR, as a measure of oxygen consumption (OC), of 2 adult females confined in a headstall respirometer during auditory and visual stimulation that elicited no overt behavioral responses. A method of correcting for distortion of the temporal OC curve, caused by gas dilution in the headstall, was developed and evaluated. Comparison of HR with corrected OC showed that both increased following stimulation. The HR and OC responses varied considerably, and the oxygen pulse (OC/HR) was not constant throughout a given response. Also, judging from the HR response pattern to certain stimuli for both animals, habituation or sensitization occurred between sets of trials. Although HR was found to be a poor measure of EE during alert reactions, we concluded that it could be used as an indicator of a non-behavioral reaction to a stimulus. Peak response in OC was equivalent to a caribou walking at approximately 4 km/h. The duration of each response was short, however, and the net cost of each single non-physical response was estimated at 1.0-4.5 ml of oxygen, equivalent to moving the body mass of the caribou 0.8-3.8 m.

This work was supported by internal funding of the Large Animal Research Station and funding from the Institute of Arctic Biology, University of Alaska Fairbanks.

Key Words: auditory stimulation, caribou, energy expenditure, habituation, harassment, heart rate, oxygen consumption, *Rangifer*, visual stimulation

PHILOSOPHICAL AND ETHICAL CONCERNS IN CARIBOU RESEARCH AND MANAGEMENT

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Abstract: The increased focus of human activities in the North associated with petroleum and mining exploration and development, tourism, and expanding transportation routes, and the changing administrative jurisdiction over wildlife resulting from resolution of native entitlements, raise philosophical and ethical questions for caribou (*Rangifer tarandus*) biologists. Professional commitment to the welfare of the wildlife resource in the interest of society may at times diverge from the goals of employing agencies or industry. The complexity of caribou ecology, in contrast to other North American ungulates, has been a handicap to our increased understanding of the species and has led to the formulation of hypotheses that are particularly difficult or not possible to test. As a consequence, caribou biologists may be drawn into controversies. Caribou biologists must walk a fine line between wildlife professionalism and the politics of resource management. The ethical guidelines for the profession published by The Wildlife Society remain relevant for those involved in caribou research and management.

Key Words: caribou, ethics, management, philosophy, professionalism, *Rangifer*, research

Is it appropriate for wildlife professionals to be discussing ethics at a workshop on caribou (*Rangifer tarandus*) research and management? Opinions may differ in response to this question. Nevertheless, professional ethics are often at issue when controversy exists between professionals, and this is particularly true when the public becomes involved. Public involvement is part of wildlife management, it is part of the political process in our democratic system, but when biological questions become politicized, pressures are generated that may challenge the professionalism of wildlifers. We must walk a fine line between wildlife professionalism and the politics of resource management.

Biologists often must decide between loyalty to an employer and their own professional integrity. Ethical guidelines do exist in our profession, and responsibility as wildlife professionals goes beyond loyalty to employers. The Wildlife Society has recognized the underlying ethical principles that provide the foundation for our profession in their published Objectives and Code of Ethics (MacDonald 1987). The objectives provide general ethical guidelines:

1. To develop and promote sound stewardship of wildlife resources and of the environments upon which wildlife and humans depend;
2. To undertake an active role in preventing human-induced environmental degradation;
3. To increase awareness and appreciation of wildlife values; and
4. To seek the highest standards in all activities of the wildlife profession.

The Code of Ethics of The Wildlife Society includes explicit ethical criteria: "Each member, in striving to meet the objectives of The Society, pledges to: Subscribe to the highest standards of integrity and conduct. Recognize research and scientific management of wildlife and their environments as primary goals.... Encourage the use of sound biological information in management decisions."

Gilbert and Dodds (1987), in their recent book, provide thoughtful discussion of the ethical responsibilities of wildlifers. They stress that wildlife researchers, to justify their activities as scientists, must adhere to the scientific method. Research design must be rigorous and based on testable hypotheses. If we make generalizations based on inadequate data, we should be aware that we may be setting ourselves up, as well as the wildlife profession in general, for loss of credibility in the future. Gilbert and Dodds point out that where our data are not adequate to yield statistically reliable results, the error that may be involved in management decisions based on these results should seek to benefit wildlife populations and not the short-term interests of the using public. If we must err, it should be on the side of wildlife conservation.

It is often in the assessment of environmental impacts that controversies develop that may pit biologist against biologist, thus threatening their credibility in the eyes of the public. Such controversies may tempt biologists to extrapolate beyond the limits of the available data solely for the sake of tilting the argument in their own favor. This is clearly a violation of professional ethics.

Environmental impact assessments (EIA's) and environmental impact statements (EIS's) engender different perspectives among the participants in their development, according to Gilbert and Dodds. They point out that those working for consulting firms view EIA's and EIS's as the opportunity to practice good science in a politically motivated way. The proponents of development view EIA's and EIS's as legally necessary but justifying only the minimal effort and cost necessary to gain acceptance for the project. Often the high public profile of the project results in EIA's and EIS's assuming a public relations role. If political options are available, it may be more expedient to invest in lobbying efforts to assure that critical questions about the project are not asked rather than to invest in the research to respond to the questions. Finally, research scientists in governmental agencies and within universities often shy away from EIA work because they believe the time constraints and the associated politics preclude the conduct of acceptable science.

It is apparent that wildlifers view the world in which they live and work with biases that parallel those of the general public. Kellert (1979) has done extensive surveys of public attitudes toward wildlife and shows their relationship to childhood experiences that are often culturally related, as well as to social and economic associations. Attitudes toward wildlife are negative if past associations have been negative, as in the case of the farmer who experiences crop damage by wildlife. Conversely, positive associations, such as hunting and recreational viewing of wildlife, yield favorable attitudes toward wildlife. Wildlife biologists, however, should have positive attitudes or biases toward wildlife, exclusive of childhood experiences, because wildlife is the very basis of their profession, employment, and economic well being. We cannot deny our humanness, nor should we, and a bias favoring wildlife should guide management decisions, but bias should not carry over into our research design and execution.

As a corollary to the suspected bias of wildlifers, does it follow that those associated with industry have a negative view of wildlife if they perceive wildlife to be an obstruction to their profit-making or a threat to their economic security? Are wildlife biologists who work for industry suspect? The answer is yes, if our logic remains consistent. But just as wildlifers working for wildlife management agencies should be able to be objective in their research and assessment of data, so should industry biologists be able to be objective scientists. They can remain ethical as long as the biases of industry do not influence their ability to be objective in their work.

Why does caribou ecology generate so much controversy? Controversy certainly colors our professional meetings; it enters the technical literature, and it provides fuel for our detractors. The complexity of the ecological relationships of caribou must be a major factor contributing to controversy. In contrast to other North American cervids, caribou appear to provide a greater number of obstacles in our efforts to understand them. Because of their migratory habits, their annual cycle spans 2 or more ecosystems. They are preyed upon by quite discrete populations of predators on their summer versus their winter ranges. Important predator species may also vary seasonally and regionally. Their complex sociality, with hierarchial structures changing seasonally in relation to antler growth and retention in both sexes, sets them apart from other cervids. Harassing and parasitic insects have an important influence on their behavior, movements, physiological status, and demography and have been an important selective factor in their evolution. Caribou exhibit long established traditions of movement and range fidelity that may, nevertheless, show annual variations related to weather or perhaps other environmental variables. Their winter food supply is often snow covered, and its availability is complicated by snow characteristics and the energy cost of digging through the snow to obtain it. Lichens, an important winter food item of caribou, are in themselves a unique association of fungi and blue-green algae that behave quite differently than vascular plants, are relatively indigestible to most other herbivores, and are little understood ecologically and physiologically. Winter ecology of caribou remains only superficially understood. Considerable variation in food and habitat selection, predator relationships, and general ecology has been shown to exist in caribou from the woodland populations (R. t. caribou) at the southern limits of distribution to Peary caribou (R. t. pearyi) in the North. These variations invariably make broad generalizations about the species vulnerable to criticism. In spite of the considerable effort that has been devoted to the study of caribou throughout circumpolar regions, there remain more unanswered questions about the ecology of caribou than for other North American ungulates.

The complexity of caribou ecology encourages the postulation of hypotheses that are, in many cases, either untestable or very difficult to test. New technological developments, such as satellite radiocollars, offer the potential for overcoming past limitations in research design to test complex hypotheses dealing with energetics, migration, body condition, predation, and insect avoidance. Up to now, however, the complexity of caribou ecology and the variation that the species exhibits throughout its circumpolar distribution have challenged the ingenuity of those who have chosen to study caribou, as well as fueling the controversy that surrounds the species.

Controversy can be healthy. It focuses attention on issues that merit our attention. It stimulates thought and generates ideas. Controversy that has revolved around caribou has generated research efforts that have increased our factual knowledge of caribou ecology, thus helping to resolve the controversy. Witness, for example, our increased appreciation of the roles of bears and eagles as predators of calf caribou as a consequence of intensive studies of causes of early mortality in caribou.

Controversy can also be detrimental. When wildlife professionals become involved in heated debate amongst themselves over issues where they claim expertise, their credibility may be eroded in the eyes of the public. The confidence of the public in the ability of wildlife professionals to manage the resources for which they have been granted responsibility may be lost. Controversy may also lead to polarization of thought among those involved. Among scientists there are all too numerous examples of individuals who have doggedly championed a controversial hypothesis to the extent that concern for their self-image overrides scientific objectivity. The challenge to these individuals is seemingly to fortify their position through their research and publications. Their research then becomes suspect, and with each succeeding publication defending their earlier published conclusions they find themselves further entrenched, with little likelihood of extraction. Professional ethics become subverted in the interest of egotism, and the whole profession suffers. No matter how important an issue of the day may appear at the time, there will be stands on future issues of equal or greater importance that will be difficult to defend in the public eye if we have sacrificed our professionalism on a past issue.

Controversy that develops over conflicts between resource uses may pit wildlifers against one another if their employers represent the uses in conflict. How should we handle situations that challenge our professional ethics? How should we respond to a request from an employer to build a case that exceeds the supporting data? Do we have any recourse when employers shut down our research efforts because the preliminary findings are inimical to their interests? If an employer "pigeon holes" our research results that are particularly relevant to an issue at hand, do we have any recourse? When is it legitimate for a public agency to withhold information from the public? Is it ethical to distort the truth in the presumed interest of society?

These are the kinds of questions that at times confront us as wildlifers. And the answers may not always be obvious. Ecological relationships are complex, and particularly so in the case of caribou. Ecology is not as exact as most other scientific disciplines, and public perception of ecological relationships is often laced with emotion. But these should not be excuses for our failure to abide by a rigorous code of professional ethics. If we wish to be perceived as scientists among our colleagues, as well as by the public, we must behave accordingly, no matter how complex the field of ecology may be nor how much emotion it engenders.

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CARIBOU BEHAVIOR AND MOVEMENTS IN THE KUPARUK OILFIELD: IMPLICATIONS FOR ENERGETIC AND IMPACT ANALYSES

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Abstract: The results of 2 published papers (Curatolo and Murphy 1986, Murphy and Curatolo 1987) on the responses of caribou (*Rangifer tarandus granti*) to oilfield development are reviewed and discussed in terms of insect harassment, disturbance, and energy balance. Elevated pipelines that closely paralleled roads with traffic had the greatest effects on caribou crossing success, activity budgets, and rates of movement; pipelines without associated traffic and roads without associated pipelines had significantly less pronounced effects. Both insect harassment and oilfield disturbance influenced caribou activity budgets by decreasing time spent lying and by increasing time spent moving; however, time spent feeding was affected by insect harassment but not by oilfield disturbance. These results are interpreted using an energetics model developed recently (Fancy 1986). An example of delineating reactive zones is presented as a possible means of refining impact assessments and predictions. Topics for future research programs are identified, and the role of biologists in formulating impact predictions and policy for caribou in oilfields is discussed.

Key Words: caribou, energetics, impact analysis, insect harassment, movements, oil development, *Rangifer*.

When questions regarding the possible effects of oil development on Central Arctic Herd (CAH) caribou (*Rangifer tarandus granti*) first arose nearly 20 years ago, there were few if any quantitative data for predicting impacts and formulating mitigation practices. Several attempts had been made to acquire an understanding of what happens when caribou encounter linear structures (e.g., Child 1974), but in the final analysis, informed opinion was what guided management decisions. At present, there is a good data base on the population status and movement patterns of the CAH, but considerable disagreement remains regarding impact assessment. Quantifying the energy costs that caribou incur as a result of interactions with oil development is among the most pressing and relevant problems regarding impact assessment for the CAH. By studying the behavioral reactions of caribou to oilfield disturbance and the energetic consequences of these reactions, a quantitative data base can be developed from which impact predictions can be formulated. This paper reviews 2 recent publications (Curatolo and Murphy 1986, Murphy and Curatolo 1987) on the effects of pipelines and roads on the movements and behavior of CAH caribou, and then discusses the energetic implications of altered movement patterns and activity budgets.

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METHODS

During summers 1981 and 1982, we recorded pipeline and road crossing success, activity budgets, and rates of movement of caribou moving through 5 study sites in an area located between the Prudhoe Bay and Kuparuk oilfields (Fig. 1). This area included sites where the frequently traveled Spine Road closely paralleled the elevated Kuparuk Pipeline (1.6-m minimum height) and sites where the Spine Road was separated from the pipeline by over 1.6 km. The "Pipe-Road Site" was situated where the pipeline accompanied the road, with traffic moving through at an average of 1 vehicle every 4 minutes; the "Pipe Site" was located where there was a pipeline and road, but virtually no traffic; and the "River-Road Site" included a road with traffic and no pipeline (crossing success data only). There also were 2 "Control" sites where neither pipelines nor traffic were present; the data acquired from these sites were combined. More than 50% of a group of caribou had to cross the pipeline and/or road in the experimental sites for the crossing to be considered successful. Crossing success in the Control refers to the frequency with which caribou crossed a hypothetical pipeline on the northern boundary of that site.

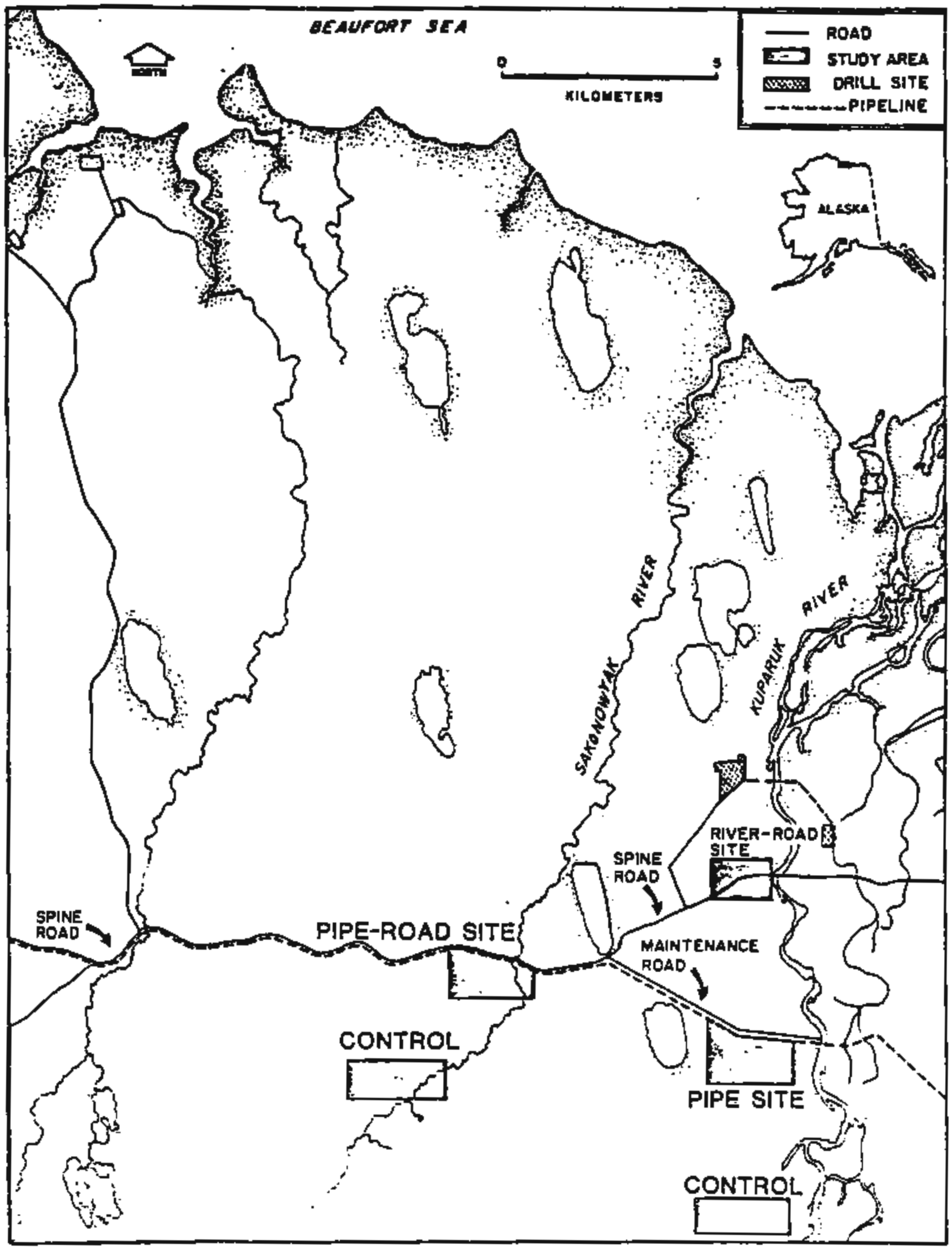

Fig. 1. Location of 5 study sites used for observing caribou behavior during 1981 and 1982 along the Kuparuk River, Alaska (from Murphy and Curatolo 1987).

When caribou were present in the study sites, we performed instantaneous scans (Altmann 1974) at 10-minute intervals, which entailed classifying the activity of each caribou as feeding, lying, standing, walking, or running. We also plotted the location of each group on large-scale maps and recorded weather and insect conditions; all data were stratified according to insect conditions. More detailed accounts of the field and analytical techniques are presented in Curatolo and Murphy (1986) and Murphy and Curatolo (1987).

RESULTS AND DISCUSSION

CAH caribou are strongly affected by insect activity during summer, and understanding the influences of mosquitoes (*Aedes* spp.) and oestrid flies (*Oedemagena tarandi* and *Cephenemyia trompe*) on caribou movements and behavior is fundamental to interpreting the effects of oilfield disturbance. In general, caribou move north to the coast during periods of mosquito harassment and then move south to preferred feeding range when mosquito activity subsides due to changes in weather (Cameron and Whitten 1979, Dau 1986). During late July and early August, oestrid flies tend to be the dominant insect pests, and their effects on caribou movements are less predictable. Caribou in the oilfield often seek unvegetated gravel pads or the shade of pipelines for relief from oestrid fly harassment (Curatolo and Murphy 1986).

Crossing Success

The crossing success of caribou groups encountering different configurations of pipelines and roads was calculated for the 3 experimental sites and the Control (Table 1). Overall crossing success in the Control was 66%, indicating that 34% of the groups that entered the Control did not cross a hypothetical pipeline. The frequency of group crossings of a pipeline adjacent to a road with traffic in the Pipe-Road Site was significantly less than expected ($P < 0.05$) during both insect-free periods (37%) and periods of mosquito harassment (31%); there were no significant differences in crossing frequency among sites when oestrid flies harassed caribou. There were no significant reductions in crossing success at the Pipe Site or the River-Road Site

(Table 1). Therefore, we concluded that there was a synergistic effect involving pipelines and roads with traffic that adversely affected caribou movements (Curatolo and Murphy 1986). Caribou are wary of structures such as pipelines, but are able to cross when given enough time; that is, when they are not disrupted in their crossing attempt by an approaching vehicle. Available evidence suggests that separating pipelines from frequently traveled roads will enhance crossing success and reduce disruption of caribou movements (Curatolo and Murphy 1986); however, very high rates of traffic (e.g., ≥ 1 vehicle/min) would probably create a barrier to caribou movements with or without an associated pipeline.

Table 1. Percentage of caribou groups that successfully crossed a pipeline with associated traffic (Pipe-Road Site), a pipeline without associated traffic (Pipe Site), traffic without a pipeline (River-Road Site), or a hypothetical pipeline (Control) in the western Prudhoe Bay Oilfield, Alaska, 1981 and 1982 (from Curatolo and Murphy 1986).

	Study site			
Insect condition	Pipe-Road Site	Pipe Site	River-Road Site	Control
None	37%[a]	75%	46%	66%
Mosquitoes	31%[a]	68%	100%[a]	64%
Oestrid flies	79%	71%	100%	67%
Overall	44%[a]	72%	75%	66%

[a] Indicates crossing frequency that was significantly different from Control (chi-square; $P < 0.05$).

Activity Budgets

Insect effects:

We monitored the activity budgets and movement rates of caribou within 1 km of the pipelines and roads and in the Control. When insects were absent, caribou in the Control spent 90% of their time engaged in activities associated with energy intake and assimilation (i.e., feeding and lying) (Fig. 2). When mosquitoes harassed the caribou, time spent feeding declined, time spent lying was reduced by nearly 50%, and standing, walking, and running increased significantly ($P < 0.05$). When

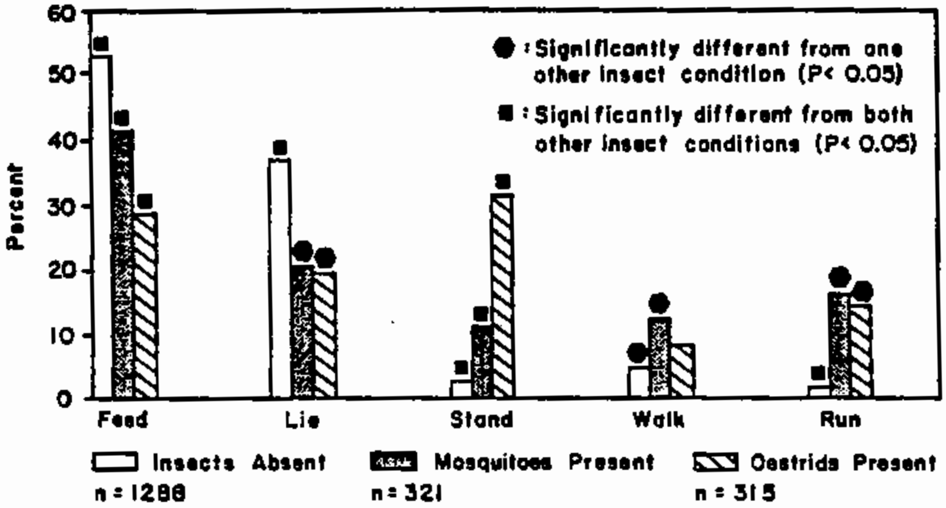

Fig. 2. Activity budgets of caribou during different insect conditions in the Control, western Prudhoe Bay Oilfield, Alaska (from Murphy and Curatolo 1987).

oestrid flies harassed caribou, the disruptive effects on the feeding and lying cycle were even more dramatic; even less time was spent feeding and more time was spent standing (Fig. 2).

The energetic costs of insect-induced changes in activity budgets were estimated by Fancy (1986); for lactating females in particular, insect harassment can cause a negative energy balance resulting in a net weight loss during the insect season. Fancy (1986) also reported that changes in energy intake variables had substantially greater effects on energy balance than did similar changes in variables influencing energy expenditure. This difference is, in part, because caribou have the lowest net cost of locomotion of any terrestrial vertebrate studied to date (Fancy and White 1987). Therefore, the 12% and 25% reductions in time spent feeding during periods of mosquito and oestrid fly harassment, respectively, were probably of greater energetic consequence than the 12-14% increases in time spent running.

Calculating the rates of caribou movement through the study sites provided another measure of changes in caribou behavior caused by insect harassment. Mean rates of travel for caribou in the Control were significantly different during each insect condition ($\underline{P} < 0.05$); caribou traveled at 0.7 km/h when insects were absent, but the movement rate increased to 2.7 and 1.6 km/h, respectively, when mosquitoes and oestrid flies were present (Table 2).

Oilfield effects:

The effects of pipelines and traffic on caribou behavior were determined by comparing caribou activity budgets and rates of movement among study sites during the 3 different insect conditions. When insects were absent, no significant among-site differences were detected in the percentage of time spent feeding, but all other activity categories differed significantly ($\underline{P} < 0.05$) between at least 2 sites (Fig. 3). The percentages of time spent walking and running differed significantly among all 3 study sites, with increases in both variables occurring under conditions of greater disturbance. The incidence of running, in particular, was substantially greater in the Pipe-Road Site (i.e., the

Table 2. Mean rates of movement (km/h) and results of statistical comparisons (* = significantly different [$P < 0.05$] from both other study sites) by insect condition for caribou groups traveling through study sites with different levels of oilfield activity, western Prudhoe Bay, Alaska, 1981 and 1982 (from Murphy and Curatolo 1987).

	Insects absent			Mosquitoes			Oestrid flies		
Study site	$\bar{x}$	SD	n[a]	$\bar{x}$	SD	n	$\bar{x}$	SD	n
Controls	0.7	1.6	1254	2.7	4.0	309	1.6	3.4	312
Pipe Site[b]	0.8	1.6	1211	3.0	3.8	432	1.9^*	3.2	209
Pipe-Road Site[c]	2.9^*	4.1	126	3.0	4.3	359	3.0^*	3.0	172

[a] n = number of 10-min activity scans.

[b] Pipeline and road, no traffic.

[c] Pipeline and road, with traffic.

study site with traffic). Rates of movement were not significantly different between the Pipe Site and the Control; however, the mean rate in the Pipe-Road Site was more than 3.5 times greater than that in either of the other 2 sites (Table 2). Time spent feeding, which was a good indicator of insect harassment in the Control, did not differ significantly among sites and thus was not adversely affected by disturbance when insects were absent.

When mosquitoes were present, the magnitude of the differences in time spent in various activities was small compared to that for periods when insects were absent, and differences among sites were not always interpretable in terms of oilfield disturbance. The amounts of time spent feeding and lying did not differ significantly between the Pipe Site and the Control (Fig. 3); however, caribou in the Pipe-Road Site spent significantly less time feeding and significantly more time lying than did caribou in either the Pipe Site or the Control ($P < 0.05$). Rates of movement did not differ significantly among the study sites when mosquitoes were present (Table 2). Considering that the total time

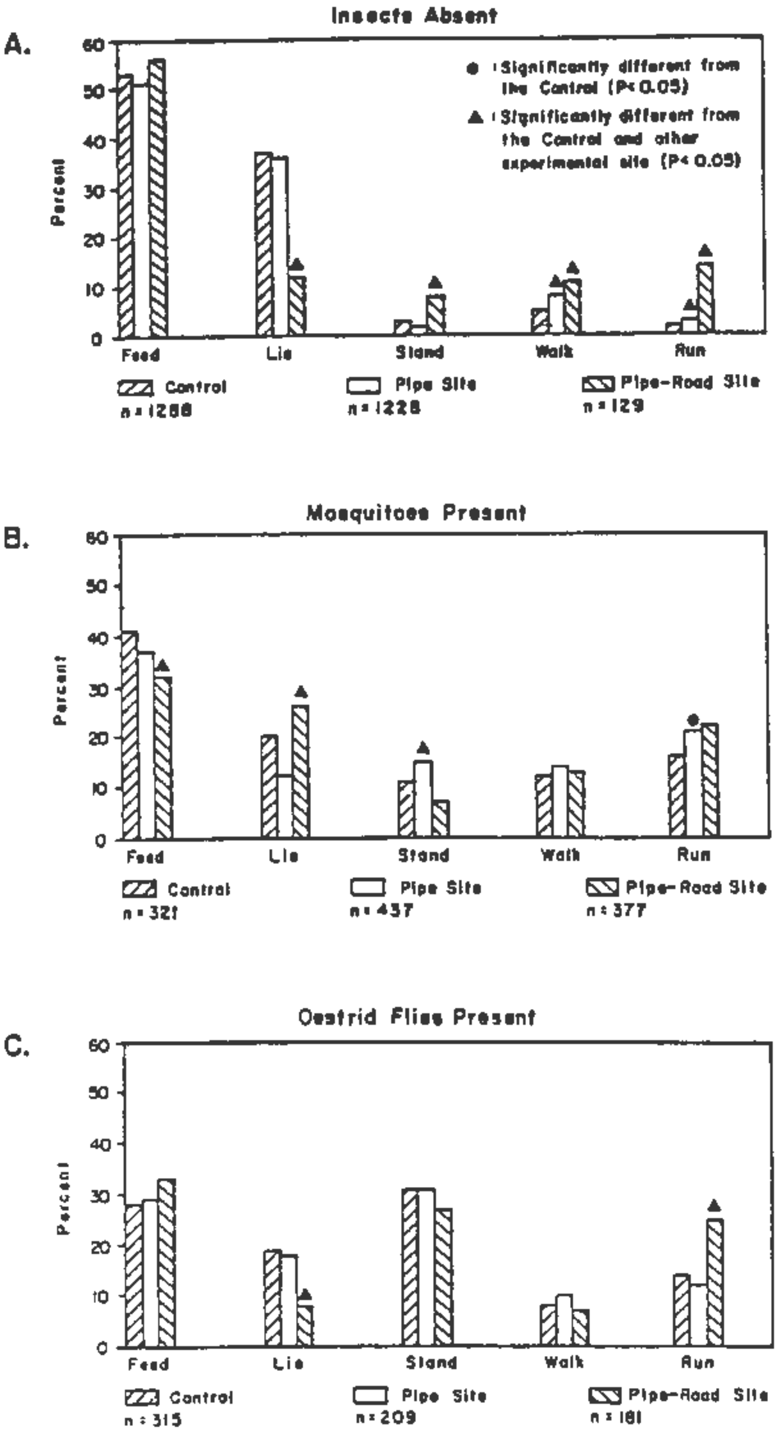

Fig. 3. Activity budgets of caribou during different insect conditions, in study sites with different levels of oilfield activity, western Prudhoe Bay, Alaska, 1981 and 1982 (from Murphy and Curatolo 1987).

spent feeding and lying was nearly equal in the Pipe-Road Site (58%) and the Control (61%), and that rates of movement were similar among sites, it does not appear that mosquito harassment and oilfield disturbance had a substantial additive or synergistic negative effect on caribou activity budgets.

When oestrid flies were present, caribou in the Pipe Site had an activity budget nearly identical to that of caribou in the Control (Fig. 3). In contrast, caribou in the Pipe-Road Site spent significantly less time lying and more time running than did caribou at the less-disturbed sites ($\underline{P} < 0.05$). Once again, there were no significant differences in time spent feeding among study sites ($\underline{P} > 0.05$). Rates of movement were significantly different among all 3 sites when oestrid flies were present ($\underline{P} < 0.05$), with higher rates recorded in the areas with more disturbance (Table 2).

Differences in activity budgets and rates of movement among study sites were most pronounced during periods when insects were absent. For this reason and because oilfield disturbance and insect harassment often had similar effects on caribou behavior, I consider the behavioral data collected during insect-free conditions to be the best for evaluating the effects of oilfield disturbance on caribou behavior. Based on the premise that changes in energy intake variables have the greatest influence on energy balance (Fancy 1986), the oilfield disturbances encountered in our study did not have the same potential for disruption of the energy balance of caribou as did insects, as time spent feeding was not significantly affected by disturbance when insects were absent. Although caribou were able to maintain levels of food intake under disturbed conditions and have relatively low energetic costs for locomotion, interruption of the feeding/lying cycle (i.e., decreased time spent lying) and increased energy expenditures due to running will negatively affect energy balance (Murphy and Curatolo 1987).

Reactive Zones

We have made an initial attempt to use behavioral data to determine the distance from a particular stimulus at which caribou alter their behavior. "Distance thresholds," or the distance from disturbance where the most clear-cut differences in behavioral responses can be identified, were used to delineate "reactive zones." This type of information is useful for determining the density of structures that caribou can tolerate and for evaluating the extent of functional habitat loss.

Figure 4 depicts empirical distribution plots (see Diggle 1983) that are based on the observed and expected cumulative percentages of caribou lying within different 100 m segments of the study sites when insects were absent (i.e., when behavioral differences among sites were most pronounced). Threshold distances were estimated from these plots by examining both the location of the deviation of the empirical distribution outside the confidence interval and the slope of the empirical distribution (Murphy and Curatolo 1987). Lying was selected as the most appropriate variable for delineating reactive zones because it indicates a low level of disturbance at that specific location. Running also is a good indicator of disturbance, but it is not necessarily site-specific because a caribou running through a study site could be reacting to a disturbance that occurred elsewhere.

In the Control, the observed distribution of lying caribou did not deviate significantly from the expected distribution ($\underline{P} > 0.01$); whereas there were significant deviations in both experimental sites (Fig. 4). At the Pipe Site, the 30th percentile, which corresponds to 300 m from the pipeline and road, appeared to be the threshold distance. At the Pipe-Road Site, the threshold distance was clearly delineated at the 60th percentile, which corresponds to 600 m from the pipeline and road. Based on these plots, zones were delineated in each of the experimental sites, and activity budgets and mean rates of movement were calculated for each zone (Table 3). Quantitative comparisons of time spent lying, time spent running, and rates of movement, both among zones and with the Control, indicated that 3 relative categories of disturbance could be discerned that were a function of both the level of disturbance and the distance from disturbance (Murphy and Curatolo 1987):

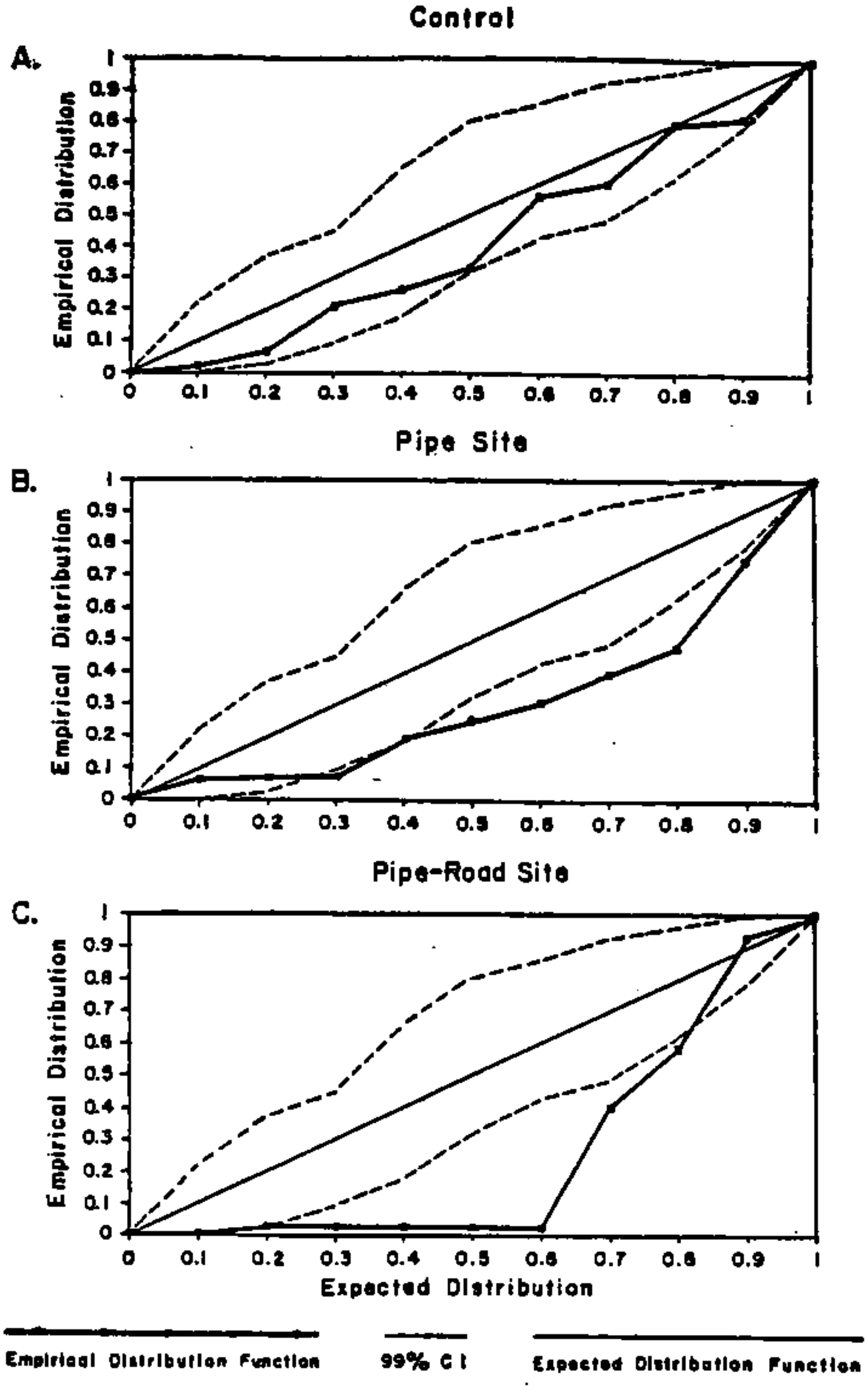

Fig. 4. Empirical distribution functions for caribou lying down during periods when insects were absent, in study sites with various levels of oilfield activity, western Prudhoe Bay Oilfield, Alaska, 1981 and 1982 (from Murphy and Curatolo (1987).

Low Disturbance - Control and Pipe Site (301-1000 m);
Moderate Disturbance - Pipe Site (0-300 m) and Pipe-Road Site (601-1000 m);
High Disturbance - Pipe-Road Site (0-600 m).

Table 3. Activity budgets and mean rates of movement for caribou during periods when insects were absent in two zones in the experimental sites (delineated by distance from the pipeline and road) and in the control sites, western Prudhoe Bay Oilfield, Alaska, 1981 and 1982 (from Murphy and Curatolo 1987).

Study site	Zone	Activity (%)					Rate of movement (km/h)	n[a]
		Feed	Lie	Stand	Walk	Run		
Control	0-1000 m	0.53	0.37	0.03	0.05	0.02	0.7	1228
Pipe Site[b]	0-300 m	0.49	0.26	0.03	0.10	0.10	1.4	211
	301-1000 m	0.51	0.37	0.02	0.07	0.02	0.7	1017
Pipe-Road Site[c]	0-600 m	0.55	0.01	0.10	0.15	0.19	3.6	61
	601-1000 m	0.56	0.21	0.06	0.07	0.09	2.2	68

[a] n = number of 10-min activity scans.

[b] Pipeline and road, no traffic.

[c] Pipeline and road, with traffic.

CONCLUSIONS

Although incomplete, our understanding of the responses of caribou to oil development in the Arctic has improved dramatically during the past 15 years. Based on the results of this and other studies (e.g., Dau and Cameron 1986), we can define with considerable accuracy the types of disturbances, in relation to season and environmental conditions, which are likely to cause problems for caribou. Similarly, we can identify situations and conditions that do not appear to pose any particular problem. Topics for future research programs that would greatly improve our understanding of caribou behavior and energetics in the oilfields include quantification of the frequency and duration of encounters between CAH caribou and development, and quantification of the extent that habituation plays in reducing impacts during the life of an individual caribou or over the life of an oilfield.

For impact predictions and management policy to be formulated from an informed position, biologists engaged in applied research in the oilfields must have positive input into the decision-making process. In an oilfield designed to minimize disturbance to caribou, the density of structures would not exceed that which would allow caribou to avoid disturbance most of the time. Furthermore, appropriate mitigative measures would be implemented to facilitate movements to minimize the frequency and duration of disturbance-induced behavioral changes, thereby reducing the likelihood of long-term energetic impacts. It is critical for biologists to supply decision-makers with defensible, quantitative data that address these issues so that impact predictions and mitigative practices can evolve at a rate commensurate with the state of knowledge of caribou biology.

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EFFECTS OF HUNTING WITH THE USE OF SNOWMACHINES ON MOVEMENTS OF WESTERN ARCTIC HERD CARIBOU, SEWARD PENINSULA, ALASKA

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Abstract: Caribou (Rangifer tarandus granti) have not occupied the western Seward Peninsula since 1880, although the viability of reindeer (Rangifer tarandus tarandus) herds ranging there since 1892 demonstrates that the habitat is suitable. Since at least 1981, winter movements of the Western Arctic Caribou Herd have extended into the eastern Seward Peninsula. From 1982 to 1987, movements of Western Arctic caribou on the Seward Peninsula were monitored by aerial observation and radiotelemetry. Caribou failed to extend movements beyond where they encountered intense hunting pressure. Hunters generally used snowmachines for access to caribou during winter, and pursuit of animals was often extensive. Avoidance of this disturbance by caribou may inhibit future range expansion near human population centers.

Key Words: caribou, disturbance, hunting, Rangifer, Seward Peninsula, snowmachines, Western Arctic Herd

Caribou were abundant on the Seward Peninsula before 1880. Petrov (1881, in Skoog 1968) reported that, in 1880, natives of Wales and Port Clarence, on the western tip of the Seward Peninsula, lived by fishing and caribou hunting. Oquilluk (1973) related numerous traditional Eskimo stories which indicate that caribou were once important in the diets of the people living on the lower Kuzitrin River in the western interior of the Seward Peninsula. For unknown reasons, caribou populations in western Alaska shifted radically soon after 1880, and caribou abandoned the Seward Peninsula. A hundred years later, in 1981, the Western Arctic Herd (WAH) moved into eastern portions of the Seward Peninsula, and each year since caribou have occupied portions of the Peninsula for varying periods between October and April.

The abundance and distribution of caribou on the Seward Peninsula have been monitored systematically since fall 1982. Although the numbers of caribou using the Seward Peninsula and the adjacent Nulato Hills have increased markedly since 1981, the limits of westernmost expansion onto the Seward Peninsula have not changed appreciably. This report describes patterns of caribou distribution on the Seward Peninsula in relation to hunting activity.

This work was supported by Federal Aid in Wildlife Restoration and by funds from the U. S. Bureau of Land Management. A number of people took part in caribou distribution surveys on the Seward Peninsula. I wish to acknowledge the contribution of the following: L. Davis, J. Coady, B. Nelson, D. Anderson, C. Lean, S. Robinson, and R. Gal.

METHODS

Surveys were flown periodically during October-April, 1982-87. Caribou were located by following tracks in snow and with radiotelemetry. Survey flight path, caribou locations, estimated numbers, and direction of movement were recorded. Human activities, caribou kill sites, and snowmachine trails were noted on maps.

RESULTS AND DISCUSSION

Early winter movements of caribou onto the Seward Peninsula followed the general pattern shown in Fig. 1 during 1982-87. The WAH increased from an estimated 75,000 in 1976 (Davis and Valkenburg 1983) to ≥229,000 in 1986 (James and Larsen 1988). Numbers of caribou using the Norton Sound region, particularly the Nulato Hills, increased notably, but caribou did not range onto the western Seward Peninsula nor south of the Unalakleet River (Fig 2).

The temporal pattern of movement has been quite consistent. Caribou moved into the Norton Sound region in late September and October, reaching their maximum westerly distribution in November. They generally withdrew to remote areas in the eastcentral portion of the Seward

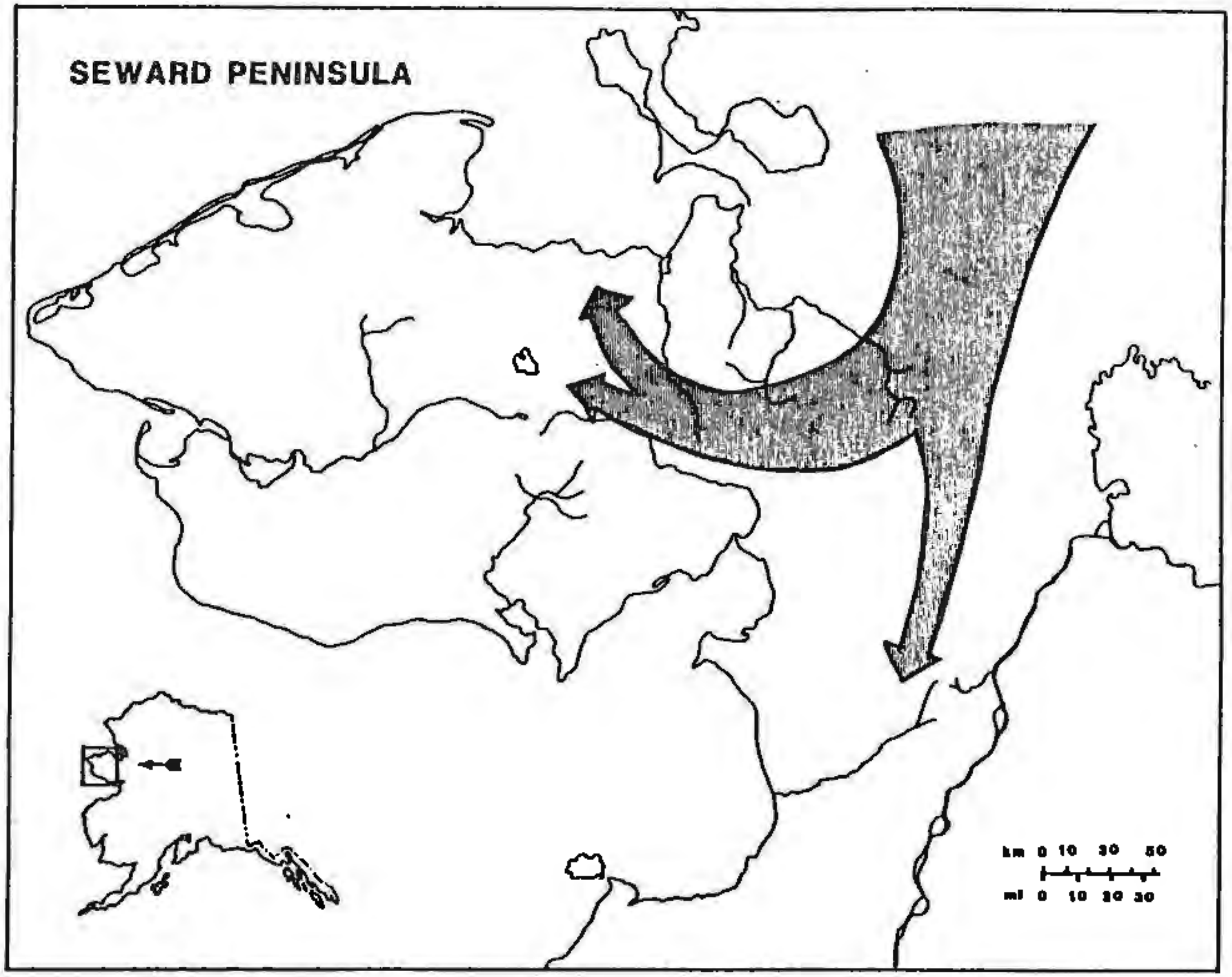

Fig. 1. Generalized movement patterns of Western Arctic Herd caribou onto the Seward Peninsula in early winter, 1982-87.

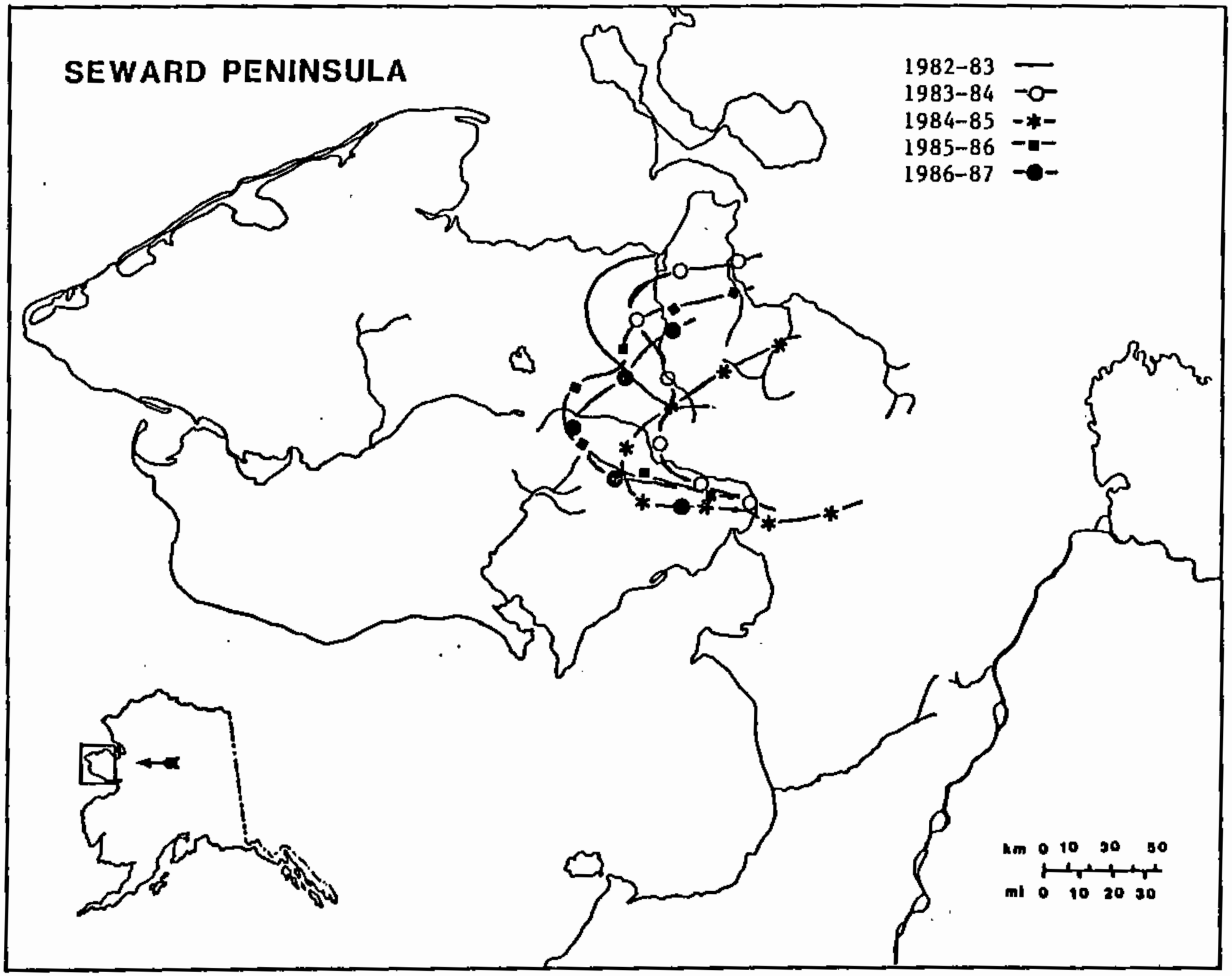

Fig. 2. Maximum westward winter distribution of caribou on the Seward Peninsula, 1982-87.

Peninsula during December, January, and February. In March and April, caribou left winter range enroute to calving grounds north of the Brooks Range.

During the period of recovery of the WAH (1976-87), tremendous advances were made in snowmachine technology. Power, fuel economy, and suspensions have been improved substantially. Modern snowmachines allow high speed operation over a wide range of terrain and, given suitable snow conditions, can overtake any terrestrial mammal. Nearly all caribou killed by hunters on the Seward Peninsula are taken with the use of snowmachines.

Temperature, slope, snow density, snow depth, and the occurrence of drifts determine the practical limits on speed and maneuverability of snowmachines. Most of western Seward Peninsula is treeless arctic tundra with few slopes too steep for snowmachine operation. Although snowmachines are used year-round, snow conditions conducive to extensive travel normally do not occur until January and improve through April when long daylight, higher temperatures, and smooth, hard snow produce optimal conditions.

Methods widely used for taking caribou in winter may be extremely aggressive, and some of the most effective methods are illegal. Acceptance of, and compliance with, regulations relating to ethical hunting practices is minimal in many rural Alaskan communities, and enforcement effort is low. Examples of these hunting methods include: driving caribou to hidden hunters, shooting with a pistol while driving with one hand, having a passenger shoot while in pursuit, and sustained firing into groups of caribou by several hunters. Although the relative frequency of use of the various methods for taking caribou is unknown, it is clear from anecdotal information that methods similar to those described above are not unusual. Furthermore, methods used by hunters from Nome, the urbanized population center, apparently differ little from those used by residents of the smaller villages.

Because of the long distances from shelter, the need to haul heavy loads of fuel and caribou meat, and the potential for mechanical failure, hunters often travel in groups of 2-4 snowmachines; 1 party of 12 machines was observed. These hunters invariably pursue the first caribou encountered and attempt to kill enough animals to accommodate all members of the party. Thus, the harvest tends to be concentrated at the periphery of caribou distribution and may involve prolonged pursuit and the killing of numerous animals. A party of hunters from Nome reportedly killed 50 caribou on a single trip. Subsequent groups of hunters frequently used the same travel routes to reach known concentrations of caribou. The same caribou may therefore be subjected to nearly continuous harassment and hunting pressure.

Communications and the ability to locate caribou have improved substantially in recent years with increased air traffic, the installation of telephones in villages, and increased mobility of rural residents. The results of surveys conducted by ADF&G are of particular interest to hunters, and they frequently consult our office for current information on caribou distribution. Soon after news is received that caribou are within snowmachine range of communities, hunting parties depart to take caribou.

As the operational range of snowmachines is fuel-limited, the difficulty of operation increases with the distance from a fuel source. My personal experience and observations of hunting patterns indicate that caribou hunting beyond 48 km (30 mi) of permanent settlements, although certainly possible, is difficult, given prevailing conditions on the Seward Peninsula. However, travel corridors with heavily used, hard-packed trails allow hunters to extend their activities farther than when traveling cross-country on unbroken snow (Fig. 3). Information on caribou movements in the southern Nulato Hills is limited, but it appears that few caribou crossed the trail between Unalakleet and Kaltag during the years 1981-87. This trail allowed hunters to efficiently detect and intercept caribou attempting to cross.

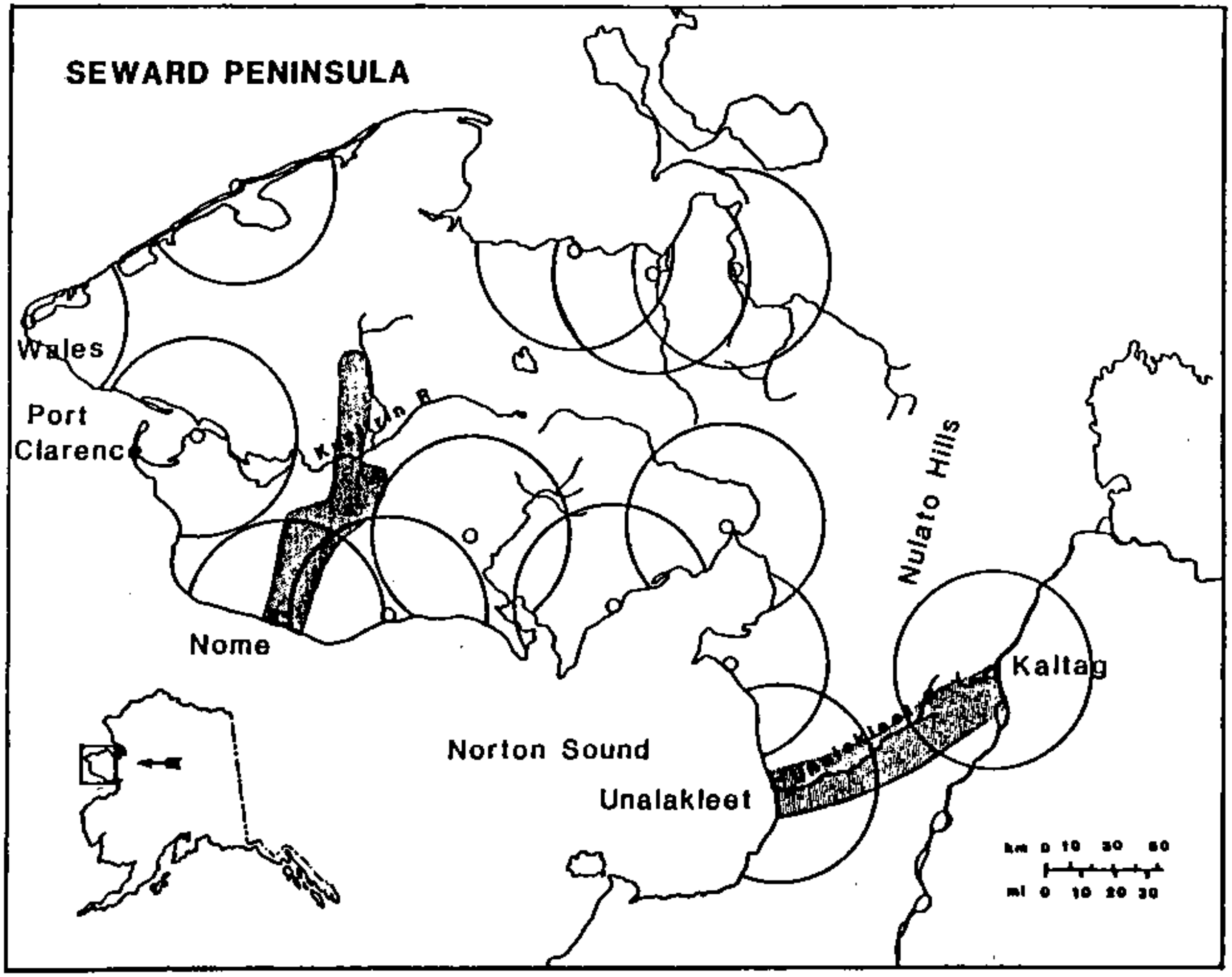

Fig. 3. Forty-eight km (30 mi) radiuses from permanent settlements on the Seward Peninsula region. This represents concentrated hunting activity by hunters using snowmachines for transportation. Shaded areas represent heavily used travel corridors.

CONCLUSIONS

While these observations do not establish a cause-and-effect relationship, the similarity between the westward limits of caribou movement on the Seward Peninsula and the effective range of hunters using snowmachines is striking (Figs. 2 and 3). Man on modern snowmachines is an efficient arctic predator, and I suggest that movements of caribou on the Seward Peninsula in recent years reflect predator avoidance.

Alternative explanations for the observed winter distribution of caribou on the Seward Peninsula do not seem plausible. Lichen ranges are reported in good condition (Swanson et al. 1985), and the year-round occupancy by 21,000 reindeer (Reindeer Herders Association, unpubl. data) suggest that habitat and climate are suitable. Predators other than man are virtually nonexistent on the western portions of the Seward Peninsula in winter.

There is no consensus on a caribou management strategy among the groups of people who would be most affected by more extensive movements of caribou on the Seward Peninsula. On the one hand, interest in harvesting caribou is considerable. Nome hunters obtained 125 caribou harvest tickets in 1986-87 even though extreme effort was required to reach caribou by surface transportation. On the other hand, the reindeer industry views the potential expansion of the WAH with apprehension. Caribou and domestic reindeer on open range are incompatible, and influxes of WAH caribou have already resulted in the loss of thousands of reindeer from the NANA herd which was held on the easternmost grazing allotment on the Seward Peninsula. The efforts of reindeer herders using snowmachines to intentionally drive caribou from reindeer grazing areas may also have contributed to recent changes in caribou distribution.

Current hunting regulations allow WAH caribou to be harvested 12 months of the year (females may not be taken from 16 May to 30 June), with no limit (except that no more than 5 animals per day can be taken). These regulations are appropriate for most of the herd's range. However, if a goal of promoting westward expansion of WAH caribou on the Seward

Peninsula is adopted, it may be necessary to modify current hunting regulations and practices.

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SERUM ANTIBODY PREVALENCE OF 3 RESPIRATORY VIRUSES IN SELECTED ALASKA CARIBOU HERDS

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Abstract: Three viral diseases, infectious bovine rhinotracheitis (IBR), bovine viral diarrhea (BVD), and parainfluenza III (PI3) are commonly referred to collectively as the "bovine respiratory group." As this generic term implies, the viruses often cause respiratory tract infection in domestic cattle. Morbidity (rate of illness) may be high in an infected population, but mortality (rate of death) is usually low. Transmission usually occurs via aerosol droplet. Serologic evidence of exposure has been previously reported for various wildlife species, including pronghorn, moose, mule deer, bighorn sheep, and others. These serologic results do not necessarily reflect actual disease, but rather only evidence of exposure to the disease agents in question.

From 1975 to 1986, we conducted a serologic survey of caribou (*Rangifer tarandus granti*) herds in Alaska (Fig. 1) by testing blood samples for evidence of exposure to IBR, BVD, and PI3. The results exhibit an interesting pattern. The 3 viruses are more prevalent in the arctic herds than in the interior herds (Tables 1). At present, we have no ready explanation for this apparent difference.

Key Words: caribou, *Rangifer*, respiratory viruses, serology

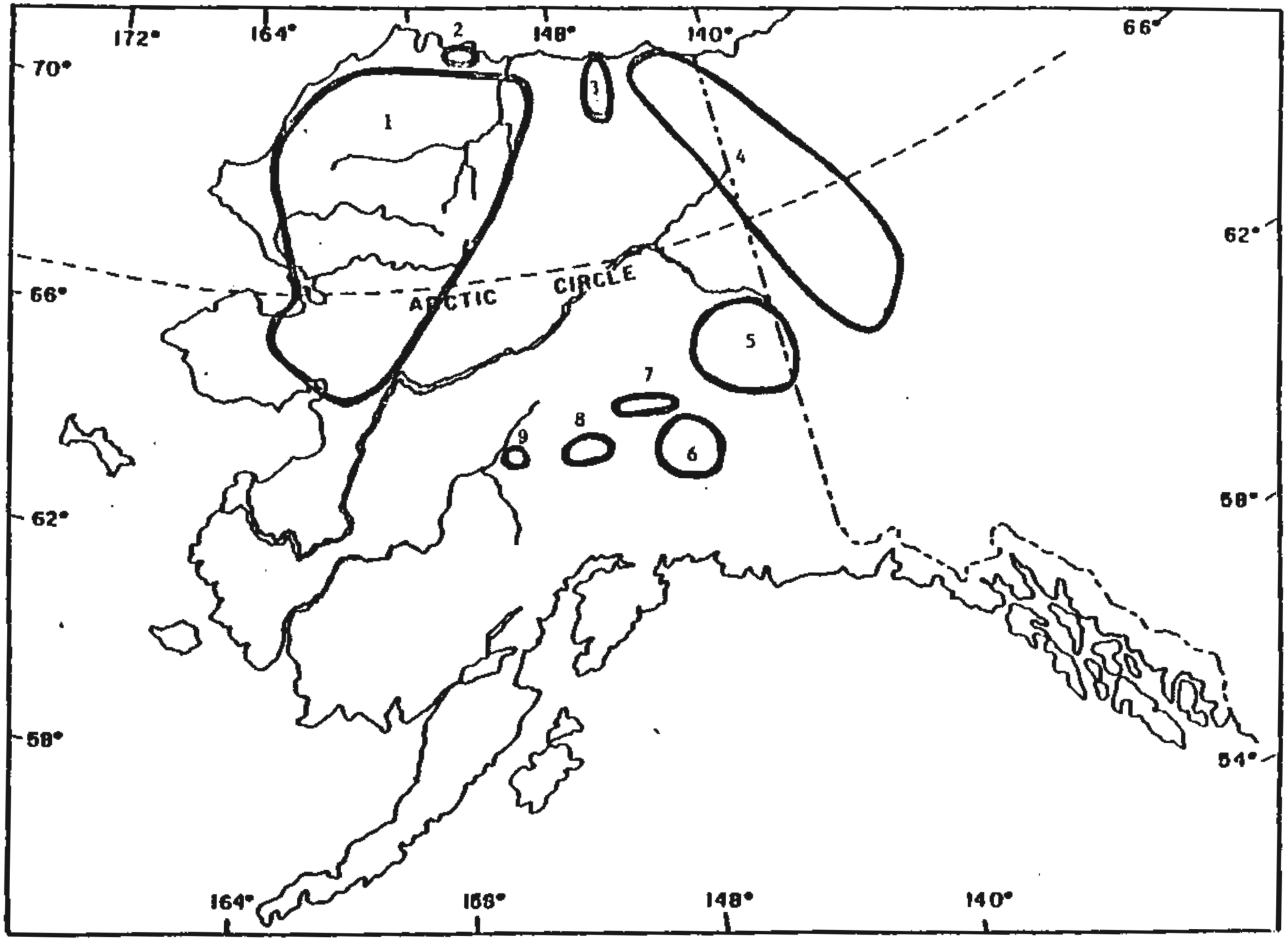

Fig. 1. Locations of caribou herds included in serologic survey: 1. Western Arctic, 2. Teshekpuk, 3. Central Arctic, 4. Porcupine, 5. Fortymile, 6. Nelchina, 7. Delta, 8. Denali, 9. Sunshine Mountains.

Table 1. Serum antibody prevalence of infectious bovine rhinotracheitis virus (IBR), bovine viral diarrhea virus (BVD), and parainfluenza III virus (PI3) in selected Alaskan caribou herds, 1975-86.

Herd	Prevalence[a]		
	IBR	BVD	PI3
Western Arctic	4/73 (5)	3/76 (4)	10/81 (12)
Teshekpuk	1/16 (6)	3/16 (19)	0/15 (0)
Central Arctic	44/174 (25)	11/170 (6)	1/155 (1)
Porcupine	8/51 (16)	3/51 (6)	10/52 (19)
Fortymile	4/17 (24)	1/17 (6)	5/17 (29)
Nelchina	1/76 (1)	0/76 (0)	0/73 (0)
Delta	0/90 (0)	0/91 (0)	0/90 (0)
Denali	0/26 (0)	0/26 (0)	0/18 (0)
Sunshine Mountains	0/9 (0)	0/9 (0)	0/9 (0)

[a] No. positive/No. tested, (%).

APPENDICES

Appendix A. Summary of population estimation information for the Wolf Lake and Finlayson caribou herds.

	Sightability correction factor	Observed population estimate (variance)			Expanded population estimate (variance)	90% UCL[a]	90% LCL[b]	90% C.I.[c] (± % of $\bar{x}$)	95% UCL[a]	95% LCL[b]	95% C.I.[c] (± % of $\bar{x}$)
		High strata	Low strata	Combined strata							
Wolf Lake Herd											
15 S.U.[d], high stratum 11 S.U., low stratum 8 intensive searches	1.3284	453 (0)	125 (3454.7)	578 (3454.7)	768 (8244.5)	940	596	22.4	982	553	28.0
14 S.U., high stratum 11 S.U., low stratum 7 intensive searches	1.3564	442 (258.9)	125 (3454.7)	567 (3713.6)	769 (9906.9)	963	576	25.1	1013	526	31.6
13 S.U., high stratum 11 S.U., low stratum 7 intensive searches	1.3564	458 (564.7)	125 (3454.7)	583 (4019.4)	791 (16645.4)	992	591	25.3	1044	539	31.9
12 S.U., high stratum 11 S.U., low stratum 7 intensive searches	1.3564	458 (956.8)	125 (3454.7)	583 (4411.5)	791 (11363.7)	998	584	26.2	1052	530	32.9
11 S.U., high stratum 11 S.U., low stratum 6 intensive searches	1.3855	474 (1455.4)	125 (3454.7)	599 (4910.1)	830 (14680.5)	1074	586	29.4	1142	519	37.5
10 S.U., high stratum 11 S.U., low stratum 5, intensive searches	1.4089	469 (2043.2)	125 (3454.7)	594 (5497.8)	837 (20464.3)	1142	532	36.4	1234	440	47.4
9 S.U., high stratum 11 S.U., low stratum 5 intensive searches	1.4089	496 (2730.1)	125 (3454.7)	621 (6184.8)	874 (22681.5)	1195	553	36.7	1292	456	47.8

Appendix A. Continued.

	Sightability correction factor	Observed population estimate (variance)			Expanded population estimate (variance)	90% UCL^a	90% LCL^b	90% C.I.^{c} (± % of $\bar{x}$)	95% UCL^a	95% LCL^b	95% C.I.^{c} (± % of $\bar{x}$)
		High strata	Low strata	Combined strata							
8 S.U., high stratum 11 S.U., low stratum 4 intensive searches	1.4621	530 (3184.3)	125 (3454.7)	655 (6638.9)	957 (33029.9)	1385	529	44.7	1535	379	60.4
7 S.U., high stratum 11 S.U., low stratum 3 intensive searches	1.6080	469 (2492.4)	125 (3454.7)	594 (5947.1)	956 (64616.0)	1698	214	77.7	2050	0	114.4
6 S.U., high stratum 11 S.U., low stratum 3 intensive searches	1.6080	451 (4280.9)	125 (3454.7)	576 (7735.5)	926 (65872.8)	1675	176	81.0	2030	0	119.3
5 S.U., high stratum 11 S.U., low stratum 2 intensive searches	2.1302	450 (7827.2)	125 (3454.7)	575 (11281.9)	1225 (402480)	5230	0	327.1	9286	0	658.2
4 S.U., high stratum 11 S.U., low stratum 2 intensive searches	2.1302	371 (7888.6)	125 (3454.7)	496 (11343.3)	1057 (310049)	4573	0	332.5	8132	0	669.2
3 S.U., high stratum 11 S.U., low stratum 1 intensive search	cannot be calculated	291 (3361.5)	125 (3454.7)	416 (6816.2)	--	--	--	--	--	--	--
<u>Finlayson Herd</u>											
39 S.U., high stratum 11 S.U., low stratum 8 intensive searches	1.741	1766 (0)	286 (6926.0)	2052 (6926.0)	3574 (70454.3)	4077	3071	14.1	4202	2947	17.6

Appendix A. Continued.

	Sightability correction factor	Observed population estimate (variance)			Expanded population estimate (variance)	90% UCL[a]	90% LCL[b]	90% C.I.[c] (± % of $\bar{x}$)	95% UCL[a]	95% LCL[b]	95% C.I.[c] (± % of $\bar{x}$)
		High strata	Low strata	Combined strata							
38 S.U., high stratum 11 S.U., low stratum 8 intensive searches	1.7419	1793 (1273.8)	286 (6926.0)	2079 (8226.22)	3622 (75619.7)	4143	3100	14.4	4272	2971	18.0
37 S.U., high stratum 11 S.U., low stratum 8 intensive searches	1.7419	1833 (2629.0)	286 (6926.0)	2119 (9555.0)	3690 (81669.1)	4232	3149	14.7	4366	3014	18.3
36 S.U., high stratum 11 S.U., low stratum 8 intensive searches	1.7419	1829 (4217.7)	286 (6926.0)	2115 (11143.7)	3684 (86276.6)	4240	3127	15.1	4378	2989	18.8
35 S.U., high stratum 11 S.U., low stratum 7 intensive searches	1.7961	1820 (5868.3)	286 (6926.0)	2106 (12794.3)	3783 (121149)	4459	3106	17.9	4634	2931	22.5
34 S.U., high stratum 11 S.U., low stratum 7 intensive searches	1.7961	1802 (7621.5)	286 (6926.0)	2088 (14326.7)	3750 (125383)	4438	3062	18.3	4616	2883	23.1
33 S.U., high stratum 11 S.U., low stratum 7 intensive searches	1.7961	1812 (9514.4)	286 (6926.0)	2098 (16440.4)	3768 (132244)	4475	3062	18.8	4658	2879	23.6
32 S.U., high stratum 11 S.U., low stratum 7 intensive searches	1.7961	1792 (11433.7)	286 (6926.0)	2078 (18359.6)	3731 (136831)	4450	3012	19.3	4636	2826	24.3
31 S.U., high stratum 11 S.U., low stratum 7 intensive searches	1.7961	1842 (13229.6)	268 (6926.0)	2128 (20155.6)	3822 (146440)	4566	3078	19.4	4758	2886	24.5

Appendix A. Continued.

	Sightability correction factor	Observed population estimate (variance)			Expanded population estimate (variance)	90% UCL[a]	90% LCL[b]	90% C.I.[c] (± % of $\bar{x}$)	95% UCL[a]	95% LCL[b]	95% C.I.[c] (± % of $\bar{x}$)
		High strata	Low strata	Combined strata							
30 S.U., high stratum 11 S.U., low stratum 7 intensive searches	1.7961	1740 (13447.8)	268 (6926.0)	2026 (20373.8)	3639 (139478)	4364	2913	19.9	4552	2725	25.1
29 S.U., high stratum 11 S.U., low stratum 7 intensive searches	1.7961	1724 (15757.7)	268 (6926.0)	2010 (22683.7)	3609 (145705)	4351	2868	20.6	4544	2675	25.9
28 S.U., high stratum 11 S.U., low stratum 8 intensive searches	1.7961	1698 (18699.3)	268 (6926.0)	1984 (25625.3)	3563 (153291)	4324	2803	21.3	4521	2605	26.9
27 S.U., high stratum 11 S.U., low stratum 7 intensive searches	1.7961	1766 (20464.8)	268 (6926.0)	2052 (27390.8)	3684 (163860)	4471	2898	21.4	4675	2694	26.9
26 S.U., high stratum 11 S.U., low stratum 6 intensive searches	1.8354	1800 (23571.8)	268 (6926.0)	2086 (30497.8)	3828 (228648)	4791	2864	25.5	5057	2598	32.1
25 S.U., high stratum 11 S.U., low stratum 6 intensive searches	1.8354	1864 (25878.6)	268 (6926.0)	2150 (32804.5)	3945 (244265)	4941	2949	25.2	5216	2674	32.2
24 S.U., high stratum 11 S.U., low stratum 6 intensive searches	1.8354	1852 (30241.9)	268 (6926.0)	2138 (37167.9)	3923 (257300)	4945	2901	26.1	5227	2618	33.2
23 S.U., high stratum 11 S.U., low stratum 5 intensive searches	1.9840	1856 (35450.4)	268 (6926.0)	2142 (42376.4)	4249 (453848)	5686	2813	33.8	6119	2379	44.0

Appendix A. Continued.

	Sightability correction factor	Observed population estimate (variance)			Expanded population estimate (variance)	90% UCL[a]	90% LCL[b]	90% C.I.[c] (± % of $\bar{x}$)	95% UCL[a]	95% LCL[b]	95% C.I.[c] (± % of $\bar{x}$)
		High strata	Low strata	Combined strata							
22 S.U., high stratum 11 S.U., low stratum 5 intensive searches	1.9840	1854 (41205.4)	268 (6926.0)	2140 (48131.4)	4244 (475436)	5714	2774	34.6	6158	2330	45.1
21 S.U., high stratum 11 S.U., low stratum 5 intensive searches	1.9840	1941 (43696.0)	268 (6926.0)	2227 (50622)	4418 (509223)	5939	2896	34.4	6399	2437	44.8
20 S.U., high stratum 11 S.U., low stratum 5 intensive searches	1.9840	1991 (48693.4)	268 (6926.0)	2227 (55619.4)	4516 (542673)	6087	2946	34.8	6561	2471	45.3
19 S.U., high stratum 11 S.U., low stratum 4 intensive searches	2.2119	1991 (58015.5)	268 (6926.0)	2277 (64941.5)	5036 (1277354)	7696	2377	52.8	8633	1440	71.4
18 S.U., high stratum 11 S.U., low stratum 3 intensive searches	2.19736	2112.77 (49553.0)	268 (6926.0)	2398.46 (56479)	5270.27 (2232375)	9633.08	907.46	82.78	11699.4	0	121.99
17 S.U., high stratum 11 S.U., low stratum 2 intensive searches	2.81285	2109.64 (60259.7)	268 (6926.0)	2395.33 (67185.7)	6737.73 (12835143)	29358.4	0	335.73	52258.5	0	675.61

[a] UCL = upper confidence limit.
[b] LCL = lower confidence limit.
[c] C.I. = confidence interval.
[d] S.U. = sample units.

Appendix B. Titles of Other Papers Presented at the 3rd North American Caribou Workshop (no written submissions).

SLATE ISLANDS CARIBOU

Arthur T. Bergerud, Biology Department, University of Victoria, Victoria, British Columbia, Canada V8W 2Y2

RUTTING LOCATIONS OF WOODLAND CARIBOU

Heather E. Butler, R.R. #1, Fulford Härbour, British Columbia, Canada V0S 1C0

Arthur T. Bergerud, Biology Department, University of Victoria, British Columbia, Canada V8W 2Y2

CARIBOU STARVATION ON RIDEOUT ISLAND

Douglas C. Heard, Department of Renewable Resources, Government of the Northwest Territories, Yellowknife, Northwest Territories, Canada X1A 2L9

LABRADOR-INUIT COMMERCIAL HUNT, GEORGE RIVER HERD

Judy Rowell, Labrador Inuit Association, P.O. Box 70, Nain, Labrador, Canada A0P 1L0

THE CARIBOU ADVISORY BOARD

Donald E. Russell, Canadian Wildlife Service, 204 Range Road, Whitehorse, Yukon Territory, Canada Y1A 3V1

Appendix C. Sources of Other Proceedings on *Rangifer*

Proceedings of the 1st North American Caribou Workshop, Whitehorse, Yukon Territory, 28-29 September 1983. Can. Wildl. Serv. Spec. Publ., Ottawa, 1985.

D. E. Russell
Canadian Wildlife Service
204 Range Road
Whitehorse, YT
Canada Y1A 3V1 cost: none

Proceedings of the 2nd North American Caribou Workshop, Val Morin, Quebec, 17-20 October 1984. McGill Subarctic Res. Pap. No. 40, 1985.

McGill Subarctic Research Papers
Centre for Northern Studies and Research
McGill University
550 ouest rue Sherbrooke
Suite 40 West Wing
Montreal, PQ
Canada H3A 1B9 cost: $20 (Can.)

Proceedings of the 4th International Reindeer/Caribou Symposium, Whitehorse, Yukon Territory, 22-25 August 1985. Rangifer. Spec. Issue No. 1, 1986.

F. L. Miller
Canadian Wildlife Service
Western and Northern Region
2nd Floor, 4999-98 Avenue
Edmonton, Alberta
Canada T6B 2X3 cost: none