Alaska Department of Fish and Game
Division of Wildlife Conservation

Federal Aid in Wildlife Restoration
Research Final Report

Movements Patterns of the Porcupine Caribou Herd in Relation to Oil Development

by

Kenneth R. Whitten

Projects W-22-5, W-22-6, W-23-1,
W-23-2, W-23-3, W-23-4,
W-23-5, and W-24-1
Study 3.34
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FINAL REPORT (RESEARCH)

State: Alaska

Cooperator: Larry Pank, U.S. Fish and Wildlife Service

Project Nos.: W-22-5, W-22-6, W-23-1, W-23-2, W-23-3, W-23-4, W-23-5, W-24-1

Project Title: Wildlife Research and Management

Study No.: 3.34

Study Title: Movement Patterns of Caribou Herd in Relation to Oil Development

Period Covered: 1 July 1985 - 30 June 1993

SUMMARY

Caribou with satellite and/or conventional radiocollars have been monitored by the Alaska Department of Fish and Game and cooperating agencies since 1981. Results of these studies have led to increased knowledge and numerous publications on population dynamics, movements, and range use of the Porcupine caribou (*Rangifer tarandus*) herd (PCH). The PCH has consistently calved at high densities on the coastal plain of the Arctic National Wildlife Refuge. Calf survival is lower when calving is displaced from this area, which is also being considered for potential petroleum development. From 1979 until 1989 the PCH grew steadily at a rate of about 5% per year and reached a peak population of 178,000. In July 1992 an aerial photocensus estimated only 160,000 caribou. The recent decline may result at least in part from severe winter weather that apparently led to low calf productivity in 1991 and low yearling recruitment in spring 1992. Adult mortality may also have increased. During this reporting period, staff of the Alaska Department of Fish and Game have continued to work on determining the relationships among calving distribution, forage quality, and forage availability.

Key Words: caribou, migration *Rangifer tarandus*, satellite radio-tracking.

CONTENTS

BACKGROUND

In 1980 the U.S. Congress set aside a portion of the coastal plain in the Arctic National Wildlife Refuge for oil and gas exploration. Results of the geological exploration indicate that the coastal plain (now commonly referred to as the 1002, or "ten-oh-two," area) is the best remaining onshore prospect for a major new oil discovery in North America.

Congress also mandated baseline ecological research of the 1002 area, and the Porcupine caribou (*Rangifer tarandus*) herd (PCH) (n = 160,000 in 1992) has thus been the subject of cooperative studies conducted by the Alaska Department of Fish and Game, the U.S. Fish and Wildlife Service, the Canadian Wildlife Service, and the governments of the Yukon and Northwest Territories. These studies have focused on seasonal movements of the PCH within both the U.S. and Canada. Satellite transmitter collars were found to be an effective addition to standard telemetry for following seasonal movements. Intensive tracking of both radio-collared cows and radio-collared calves yielded valuable information on timing and distribution of calving and spatial variation in calf survival. In most years, about 50-75% of the calves in the PCH are born in an area that comprises only about 25% of the overall calving grounds. Calf survival tends to be particularly high when calving occurs in the low-lying coastal plain portions of this traditional high-density calving area rather than in nearby foothills and mountains where predators are more abundant.

The 1002 area overlaps most of the coastal plain portion of the traditional calving area. All of the 1002 area is used as postcalving habitat by the PCH, and much of the western part of the 1002 area is used by the Central Arctic herd (CAH) (n = 23,400 in 1992) as late summer and winter range. Studies of the CAH in the Prudhoe Bay and Kuparuk Oilfield areas have indicated a potential for displacement of caribou from traditional ranges and disruption of traditional movement patterns. The overall goals of the current study are to continue to identify potential conflicts between caribou and oil development and to recommend measures for minimizing the impact of oil development on caribou and their habitat. Emphasis is now shifting away from the use of satellite and conventional telemetry to study general movement and distribution patterns and toward intensive visual relocations, serial recaptures, and weighing of conventional collared cows and calves to investigate the importance of specific coastal plain habitats to summer nutrition of caribou.

OBJECTIVES

To synthesize existing knowledge on migration routes between seasonal ranges, selection of calving areas on the arctic coastal plain, selection of winter ranges, and long-term natality and mortality rates of radio-collared caribou.

STUDY AREA

The study area encompasses the entire range of the PCH in northern Alaska and in the Yukon and Northwest Territories in Canada.

METHODS

Migration Routes

Migration routes between summer and winter ranges were determined primarily from cumulative location data from satellite-collared caribou. Details of the satellite telemetry system were reported by Fancy *et al.* (1989*a,b*) and Whitten and Fancy (1991). For the purposes of analyses conducted so far, fall migration has been considered to occur during September and October and spring migration during April and May (Whitten and Fancy 1991). Extensive movements between distant ranges also occur during other times of the year, however, and future analyses may consider these other movements as well.

Selection of Calving Sites

Movement toward calving areas was monitored primarily by tracking satellite-collared cows. Movement toward specific calving sites within the overall calving area was monitored by intensive (daily) tracking flights to visually locate both satellite and conventional collared cows. General calving areas and specific calving sites were compared with topographic features, forage quality and availability, predator distribution, and annual variation in snow cover.

Sensitive Habitats

Seasonal ranges have been determined by plotting distributions of both satellite and conventional collared caribou, with additional data from general aerial surveys. This information is currently being used to prepare a report on sensitive habitats of the PCH for submission to the International Porcupine Caribou Board. Sensitive habitats will be designated according to criteria on frequency and duration of use, availability of alternatives, sex/age status of caribou using the sites, and vulnerability of caribou to various factors at particular times of the year.

The hypothesis that individual caribou maintain long-term fidelity to specific winter ranges has been tested using multi-year data from individual collared caribou and by comparing the relative numbers of collared caribou using various areas each year.

Long-term Natality Rates of Radio-collared Caribou

Natality of collared cows was determined annually by extensive monitoring on the calving grounds. Parturition status was determined using a combination of observations, including presence or absence of a calf, antler condition, and udder distension. Individual collared cows were relocated frequently from about 28 May to 10 June because past experience indicated that point-in-time observations do not positively identify all parturient females. Radiocollar batteries usually lasted 3-5 years, and we also recaptured many cows and fitted them with new collars so that a sizable sample of females with >2 years of natality data is now available for analysis.

Long-term Mortality Rates of Radio-collared Caribou

We studied long-term mortality by using data from radio-collared calves, yearlings, 2-year-olds, and adults. Annual mortality rates were calculated using a staggered entry, product-limit design (Pollack *et al.* 1989).

RESULTS AND DISCUSSION

Many results of this study have already been published in Annual Progress Reports, in U.S. Fish and Wildlife Service publications, and in professional journals. Only major findings are summarized here, along with new data from the current reporting period. A list of pertinent publications resulting from this project is provided in Appendix A.

A synthesis of available data on PCH calving ground use and calving site selection has confirmed traditional use of a high-density calving area overlapping the 1002 area. Survival of calves is higher when parturient cows are able to use this area and lower when they are displaced (by adverse snow conditions) to areas with more predators (Whitten *et al.* 1992*a,b*). Researchers continue to monitor the general correlation between a more coastal calving distribution and higher calf survival. However, research emphasis is currently shifting to the role of nutrition, forage quality, and forage quantity in calving site selection. The nutrition/habitat aspects of this work are being conducted primarily by the U.S. Fish and Wildlife Service, while ADF&G continues to be the lead agency in providing data on caribou distribution.

Calving surveys in 1993 were hampered by inclement weather that forced researchers to prioritize between daily tracking of collared cows, and capture and habitat use monitoring of collared calves. After obtaining minimally adequate data on calf habitat use, insufficient time and manpower remained to search adequately for collared cows outside the traditional high-density calving area, or to obtain visual locations of cows in peripheral portions of the coastal plain. Only 63 radio-collared adult cows were observed visually in early June, while 15 other cows were not seen until the end of the month. By combining data from early and late June, it appeared that 53 of 78 collared cows were parturient, 12 were definitely not parturient, and 13 were not seen until it was too late to determine parturition status. The 1993 parturition rate was thus between 68% and 85% (53/78 to 66/78), with a mean estimate of 76.3%. First month calf mortality was at least 34% (18/53 known to have been born). Mortality could have been as high as 47% (31/66) if the 13 cows of uncertain status had calves and lost them. The mean estimate for mortality would be 41.2% (calculated as the mean number of deaths divided by the mean estimate for number of calves born).

The observed calf:cow ratio at the end of June 1993 was 45% (35/78) which is also the product of the mean estimates for parturition and survival (1 minus mortality). This is the lowest late June calf:cow ratio ever observed among radio-collared adult cows in the PCH. Because of the 13 cows with undetermined parturition status, it remains uncertain whether to attribute the low calf:cow ratio to low birth rate, poor survival, or some combination of these factors, although circumstantial evidence allows some speculation. Radio signals from five of the cows of uncertain status were not even heard during calving surveys, suggesting those cows were not on the traditional calving grounds. Signals from the other uncertain cows were heard in peripheral areas, but they were never seen. Cows not on the main calving grounds at calving time are generally less likely to be parturient (Whitten *et al.* 1992*b*). Also, mean cow weights in November 1992 were similar to weights in November 1990, which correlated with low parturition; mean weights were higher in November 1991, when there was high parturition the following spring (D. Russell, Canadian Wildlife Service, pers. commun.).

The lowest calf survival ever recorded in the PCH was 57% in 1992. Mean weights and body condition scores of cows in late June 1993 were higher than in 1992 (D. Russell, Canadian Wildlife Service, pers. commun.), which should have correlated with better calf survival in 1993 (Cameron *et al.* 1993). Calf survival among the 53 cows known to have given birth in 1993 was 66%, and assuming calf mortality rather than nonpregnancy for the uncertain cows in 1993 would tend to drive this estimate too low relative to 1992. Therefore, it seems most likely that the low calf:cow ratio in late June 1993 was due primarily to unusually low parturition, but possibly exacerbated by poor calf survival.

Parturition rates for most caribou herds in Alaska were low during 1993, and the low-end estimate for the PCH (68%) was still higher than most other herds (P. Valkenburg, Alaska Department of Fish and Game, pers. commun.). PCH calf survival through the first month of life was probably also higher than most other herds. Nevertheless, the calf:cow ratio in the PCH at the end of June was probably not sufficient to sustain herd growth unless offset by excellent overwinter survival for all age classes.

A paper on field techniques for determining natality in free-ranging caribou has recently been completed and submitted for publication and is presented here as Appendix B. Work continues on long-term reproductive histories of individual females in the PCH. A decision will soon be made on whether to publish those data as a free-standing paper or to incorporate them with data from other herds in a more far-ranging examination of caribou productivity in relation to nutrition, weather, physiological condition, and individual female reproductive history.

Long-term data on population dynamics, including changes in population size, natality, and mortality, continue to be gathered on a routine basis. An aerial photocensus of the PCH was completed in July 1992. Quality of the photographs was adequate, and 156,800 caribou were estimated from the prints. However, the camera malfunctioned while photographing a group estimated to contain 3,000 caribou, and only 326 showed up on photos. Another 573 caribou were counted from 35mm photos of two small groups, and 432 caribou were counted directly and were never photographed. The final 1993 population estimate was raised to 160,000 to account for these additional caribou.

The 1993 estimate represents a 10% decline from the 178,000 counted in 1989 (-3.5%/yr). Poor calf production in 1991 and poor overwinter calf survival in 1991-92 were probably factors in the decline. Recent population dynamics of the PCH are discussed more thoroughly in Appendix C. A summary of the population dynamics and ecology of the PCH will also be presented as an invited paper at the Sixth North

American Caribou Workshop to be held in Prince George, B. C., Canada in March 1994.

A paper on winter range fidelity of the PCH was presented as an appendix in an earlier progress report (Whitten 1990) but has not yet been accepted for publication in a professional journal. This paper will be revised and resubmitted or presented at the Sixth North American Caribou Workshop.

Budget reductions and changes in research priorities among cooperating agencies over the past 2-3 years have resulted in deployment of fewer satellite collars (generally <10 and often <5) and infrequent and incomplete tracking surveys except during summer. This has greatly slowed the accumulation of new data on migration routes and winter range use, but the Alaska Department of Fish and Game will continue to cooperate with the U.S. Fish and Wildlife Service and other agencies to analyze existing data as well as new data that will continue to accumulate.

Finally, a new research project on the relationships between female body condition, calf production, and calf survival has been approved under the State of Alaska Capital Improvement Projects program. This project is also being funded by Federal Aid in Wildlife Restoration Project 3.39. Results of this project should provide background information on PCH physiological condition and reproductive potential under undisturbed conditions and will aid in detecting the occurrence and magnitude of the effects of any future development.

ACKNOWLEDGMENTS

Valuable assistance to this project was provided by Larry Pank, Noreen Walsh, Brad Griffith, and Tom McCabe of the U.S. Fish and Wildlife Service; Wayne Regelin, Dan Reed, Pat Valkenburg, and Bob Hunter of the Alaska Department of Fish and Game; Don Russell and Debbie van de Wettering of the Canadian Wildlife Service; Cor Smits and Dorothy Cooley of the Yukon Department of Renewable Resources; and Karen Gerhart of the University of Alaska-Fairbanks.

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APPENDIX A. Representative publications based on work funded all or in part by Federal Aid in Wildlife Restoration Project 3.34.

This list includes journal publications and agency completion or summary reports. It does not include agency annual or progress reports.

Fancy, S. G., L. F. Pank, D. C. Douglas, C. H. Curby, G. W. Garner, S. C. Amstrup, and W. L. Regelin. 1989. Satellite telemetry: a new tool for wildlife research and management. U.S. Fish and Wildl. Serv. Resour. Publ. No. 172. 54pp.

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Appendix B. Manuscript submitted to Journal of Wildlife Management, September 1993 (with minor format changes for presentation in this report).

27 August 1993
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RH: Estimation of Parturition Rates in Caribou · Whitten

USE OF ANTLERS AND UDDERS TO ESTIMATE PARTURITION RATES IN FREE-RANGING CARIBOU

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Abstract: Observations of antler retention and udder distension relative to parturition status were obtained from 23-89 radio-collared Porcupine Caribou (Rangifer tarandus) Herd females observed repeatedly during the calving seasons of 1983-90. Among cows that grew antlers, 99% with ≥1 hard antler (n = 303) at the onset of the calving period were parturient and 86% with shed antlers (n = 164) were not parturient. Most (91%) of the parturient females with antlers kept at least 1 antler until after their calves were born. Although not all parturient cows developed distended udders, most showed some distension before giving birth (91%; n = 160 with pre-partum data). Cows with distended udders usually retained them for some time after their calves died, but the duration was highly variable. Parturition determinations based on antler retention, udder distension, and/or presence of a calf were highly reliable early in the calving season and somewhat less so later on. Estimation of early calf mortality based on differences in proportions of cows with distended udders and cows with calves was problematical because cows with dead calves and pregnant cows could both have large udders. Nevertheless, low calf:cow ratios could be attributed qualitatively to low natality versus poor survival.

J. WILDL. MANAGE. 00(0):000-000

Key words: antlers, caribou, parturition, Rangifer, udders.

Caribou and reindeer (Rangifer tarandus) are the only cervids in which females regularly bear antlers, although non-antlered females can be common in some populations (Bergerud 1976, 1978; Butler 1986; Thing et al. 1986). Antlered females occur very rarely in other cervids (Whitehead 1972, Bubenik 1983). Non-pregnant Rangifer females tend to shed antlers during late winter, while pregnant cows retain theirs until parturition. Thus, pre-calving counts of antlered versus unantlered females can be used to estimate parturition rates (Lent 1965, Skjenneberg and Slagsvold 1968, Skoog 1968, Bergerud 1978).

Udder distension can also be used to estimate parturition and calf mortality rates for Rangifer (Bergerud 1964, 1971, 1978). In parous females, visibly distended udders develop slightly before or after parturition, persist during lactation, and remain visible even after a calf dies.

In this paper I discuss antler retention and udder distension in free-ranging cows of the Porcupine Caribou Herd that were observed repeatedly during calving time. Commonly overlooked errors in both antler and udder survey techniques are identified, and guidelines and limitations on their use in estimating calf production and survival are suggested.

Funding was provided by the Alaska Department of Fish and Game (Federal Aid in Wildlife Restoration Funds) and the U.S. Fish and Wildlife Service (Arctic National Wildlife Refuge and Alaska Fish and Wildlife Research Center). F. J. Mauer and S. G. Fancy helped with aerial observations of calving caribou. D. C. Miller and P. Valkenburg safely and efficiently piloted aircraft and also helped with observations. R. D. Boertje, J. L. Davis, D. J. Reed, and P. Valkenburg critically reviewed the manuscript.

METHODS

Radio-tracking surveys of the Porcupine Herd range in northeastern Alaska and the northern Yukon Territory were flown daily (weather permitting) from about 27 May through 30 June 1983-90; essentially all calves were born during this period annually. Caribou were observed visually with a low, slow pass (6-15 m AGL, 100 km/hr) from a Piper PA-18 Super Cub or Bellanca Scout aircraft. Location, presence or absence of a calf, antler status (0, 1, or 2 hard antlers remaining; new velvet antler stubs present), udder condition (large, medium, small, or no visible udder), and any qualitative information pertinent to possible pregnancy (i.e., grossly distended abdomen or bloody vulva) were recorded.

Numbers of collared females varied from 23 in 1983 to 89 in 1988, and a total of 491 potential calving events was monitored. Presence of 1 or more hard antlers or of a distended udder was considered to indicate pregnancy. Females showing these traits were relocated every 1-2 days until a calf was observed or until the indications of pregnancy disappeared. Following parturition, females were relocated at approximately 2- to 3-day intervals to check for calf mortality. Antler status was monitored regularly after parturition, but udder distension was not recorded as long as the calf remained alive. If a known parous cow was observed without her calf, she was relocated at least once more to confirm calf mortality. Females without hard antlers or distended udders (usually with new velvet antlers and located toward the periphery of the traditional calving area) were relocated at least twice before being judged not to be parturient.

Frequency of relocation among individuals also varied due to logistic constraints such as locally bad weather or distance from the operations base. Time gaps in relocation data often necessitated use of intervals rather than a specific number of days for antler drop or udder distension relative to parturition. Sample sizes for various analyses differ because not all data could be recorded for each sighting. For example, presence of a calf and antler status were often observed during turbulent flying conditions, while udder condition was not. Or, if a cow already had a calf when first observed, pre-partum udder condition could not be recorded, but retention of antlers post-partum (i.e., ≥ 1 day) could. All data were gathered incidental to a larger calf production/mortality study (Whitten et al. 1992), and many cows were no longer monitored once their calves were confirmed dead. Therefore data on udder regression are limited.

Capture records of radio-collared females were examined for evidence of polled (i.e., never growing antlers) or 1-antlered individuals. Antler status for females collared in March or April was compared with antler and parturition status 6-8 weeks later during calving.

Parturition status of collared cows estimated from single observations was compared with the determination based on all observations to approximate the error rate in estimating parturition from point-in-time samples versus multiple observations of marked individuals. Comparisons were made for a survey early in the calving period (i.e., observation nearest to 1 June) and a survey after most calving had already occurred (i.e., observation nearest to 10 June).

Nine parous cows were captured and radio-collared on 1 and 2 June 1987 and their calves taken away to be used in feeding/nutrition studies at the University of Alaska, Fairbanks. These females, for which calf loss date was positively known, were relocated on 12 June and their antler and udder status was recorded.

RESULTS

Incidence of Polled and One-antlered Phenotypes

Three percent of the Porcupine Herd females captured as adults from 1981 through 1990 ($\underline{n}$ = 146) were polled (possessed no antlers, pedicels, broken stubs, or shed antler scars and had apparently never grown antlers). However, this sample was biased because large-antlered females were captured preferentially during the first few years of this study. An unbiased sample of females originally captured as newborn calves in 1983, 1984, and 1988 indicted 13% polled females ($\underline{n}$ = 24). None of the polled cows developed antlers in any subsequent years. All those captured as adults had calves the next spring. Those captured as calves first gave birth as 3-year-olds, which is the norm for Porcupine Herd cows (Whitten et al. 1992). Cumulatively, the polled cows produced calves in 11 of 13 possible cases.

Four females captured as adults (3%; $\underline{n}$ = 146) possessed only 1 antler and had no shed antler scar on the other side. One died before the next calving season and the others were again 1-antlered in 7 of 10 possible calving events. The exceptions were cases where 2 antlers were recorded on the first observation of a season but were never confirmed by a second sighting. Cumulatively, the "1-antlered" cows produced calves on each of 10 possible occasions.

Antler Shedding Prior to the Calving Period

Antler status of radio-collared cows prior to the calving period was noted only if they were captured in March or early April. In addition to the polled and 1-antlered animals mentioned above, 1 female appeared antlerless and 5 appeared to have only 1 antler due to breakage close to the skull. The only evidence of shed antlers at capture was for 2 cows that had each shed 1 antler, but both had calves in June. Fifteen percent of the cows with 2 antlers in March or April ($\underline{n}$ = 145) were later determined not to be pregnant.

Many cows known to possess antlers or to be capable of growing antlers had lost them by the onset of calving at the end of May. Most (86%; $\underline{n}$ = 164 with shed or possibly broken antlers) were never seen with a calf and never developed distended udders. However, 10% did give birth and 4% developed distended udders. Ninety-three percent of females with 1 or more hard antlers remaining at the onset of calving ($\underline{n}$ = 303) were later observed leading calves and another 6% developed distended udders; less than 1% were never seen with a calf or a distended udder.

Antler Shedding During the Calving Period

Most parous females known to possess antlers did not complete antler drop until after their calf was born (Table 1). Individual cows usually shed both antlers within a 4-day period. Only about 2% dropped 1 antler more than a week before the other, but the longest observed interval between losing antlers was $\geq$45 days (i.e., for the 2 cows that had already shed 1 antler in April). Ninety-one percent kept at least 1 antler after parturition, and 80% retained both. In 10% of the parous cows the last antler was shed >1 week post-partum (maximum = 20 days). Only 5% of the parous cows with antlers had already shed both before calving surveys began, but 9% dropped both antlers pre-partum. At least 17% lost 1 antler before parturition. Thus hard antlers on females during the calving period were a strong indicator of parturition but not of whether cows were pre- or post-partum.

Udder Distension Relative to Parturition Date

At least 96% of known parous cows that were observed pre-partum (n = 160) developed distended udders before parturition. The remainder could have developed udders between the last pre-partum sighting and calf birth. The longest recorded pre-partum distension was 21 days. At least 31% of the parous females had distended udders $\geq$5 days pre-partum, 16% $\geq$7 days, and 8% $\geq$10 days. These are minimum figures because many cows already had distended udders when first sighted. Seven percent had no visible udders on 1 or more days after the udder was first noted, implying that udder distension, or the ability to discern it, could vary.

Udder Distension After Loss of Calves

Female caribou usually retained large distended udders after their calves died, but the duration of distension varied greatly. Eleven cows retained large udders for as long as they were watched; 4 of these were followed <5 days after their calves died, 4 more for 6-10 days, and 3 for 23-27 days. Thirteen cows were observed until their udders regressed to the point where they were no longer visible; maximum duration for udder distension was <5 days for 2, 6-10 days for 3, 11-15 days for 3, 16-19 days for 3, and 20-21 days for 2. Four cows showed no udder distension either pre-partum or after their calves died. These cows may have failed to lactate. Another cow had no visible udder 5 days after calf loss, did show an udder 10 days after, and had none again 15 days after. Perhaps this cow did not lactate in time to nourish her calf, which died.

Udder Distension in Cases of Inferred Parturition

There were 26 instances where parturition was inferred from udder distension but never corroborated by observation of a calf (20 of these cows also had hard antlers). In 17 such cases the distension period exceeded 10 days (maximum = 28 days) but, because of gaps in relocation data, could have included several days of lactation as well as pre-partum and post-calf-loss distension. In 1 female, udder distension definitely did not exceed 6 days, and in the remaining cases udder data were recorded too infrequently to accurately determine the duration of distension.

Parturition was inferred for 2 females based on antler retention only. One had no distended udder $\pm$2 days from dropping its antlers, and the other had no udder for 9 days after shedding antlers.

Discrepancies in Determination of Parturition Status From Single Versus Multiple Observations of Marked Cows

On a given day, any or all of the positive indicators of parturition (distended udder, hard antlers, or presence of a calf) might be missing. Thus a determination of parturition status based on observations for that day only could be in error. No single criterion nor any set of criteria for determining parturition was invariably infallible when applied only once (Table 2). Presence of a calf was a poor indicator of parturition rate both early and late in the calving period because it accounted for neither pregnancy nor calf loss. Nevertheless, presence of a calf was very useful as a positive indicator because it was easy to detect and obviated the need to look for any other criteria. Both udder data and antler data resulted in moderately low errors (ca. 10%) early in the calving period, when essentially all cows were being monitored. The combined use of all indicators of parturition was more reliable than any single criterion and resulted in low error rates (ca. 3%) early in the calving period.

Although antler shedding severely reduced the usefulness of antler data for determining parturition by 10 June, the error rates for udder distension and all criteria combined appeared to remain low (ca. 5%) and not significantly different from the rate for all criteria combined on 1 June (Table 2). However, the actual error rates for all criteria on 10 June were probably higher than the values presented in Table 2 because many cows known to have lost calves were no longer being monitored. That such cows may have introduced more errors is demonstrated by data from 9 cows whose newborn calves were taken away on 1 and 2 June 1987 (Table 3). By 12 June, only 4 of these cows appeared to be parturient based on udder distension alone, 4 based on antler retention alone, and 6 based on antlers and/or udders.

Use of Udder Data to Estimate Calf Mortality

Udder surveys to estimate calf mortality assume that all parturient cows have udders and that all cows with udders, but no calves, have lost their calves (Bergerud 1964, 1978). Not all parturient Porcupine Herd cows had distended udders at the same time. Among the parturient cows for which udder distension was recorded on 10 June ($\underline{n}$ = 306; Table 2), 16 (5.2%) had no visible udders, 6 of these had lost calves, 3 were pregnant, and 4 were of uncertain status (i.e., their calves were never actually seen). Underestimation of parturition may have actually exceeded 5.2% because many cows that had lost calves were not included in the 10 June surveys.

Furthermore, lack of a calf at heel did not equate with calf mortality. Of 46 cows with udders, but no calves on 10 June (all years combined), only 12 had definitely lost calves, 18 were still pregnant, and 16 were of uncertain status (i.e., their calves were never actually seen and may or may not have already been dead by 10 June).

DISCUSSION

Porcupine Herd females with hard antlers during calving were almost certainly (99%) parturient. Skoog (1968), Bergerud (1976), and many other researchers and managers have also concluded that the incidence of non-pregnant females with hard antlers at calving time must be insignificant in wild Rangifer populations, based on close agreement between pre-calving antler counts and subsequent calf:cow ratios. In contrast, Lent (1965) warned that up to 20% of the antlered females on calving grounds might be barren, but Skoog (1968) pointed out that Lent had probably erred in assuming calving was complete at the time of his survey, when in fact many antlered cows were still pregnant. Nevertheless, the possibility of barren cows retaining hard antlers into the calving period should not be categorically dismissed. Espmark (1971) reported that 3 of 11 non-pregnant reindeer cows raised in pens shed their antlers during the normal calving period and not before. Skjenneberg and Slagsvold (1968) also warned that predictions of natality based on antler counts do not always prove true.

Visibly distended udders were also highly indicative of parturition in Porcupine Herd cows during the calving period. Although some lactating cows still showed visible udders during September, close examination of several hundred shot or immobilized cows from the Porcupine Herd and the adjacent Central Arctic Herd indicated no udder distension during March through mid-May such as occurs at calving time and would be visible from an aircraft. Thus, during the calving period non-pregnant cows would be unlikely to retain any visible udder distension from the previous year. Nevertheless, false indications of current year parturition based on overwinter persistence of a distended udder cannot be completely discounted. Skjenneberg and Slagsvold (1968) stated that abandoned reindeer calves can be saved by presenting them to a non-parturient female still nursing her yearling. Possibly, then, some of the females in this study that had only small distended udders and were never observed with newborn calves were really nursing yearlings.

Unfortunately, there are no similarly reliable indications for determining when caribou are not pregnant. Pre-partum shedding, resulting in antlerless but parturient cows, occurred in about 10% of Porcupine Herd females. In the Porcupine Herd, most pre-partum shedding occurred after the first calves in the herd had been born. However, in some populations, especially on particularly good range, pre-partum shedding may be more common and may occur well before calves are born (Skjenneberg and Slagsvold 1968, Wika 1980, Gagnon and Barrette 1992). More importantly, genetically polled females (which probably occur in all populations and are common in some) are always antlerless, and the polled condition has no bearing on pregnancy status. Finally, breakage can cause females that actually have antlers (and are thus likely parturient) to appear antlerless.

Growth of new velvet antlers may be a more reliable indicator of non-pregnant status than the mere absence of hard antlers. Many Porcupine Herd females presumed to be non-parturient were already growing new velvet antlers by 1 June, whereas cows known to be parturient did not begin new antler growth until about 12-15 June. Parturition in polled cows would still be indistinguishable by this characteristic, however, and velvet antlered females have been known to give birth (Bergerud 1976, Wika 1980, Gagnon and Barrette 1992). In 1985 an uncollared Porcupine Herd female with 15- to 20-cm forked velvet antlers was observed guarding the carcass of a newborn, underweight calf.

Lack of a distended udder also does not necessarily indicate that a cow has not been pregnant. Some parturient females may simply fail to lactate. More important, however, is the variation in time over which udder distension occurs in individual females relative to the period during which calving occurs in a population. At no time during the calving period did all parturient Porcupine Herd cows have distended udders simultaneously. Some females did not develop distended udders until shortly (1-3 days) before parturition, some showed udders only a short time after calf mortality, and udders on some cows were visible on some days but not others.

Characteristics such as an enlarged abdomen or bloody discharge from the vulva are very limited as corroborative evidence of parturition status. Few Porcupine Herd cows obviously "looked pregnant," even within a few days of parturition, and many cows that did not look pregnant were. Physical appearance might be useful in studies relying on long-term, close-range observations from the ground, but is probably worthless for aerial surveys.

In this study, most cases of parturition were eventually corroborated by observation of a calf. In contrast, non-pregnant status could never be absolutely confirmed. Some cows without antlers or udders were pregnant, and observations on 2 or more days were sometimes necessary before a diagnosis of not pregnant could be confidently assigned. Non-pregnancy was ultimately assumed only for females never showing any signs of pregnancy, although some of these could have given birth and lost calves between sightings or before surveys began.

The cumulative parturition rate determined in this study was 4% for 2-year-old females (n = 53 possible calving events) and 79% for adults aged 3 years or older (n = 438). These figures are in general agreement with data from other North American caribou populations, where few 2-year-olds but most older females are parturient (Bergerud 1978, 1980).

CONCLUSIONS AND RECOMMENDATIONS

Reliability of natality estimates depends not only on obtaining a representative sample, but also on accurately recognizing which animals are parturient. In contrast to most mammal species, parturiency in barren-ground caribou is fairly easy to recognize because of antler retention, udder distension, and high visibility on the usually open and gentle terrain of calving habitats. In the past, failure to take advantage of these traits and to conduct natality surveys has led to unnecessary arguments over whether pregnancy failure or poor calf survival is affecting populations.

Determining reproductive rate in populations of free-ranging caribou still presents some problems, however. Neither antler retention nor udder distension are infallible indicators of parturition, and geographic segregation of pregnant and non-pregnant cows makes representative sampling difficult.

The ideal time to estimate parturition rate is probably at about the beginning of the peak calving period, or a few days after the first calves are born. In the Porcupine Herd, this would be about 1 June. All cows with calves, hard antlers, and/or udders should be considered parturient. The error rate using this technique on 1 June in the Porcupine Herd was only about 3%. Reliability of natality estimates diminishes after the peak calving period for several reasons. Antler data become unreliable (due to shedding), and estimates become more dependant on udder data alone, especially if early calf mortality is high. In the Porcupine Herd, the error rate in distinguishing parturient cows just after the peak of calving increased to about 5% (and in reality was probably considerably higher).

Reliability of natality estimates may be compromised in populations with high proportions of polled females, again because the estimate becomes more dependent on udder data without the compensatory data on antler retention. In the Porcupine Herd, the polled and probably the 1-antlered conditions were genetic (i.e., permanent). Where genetically polled females are a factor, a parturition estimate could be calculated based on the proportion of antlered females in the herd (Bergerud 1964, 1978), although estimation of that figure would in itself be difficult. In some herds, possession of antlers may be affected by nutrition, and parturition rates among antlered and unantlered cows may differ (Thing et al. 1986). Antler data would then be useless for estimating natality.

Comparison of distended udder counts with counts of calves at heel to determine early calf mortality must be approached very cautiously. Empirical data from the Porcupine Herd indicate that such surveys may result in biased calf mortality estimates. Udder condition cannot distinguish between a near-term pregnant cow and one that has lost her calf. Surveys conducted up to a week after the peak of calving can substantially overestimate calf mortality by mistaking still pregnant cows as having already lost calves. Only counts conducted long after the peak of calving can eliminate this bias, but by that time ability to even determine which cows are parturient will have declined significantly. This is not to say that udder data are useless for determining early calf mortality, however. A large difference between the proportions of cows with udders and cows with calves late in the calving period would undoubtedly indicate high calf mortality, although precisely quantifying the mortality or positively detecting a low rate would remain problematic.

As a final caution, the literature on Rangifer suggests that populations differ in antler characteristics according to both genetic and nutritional conditions. Udder distension may also vary with nutrition. Therefore, the results presented in this paper should be considered as indicative of the Porcupine Herd. Other researchers should first corroborate these relationships or determine more appropriate herd-specific relationships before relying on antler and udder observations to investigate parturition.

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Table 1. Antler loss relative to parturition date for radio-collared Porcupine Caribou Herd females, 1983-90.

	Minimum interval before (days)[a]											Minimum interval after (days)[a]														
	>10	10	9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9	10	11	12	13	>13	Total
1983									1[b]			2		3	2	3	1	4					1			17
1984											2	4	1	4	3	2	1			1						18
1985	2											6	2	5	8	3		4		1	1		1	1		34
1986												13		1				1	1							16
1987								1				8	2	6	4	1	2		4		1					29
1988	1			2							4	20	4	2	6	10	5	1	2	1	1		1			60
1989						1				1	2	2		13	10	8	7		4							49
1990						1	1	2		3		1	2	15	3	9	5	4	3	1						50
Total	3			2		2	1	3	1	4	8	56	11	49	36	36	21	14	14	4	3		3	1	1	273

9%[c] 91%

6% 10%

[a] Minimum interval for loss of both antlers. Data are compressed toward parturition date because caribou were not observed every day, and actual intervals could have been longer.

[b] Number of females observed.

[c] Percent of 273 parturient females for which antler shedding data were recorded.

Table 2. Errors[a] in determining parturition status for radio-collared Porcupine Caribou Herd females on 1 June and 10 June 1983-90.

Year	1 June criteria				10 June criteria			
	Udder distension	Antler retention	Calf at heel	Combined	Udder distension	Antler retention	Calf at heel	Combined
1983	3/13[b]	0/21	17/21	0/21	2/19	9/20	6/20	2/20
1984	3/10	3/30	22/30	2/30	1/22	16/28	5/28	3/28
1985	6/56	6/60	21/60	1/60	2/42	29/43	12/43	2/43
1986	Insufficient Data							
1987	0/26	6/45	28/48	1/48	4/42	28/48	12/48	6/48
1988	9/75	13/86	37/86	4/86	4/72	53/79	18/79	6/80
1989	4/76	8/76	40/76	2/76	0/53	39/53	10/53	0/53
1990	2/64	13/67	27/67	1/67	0/51	22/51	6/51	0/51
All years	27/320 8.4%	49/385 12.7%	192/388 49.5%	11/388 2.8%	16/306 5.2%	195/322 60.6%	69/322 21.4%	17/322 5.3%

[a] Errors resulted when a parturient cow lacked a distended udder, antlers, a calf-at-heel, or all three on a particular survey date.

[b] Number of errors/number of females sampled.

Table 3. Antler and udder status on 12 June 1987 of 9 radio-collared female caribou whose calves were removed on 1 or 2 June 1987.

	Udders		
Antlers	None	Small	Large
0	3[a]	2	0
1	1	0	0
2	1	0	2

[a] Number of caribou.

APPENDIX C.

DEMOGRAPHY OF THE PORCUPINE CARIBOU HERD, 1982-1992

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Fancy, S. G., K. R. Whitten, and D. E. Russell. Demography of the Porcupine caribou herd, 1982-1992. Can. J. Zoology

Abstract: Population size, parturition rates, and sex- and age-specific survival rates were determined for the Porcupine caribou herd (Rangifer tarandus) in northeastern Alaska and northwestern Canada between 1982 and 1992. The herd increased at an annual rate of $r = 0.0467$ between censuses in July 1983 ($n = 135\,000$) and July 1989 ($n = 178\,000$). The mean parturition rate for 225 radio-collared cows aged ≥3 years monitored for 603 animal-years was 79% and did not differ among years. First-year survival of calves was 51%. Survival of calves through their first month differed among years (range 57-90%). Annual adult survival rates were 84.2% for 225 females and 82.6% for 42 males. Hunting mortality for the herd was 2-3% annually. Population estimates generated by a computer model using parturition and survival rates for the herd closely tracked population trends determined from photocensus data. Growth of the herd is most sensitive to annual variation in survival of adult females, followed by measures of calf production and survival.

Key words: caribou, population dynamics, demographics, population model, Alaska, Yukon Territory, radiotelemetry, survival

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Introduction

The Porcupine caribou herd (PCH; Rangifer tarandus granti) has received considerable attention since 1970 because of its migration between the United States and Canada, its importance to subsistence hunters, and concerns about potential effects of roads and industrial development within its range. Intensive field studies and monitoring of caribou using radio- and satellite telemetry have been conducted cooperatively by the U.S. Fish and Wildlife Service (USFWS), the Alaska Department of Fish and Game (ADFG), the Canadian Wildlife Service (CWS), and the Yukon Department of Renewable Resources (YDRR), to address concerns related to increased harvest along the Dempster Highway and potential oil and gas exploration and development on the PCH calving grounds.

Because of the high costs and considerable logistical difficulties associated with studies of barren-ground caribou herds, much of our understanding of the dynamics of these large populations has been inferred from small sample sizes or studies lasting only a few years. The importance of factors such as predation, weather, and food supply in limiting or regulating caribou populations is still very much in debate (e.g., Bergerud 1980; Messier et al. 1988). The accuracy of the commonly-used methods of using udder counts to estimate parturition rates (Bergerud 1964) and conventional life table analyses to estimate survival has recently been questioned (Bergerud 1980; Martell and Russell 1983; Whitten 1991a). The current practice for many herds of using radio-collared caribou to estimate population parameters should lead to more reliable results and, consequently, improved understanding of caribou population dynamics.

This paper summarizes the demography of the PCH between 1982 and 1992. We quantify herd size and trend based on photocensus data, and we present estimates of parturition and age-specific survival rates for the herd based on relatively large samples of radio-collared animals. We also describe a computer model that we developed using our estimates of parturition and survival, that closely tracked herd size based on photocensus data. Sensitivity analyses using the model point to the importance of adult female survival and calf production and survival as determinants of herd growth.

Methods

Study Area

The range of the PCH (ca. 250 000 km^2) includes the arctic coastal plain of northeastern Alaska and the northern Yukon Territory, and mountainous and forested habitats of northeastern Alaska, the northern Yukon Territory, and the Northwest Territories of Canada (Fig. 1; Fancy et al. 1989). Primary wintering areas occur in the Ogilvie and Richardson mountains in Canada and in the Chandalar, Sheenjek and Coleen drainages south of the Brooks Range in northeastern Alaska. Most calves are born between 28 May and 12 June on the coastal plain between the Canning River in Alaska and the Babbage River in Canada, with more concentrated calving occurring in the Arctic National Wildlife Refuge south of Kaktovik, Alaska (Fancy and Whitten 1991). Vegetation, geomorphology and climate of the study area have been described by Spetzman (1959), Wiken et al. (1981) and Garner and Reynolds (1986).

Capture and Radio-tracking

Adult and yearling caribou were captured with a helicopter and net gun or dart gun (Fancy et al. 1989; Fancy and Whitten 1991). Caribou were fitted with radiocollars, most containing a sensor that increased the pulse rate if the collar was motionless for ≥4 h. Expandable radiocollars were placed on 1-3-day-old calves using methods described by Garner et al. (1985) and Whitten et al. (1992b). Projected battery life was 18 months for calf transmitters and 40 months for transmitters placed on yearlings and adults. Some transmitters functioned considerably longer, and many caribou were recaptured and recollared. Age of captured caribou was determined by tooth eruption patterns and body size (Miller 1974).

Instrumented caribou were monitored from a variety of fixed-wing aircraft using standard techniques. Generally, we used a high-performance Piper Supercub[1] and Cessna 185 aircraft in summer to locate caribou visually, and mapped their locations precisely. During most winter flights we used larger, faster aircraft and sometimes recorded only approximate positions and whether the transmitter pulse rate was normal or fast (i.e., indicating probable mortality).

Population Size

Photographic censuses (Davis et al. 1979; Valkenberg et al. 1985) of the PCH were conducted during early July in 1979, 1982, 1983, 1987, 1989 and 1992. Formation and distribution of large post-calving aggregations was monitored by intensive aerial reconnaissance, radio-tracking, and satellite telemetry to determine when the caribou were optimally aggregated for photographing. All active transmitters were accounted for prior to or during each census. When caribou were suitably aggregated, they were photographed with a Fairchild T-11 aerial mapping camera mounted in the belly of a DeHavilland Beaver aircraft. Photographs of large groups overlapped by approximately 30% within and between transects to ensure complete coverage. Photo scale varied between 1:1000 and 1:3000 depending on the size and configuration of each group.

We used terrain features or recognizable caribou to determine overlap between adjacent photos. We then drew lines directly on black and white contact prints (23 x 23 cm) to denote which portion of each photo to count so that caribou appearing on adjacent photos where counted only once. We used acetate grid overlays, magnifying lenses, and hand-held tally registers to facilitate counting the caribou. Numbers of calves and adults were tallied separately.

In 1983, 5-10 counters practiced counting representative photos until their tallies were consistent. The census photos were then divided among the counters and their individual tallies were summed to give the population total. Beginning in 1987, we assessed accuracy and consistency among 10 observers participating in each count by comparing tallies of a series of reference photos distributed blindly through each observer's stack of photographs. A mean count across observers was calculated for each reference photo. Weighted least squares through the origin (Draper and Smith 1981, p. 108) was used to estimate a correction factor for each observer as described by Fancy et al. (1992). The correction factor for each observer was applied to each observer's total count so that the final, overall total for all photographs could be adjusted as if a single "average" observer had done the entire count (Fancy et al. 1992).

Parturition Rates

We estimated parturition rates by intensively monitoring radio-collared cows from about 28 May to 30 June each year. A female's parturition status was determined from a combination of criteria, including presence or absence of hard antlers, udder distension, and presence of a live or dead calf (Whitten 1991a). Cows not showing any overt signs of parturition but not obviously barren (e.g, located along migration trails far from the calving area or already growing new velvet antlers), were relocated 1 or more additional times to ensure that no pregnancies were missed.

Survival Rates

Previous studies indicated that substantial mortality of Porcupine Herd calves occurs during the first 48 h of life (Whitten et al. 1992b). (Survival estimates based solely on the fate of radio-collared calves would overestimate survival because many calves die before they can be collared.) Therefore, we estimated calf survival for the first month of life (i.e., June) by intensively monitoring collared cows and recording the survival or disappearance of their calves.

During 1983 through 1985, and in 1988, we captured and attached mortality-sensing radio collars to 1-3-day-old calves to study the chronology, causes, and geographic patterns of mortality on the main calving grounds (Fancy and Whitten 1991; Whitten et al. 1992b). The fate of these calves was used to calculate a survival rate for the following 11-month period, from July 1 through May 31.

We determined survival of yearlings and 2-year-olds by monitoring known-age radio-collared animals. Known-age individuals included caribou captured in March 1983 when they were 10 (n = 37) or 22 months old (n = 6), and the survivors of calves collared in 1983-1985 and 1988. Survival rates for calves, yearlings and 2-year-olds were calculated by product-limit estimators (Kaplan and Meier 1958) using the staggered entry design (Pollack et al. 1989). Because of small sample sizes, data for yearlings and 2-year-olds for all years were pooled into monthly intervals.

We calculated separate survival rates each year for adult females and males. Because of logistical difficulties in covering our large study area, we varied the number and duration of time intervals each year depending on the timing of surveys and the occurrence of dead and missing animals during each survey. Tracking flights to detect mortalities were flown almost daily from late May through mid-July in most years, but surveys during the rest of the year were irregular and less frequent (e.g., usually 3-6 winter flights each year). Some flights covered the PCH's range in only Alaska or Canada, and it was necessary to combine such flights to obtain a complete survey of the herd. Winter surveys usually covered only winter range, and summer surveys covered only summer range. Therefore, mortalities were sometimes not detected until long after they occurred.

Whenever possible, we assigned deaths to the time period in which they most likely occurred. For example, an animal that was heard on "live" transmitter mode in November, and was not heard again until it was found dead near the same location the following October, would be assigned as dead in the period following the November location rather than in the period when its carcass was found. We seldom found all functional transmitters on a single survey except in midsummer when the entire herd was concentrated in a small area. Therefore, we censored caribou from the samples only if they were never found again. Transmitters on the majority of caribou that were censored had outlived their projected battery life, or were among a batch of inferior transmitters purchased in 1987.

We estimated hunting mortality by repeating the above analyses for adult caribou, but including as dead only those animals that were shot by hunters. Caribou that died of other causes were censored from the sample.

Population Modelling

We developed a computer model to determine whether we could accurately simulate herd growth (as determined by photocensus data) from our estimates of population parameters for the herd. We also wanted to determine the sensitivity of the model to changes in various population parameters. We applied parturition and survival rate estimates to a computer simulated caribou population to estimate its rate of change between 1983 and 1989. We chose that period because photocensus data indicated steady population growth, and because we did not collect data on overwinter calf survival, yearling and 2-year-old survival, and 2-year-old productivity after 1989. The model for the simulated population was constructed in computer spreadsheet format by (1) assuming a starting population size of 135 000 caribou on 1 July 1983, as determined by the 1983 photocensus of the PCH; (2) apportioning the 135 000 caribou among sex and age classes using composition data obtained during photocensuses and winter counts between 1980 and 1987 (International Porcupine Caribou Board 1990; our unpubl. data); (3) assuming a sex ratio of 50:50 at birth (Kelsall 1968; Miller 1974); (4) applying mean parturition rates for 2-year-old and ≥3-year-old females to the number of cows alive on 1 June each year; (5) applying mean survival estimates to the appropriate sex and age classes; and (6) calculating recruitment as the product of mean June calf survival and mean calf survival from July to May.

The model calculated the number of caribou in each sex and age class on 1 July of each year, 1983-1989. Rate of increase determined by the model was compared with that determined from photocensus data by testing for equality of slopes of the log linear regressions (Zar 1984, p. 292).

Results

Population Size and Trend

The Porcupine herd increased steadily from 1979 to 1989 (Fig. 2). The minimum estimate of herd size in 1983 was 135 000 adults and calves. In 1987, we actually counted 172 361 caribou on the photographs, but adjusted the count to 165 000 because approximately 7000 caribou from the adjacent Central Arctic Herd (CAH; n = 23 000 in 1992) were included in the photographs. Assignment of those caribou to the CAH was based on the distribution of radio-collared caribou from the CAH and a visual estimate of numbers of CAH caribou in the area just before the distributions of the 2 herds overlapped. The 1989 adjusted estimate of 178 000 caribou (± 463 SD) was similarly determined from an initial count of 187 944 caribou from the PCH and CAH on the photographs, and an estimate of 10 000 CAH caribou in the area. Between 1983 and 1989, the finite rate of increase for the PCH was 1.048 (r = 0.0467; Fig. 2).

In 1992, 156 800 caribou were counted on census photos. The camera malfunctioned while photographing a group estimated to contain 3000 caribou, and only 326 caribou were counted on the photos. Two small groups photographed with 35 mm film contained 573 caribou, and another 432 caribou were counted directly but never photographed. The final 1993 population estimate was increased to 160 000 to account for these additional caribou. The rate of decline between 1989 and 1992 was $\underline{r} = -0.0355$.

Parturition Rates

We found no evidence of Porcupine herd females giving birth as yearlings. Parturition among 2-year-olds was also rare, with only 2 of 53 (3.8%) giving birth. Most females first gave birth at 3 years old, although there was some evidence that 3- and 4-year olds had lower parturition rates than those aged ≥5 years (Whitten 1991b). Annual parturition rates for 225 cows aged ≥3 years monitored for 603 total reproductive attempts were 74 to 89% between 1982 and 1992 (Table 1). The 1983-1989 mean was 79%. We found no difference among years for adult female parturition rates (log likelihood test, $\underline{G} = 7.01$, $\underline{p} = 0.725$).

Survival Rates

The two calves born to 2-year-olds did not survive >48 h; therefore, 2-year-old cows do not appear to contribute to recruitment. June survival for calves born to cows aged ≥3 years averaged 73.4% between 1983-1989 and differed among years (log likelihood test, $\underline{G} = 24.93$, $\underline{p} = 0.002$). Perinatal calf survival (i.e., survival ≤48 h of birth) was not related to geographic distribution of calving (Whitten et al. 1992a). Post-perinatal calf survival was higher for years when most calving occurred on the coastal plain in Alaska than in years when calving occurred in the foothills or mountains or in Canada (Whitten et al. 1992a,b).

We found no differences between 11-month survival estimates (1 July - 31 May) for female and male collared calves in any of the 4 years for which we have data. Data for both sexes were therefore pooled to test for differences in calf survival among years. Calf survival functions were similar for all 4 years (K-sample test; $\underline{X}^2 = 11.9$; 3 df; $\underline{p} = 0.76$; Lee 1980, p. 144). Overall survival for 245 calves between 1 July and 31 May was 70.1% (Table 2). Estimated annual survival of calves, calculated as the product of June survival of calves of collared cows, and 11-month survival of collared calves, was 51.0%.

Survival functions were similar for female and male yearlings (Table 3; log-rank test; $\underline{X}^2 = 1.31$; $\underline{p} = 0.25$). We also found no difference between survival of female and male 2-year-olds ($\underline{X}^2 = 0.58$; $\underline{p} = 0.45$). None of the 15 2-year-old males at risk on June 1 died during the year that they were monitored.

Mean annual survival during 1983-1989 was 84.2% for adult cows and 82.6% for adult bulls (Table 4). Hunting mortality as determined from radio collars was 1.8% for adult cows and 3.9% for adult bulls. The estimated annual harvest based on harvest reports from sport hunters and villages during 1985-1989 was <3% (International Porcupine Caribou Board 1990).

Population Modelling

We entered age-specific parturition rates and age- and sex-specific survival rates for 1983-1989 into the spreadsheet model, and found no difference between the growth rate of the simulated population (r = 0.0306) and that determined by periodic photocensus data for the PCH during the same period (r = 0.0467; t = 0.170, 2 df, p > 0.50). Furthermore, calf/cow ratios for the simulated July population (50:100) were consistent with those obtained by direct counts of the PCH (International Porcupine Caribou Board 1990).

We determined the sensitivity of the model to each estimate of parturition and survival by determining for each parameter the difference between the empirical estimates used in the model (1983-1989 values) and the value needed to cause a 10% decrease in the modeled 1989 population estimate of 161 887 (Table 5). The most sensitive parameter was the survival rate for adult females; the projected population would decrease by 10% if the female survival rate decreased by only 3%. The model was also sensitive to changes in calf survival and the parturition rate for adult females (Table 5). The projected population would decrease by 10% if calf survival or adult parturition rates were ca. 8-10% lower than empirical estimates.

The model was least sensitive to survival rates for yearling and 2-year-old males, and the parturition rate for 2-year-old females.

Discussion

Estimates of herd size from the 1970's and in 1982 suggest that the Porcupine herd increased slowly but consistently during the decade preceeding our study (Fig. 2). Between 1983 and 1989, the herd increased at a finite rate of increase (λ) of 1.048 (based on photocensus data), but the recent 1992 estimate of 160 000 caribou indicates that the herd declined (λ = 0.965) between 1989 and 1992. We are confident that the herd increased between 1983 and 1989 and then decreased between 1989 and 1992 in spite of adjustments that had to be made to the 1987, 1989 and 1992 census data. Our estimates of annual survival for adult cows between 1989 and 1992 were similar to the long-term mean, giving us no reason to suspect that increased adult mortality was an important factor in the decline. However, a decline of 3-5% in adult female survival would fall within the confidence interval of our estimates and would be sufficient to stabilize population growth. Our estimated parturition rate for adult cows in 1991 was only 74%, and low calf production in that year probably contributed to the herd's decline. June calf survival in 1992 was only 57%, the lowest on record. We did not collect any radiotelemetry data to monitor calf survival after June between 1989 and 1993. Spring composition surveys conducted in March 1990 suggested good overwinter survival of calves (43 calves/100 cows), but counts in 1992 showed poor survival (21 calves/100 cows). Thus, we suspect that recent increases in late summer through winter mortality of calves may also have been a factor in the herd's decline.

We found significant variation in calf survival between 1983-1989, when the herd was growing steadily. Calving date and early calf survival are influenced by maternal condition during late pregnancy (Cameron et al. 1993). In a study of perinatal (i.e., within 48 h of birth) mortality of PCH calves, Roffe (1993) found that the majority of calves found dead shortly after birth were stillborn or died of emaciation or malnutrition; these conditions are determined primarily by maternal condition during gestation and early lactation (Thorne et al. 1976; Verme 1977). Whitten et al. (1992b) found that predation by wolves, grizzly bears, and golden eagles (Aquila chrysaetos) was the primary cause of mortality for calves between 3 and 30 days of age. Higher post-perinatal mortality of calves occurs in years of late snowmelt when calving is displaced further south and east of the primary calving area south of Kaktovik (Fancy and Whitten 1991; Fancy et al. 1992; Whitten et al. 1992a,b).

Our survival rate for adult males is probably an overestimate. The number of males at risk each year (mean = 9.7, as compared with 53.8 for adult females) was too small to provide a reliable estimate. In most ungulate populations, males suffer higher mortality than females, presumably because of energetic stresses during the rut (Geist 1971; Clutton-Brock et al. 1985). The skewed adult sex ratio in the PCH (62 bulls/100 cows) also indicates that survival of males is lower than that of females. When our estimate of adult male survival is used in the population model, the resulting bull/cow ratio is higher than expected based on composition counts, and increases each year. To maintain a 62:100 bull/cow ratio throughout the model projection, the adult male survival rate would need to be 0.72.

We probably overestimated yearling survival as well because of the relatively high number of censored animals (Table 3). Most (31 of 34 females and 28 of 31 males) of the censored yearlings were captured as calves and fitted with expandable radiocollars with an expected battery life of 18 months. If any of these yearlings died after their transmitters failed or were shed, then our estimates of yearling survival would be inflated.

Messier et al. (1988) compared values of several demographic parameters for two expanding caribou populations, the Avalon Peninsula herd (Bergerud et al. 1983) and the George River herd prior to 1984. For the Avalon Peninsula and George River herds, respectively, Messier et al. (1988) reported a mean adult sex ratio (M:F) of 64:100 and 63:100; pregnancy rates of 73% and 67%; percentage of calves in the autumn population of 25% and 23%; and natural adult mortality rates of 6% and 8%. Comparable values for the PCH are 63:100 for the adult sex ratio, a parturition rate of 74% (adjusted to include 2-year-olds; n = 656), a 20% autumn calf percentage, and 13-14% natural mortality for adults. Thus, the main difference between demographic parameters for the PCH and those for two rapidly expanding herds (r = 0.12 for the Avalon Peninsula and r = 0.11 for the George River herd) is the higher natural mortality of adults in the PCH.

Because of the importance of the PCH to subsistence hunters and potential threats of oil and gas development in its range, we benefited from a much higher level of funding for our research than most agencies could obtain. We were able to obtain relatively large sample sizes, and our estimates of parturition and survival were sufficiently accurate to model population trend from 1983-1989. However, because we did not collect adquate data on all of the important population parameters after 1989, we were unable to predict the population decline between 1989 and 1992. Studies are now underway to determine whether the size of the PCH peaked in 1992, and to investigate the role of maternal nutrition on calf production and survival. Our results indicate that with adequate data, changes in population size can be predicted over periods of a few years. However, photocensus data remain as the most reliable means of monitoring size and trend of barren-ground caribou herds.

Acknowledgements

We thank R. D. Cameron, J. Carey, G. W. Garner, D. B. Griffith, R. B. Harris, G. M. Lortie, L. D. Martin, M. A. Masteller, F. J. Mauer, T. R. McCabe, E. J. McDonald, D. C. Miller, G. A. Muehlenhardt, W. A. Nixon, L. F. Pank, C. Smits, D. Sowards, P. Valkenburg, N. E. Walsh, G. J. Weiler and D. Young for assistance with caribou capture, radio-tracking, and censuses. J. C. Greslin and D. J. Reed assisted with computer programming and data analyses. G. W. Garner, T. R. McCabe, L. F. Pank, and W. L. Regelin obtained funding and administered the study. We appreciate critical reviews of the manuscript by W. B. Ballard, D. J. Reed, and P. Valkenburg. This study was supported in the United States by research and operational funds from the USFWS, administrative funds from the Pittman-Robertson Program, and funds from ADFG through Federal Aid in Wildlife Restoration Projects W-22-5 and W-22-6. In Canada, funds were provided by the Northern Oil and Gas Action Program, the Northern Roads and Airstrips Division, Indian and Northern Affairs Canada; the Polar Continental Shelf Project, Energy, Mines and Resources Canada; and research funds from the CWS and YDRR.

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Table 1. Parturition rates for 225 adult (≥3-year-old) cows and survival of their calves through June, Porcupine herd, northeastern Alaska-northwestern Canada, 1982-1992. No data are available for June calf survival in 1982 or 1986.

Year	n	No. giving birth	Parturition rate	No. Monitored through June	Survival rate	Calves/100 Cows on 1 July
1982	9	8	0.89			
1983	23	20	0.87	20	0.65	57
1984	31	25	0.81	25	0.84	68
1985	56	43	0.77	43	0.65	46
1986	42	31	0.74			
1987	51	40	0.78	40	0.70	55
1988	91	76	0.84	71	0.71	62
1989	74	58	0.78	57	0.74	58
1990	74	61	0.82	54	0.90	74
1991	74	55	0.74	54	0.82	61
1992	78	67	0.86	67	0.57	
	49					

Table 2. Eleven-month Kaplan-Meier survival estimates for radio-collared calves of the Porcupine caribou herd alive on July 1 in 1983, 1984, 1985 and 1988.

	Females			Males			Both sexes			Log-rank test[a]	
Year	n	Survival	95% CI	n	Survival	95% CI	n	Survival	95% CI	X^2	P
1983	28	0.7669	0.5855-0.9483	24	0.7895	0.5754-1.0035	52	0.7445	0.5836-0.9055	0.087	0.768
1984	23	0.7391	0.5694-0.9089	32	0.6207	0.4610-0.7805	55	0.6676	0.5401-0.7952	0.703	0.402
1985	26	0.7379	0.5467-0.9291	25	0.7350	0.5496-0.9204	51	0.7379	0.5980-0.8779	0.001	0.975
1988	46	0.6649	0.4701-0.8597	41	0.5626	0.3604-0.7649	87	0.6178	0.4363-0.7994	0.051	0.821
Combined							245	0.7007	0.6259-0.7754		

a Log-rank test comparing survival functions for male and female calves each year.

Table 3. Kaplan-Meier survival estimates for yearling and 2-year-old radio-collared caribou from the Porcupine herd.

Sex	Age	At risk on June 1	Died	Censored	Survival	95% CI
Female	1	84	4	34	0.9289	0.8580-0.9997
	2	49	1	0	0.9592	0.9044-1.0140
Male	1	53	4	31	0.8474	0.6986-0.9963
	2	15	0	1	1.0000	

Table 4. Kaplan-Meier survival estimates for adult (≥3-year-old) cow and bull radio-collared caribou from the Porcupine herd, 1 June 1982 to 31 May 1992.

Year	At risk on June 1	Died	Censored	Added[a]	Survival	95% CI
Cows						
1982	10	1	0	15	0.9000	0.7837-1.0163
1983	24	2	2	14	0.9205	0.8243-1.0166
1984	34	7	4	35	0.7793	0.6524-0.9061
1985	58	6	10	5	0.8896	0.8013-0.9780
1986	47	11	12	37	0.7498	0.6414-0.8582
1987	61	4	9	43	0.9302	0.7787-0.9603
1988	91	20	8	12	0.7793	0.6990-0.8595
1989	75	13	6	12	0.8292	0.7512-0.9073
1990	68	12	10	24	0.8419	0.7666-0.9172
1991	70	14	4	18	0.8190	0.7426-0.8953
Bulls						
1982	7	0	1	5	1.0000	
1983	11	1	2	0	0.9000	0.7236-1.0764
1984	8	2	3	8	0.7500	0.5284-0.9716
1985	13	3	1	0	0.7552	0.5344-0.9761
1986	9	1	1	4	0.9167	0.7669-1.0664
1987	12	1	1	5	0.9091	0.7704-1.0478
1988	15	4	4	0	0.7222	0.4584-0.9860
1989	8	0	2	1	1.0000	
1990	7	0	2	2	1.0000	
1991	7	2	0	10	0.7143	0.5211-0.9075

[a] Number of new caribou captured or that became 3 year old during annual interval.

Table 5. Sensitivity of a simulated caribou population to changes in single demographic parameters. Empirical estimates are compared with the value of each parameter needed to cause a 10% decrease from the modeled 1989 total population of 161 887.

Parameter	Empirical estimate	Value needed for 10% decrease	Difference
Parturition rate, adult cows	0.7900	0.6940	0.0960
Parturition rate, 2-year-olds	0.0377	0.5365[a]	0.4988[a]
June calf survival	0.7280	0.6402	0.0878
July-May calf survival	0.7007	0.6105	0.0902
Yearling male survival	0.8474	0.4631	0.3843
Yearling female survival	0.9289	0.7447	0.1842
2-year old male survival	1.0000	0.4612	0.5388
2-year old female survival	0.9592	0.7756	0.1836
Adult male survival	0.8260	0.6558	0.1702
Adult female survival	0.8420	0.8113	0.0307

[a] The 1989 population projection would decrease by only 0.7% if the parturition rate for 2-year-old cows was zero. The 1989 population would be 10% greater than 161 887 if the parturition rate for 2-year-olds increased to 0.5365.

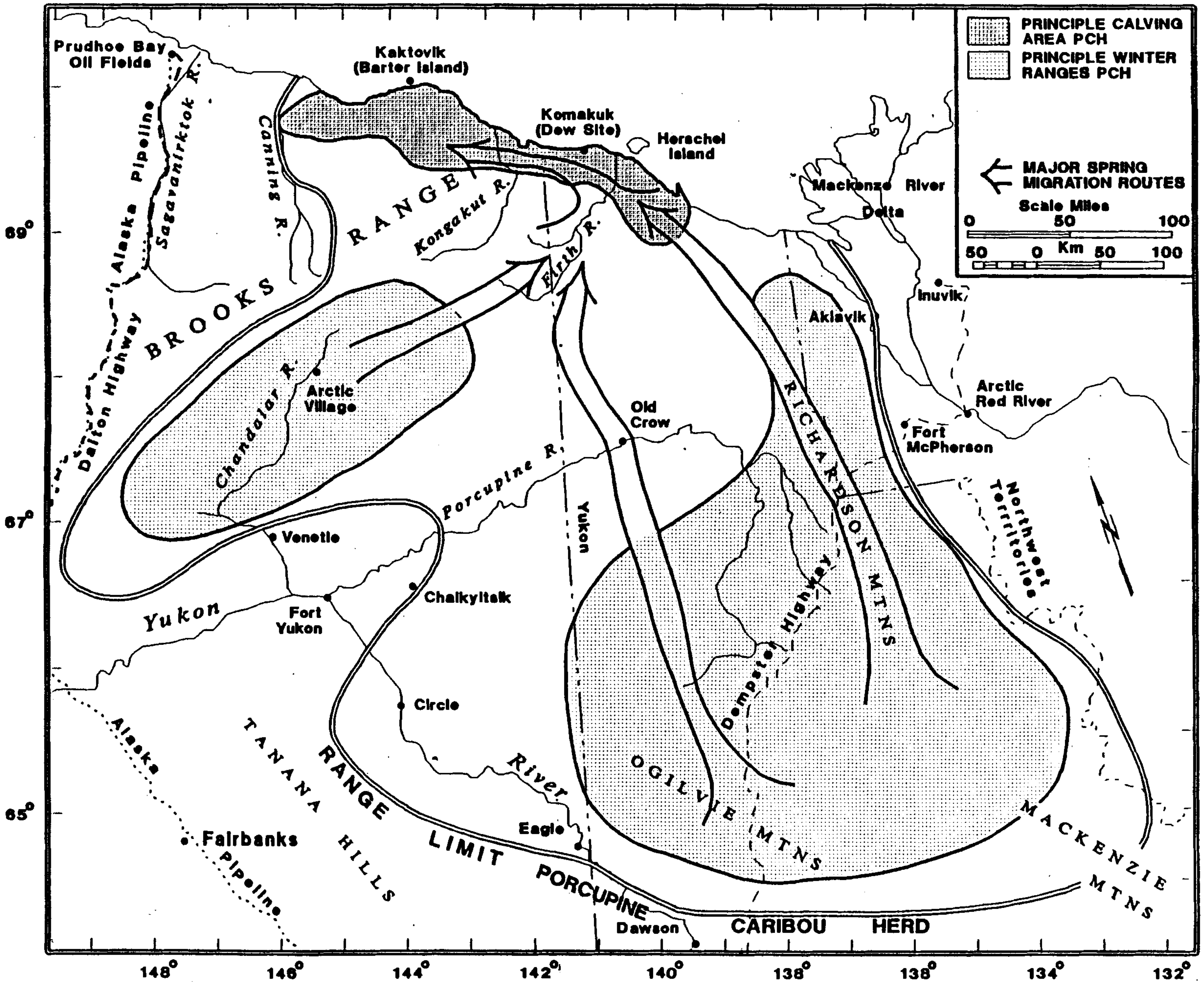


Figure 1. Annual range of the Porcupine caribou herd.

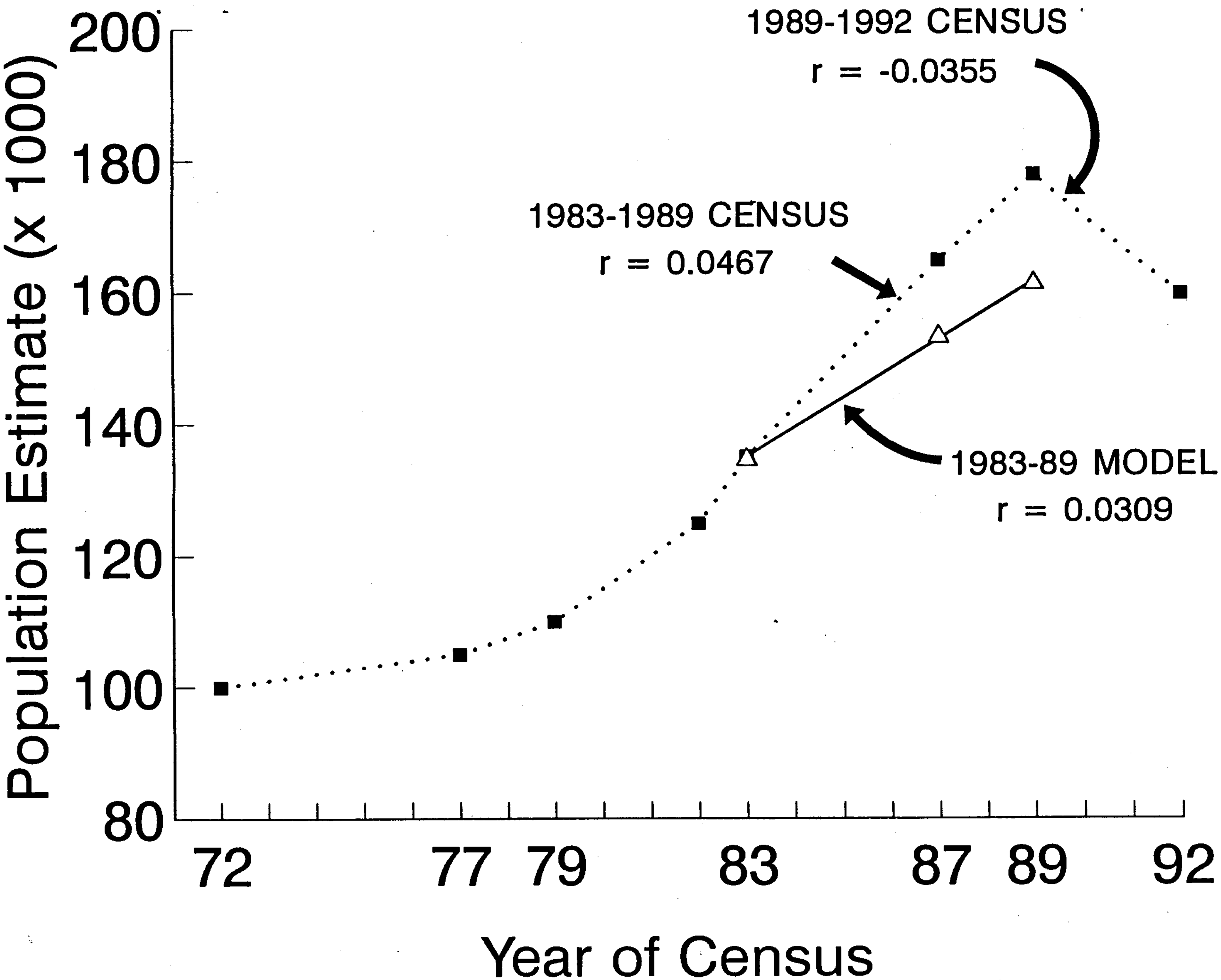
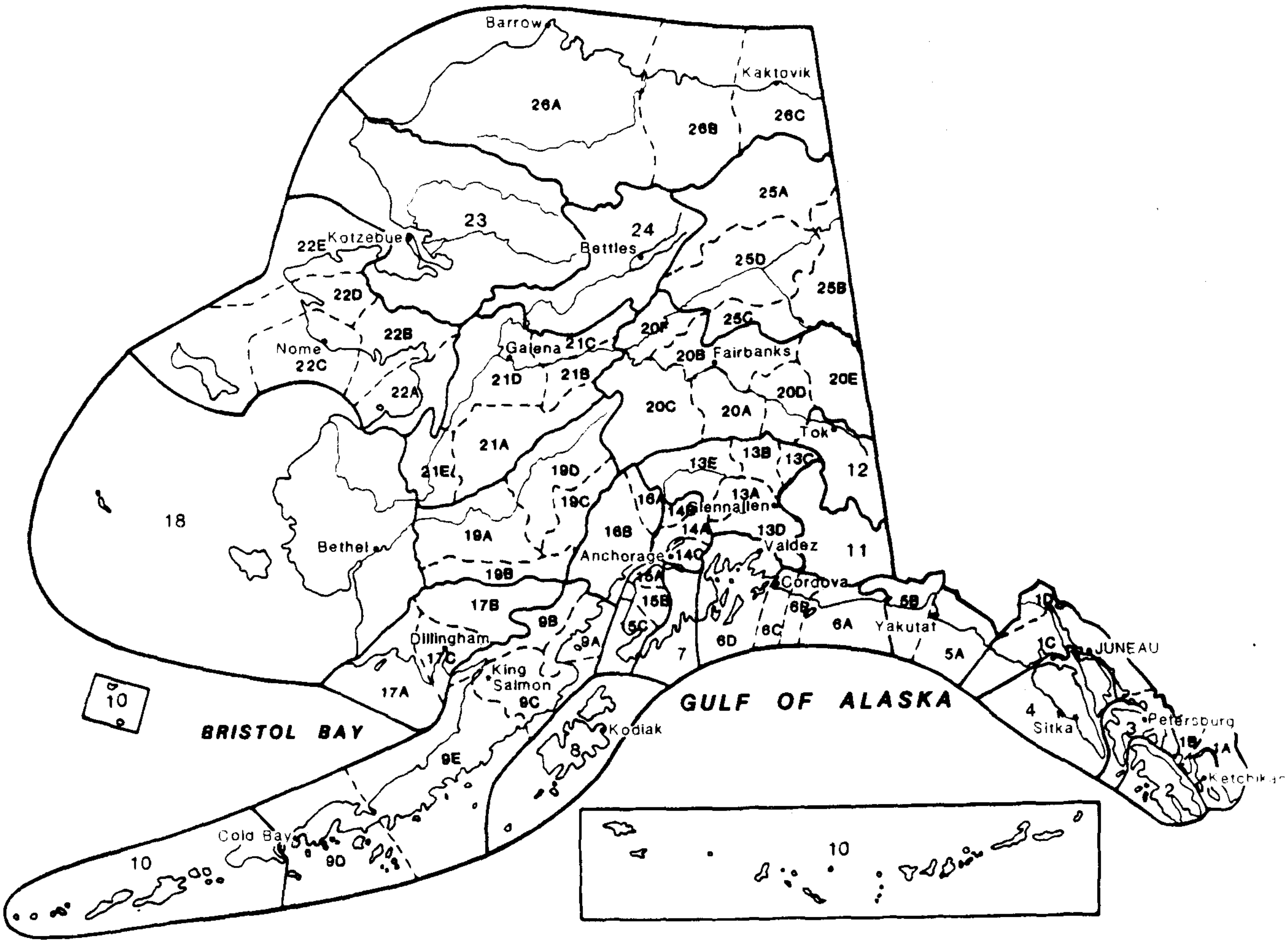


Figure 2. Estimates of population size for the Porcupine caribou herd as determined by photocensus data (solid squares) between 1972 and 1992. Open triangles show estimates from a population model based on mean estimates of parturition and survival, 1983-1989.

Alaska's Game Management Units



Federal Aid in Wildlife Restoration

The Federal Aid in Wildlife Restoration Program consists of funds from a 10% to 11% manufacturer's excise tax collected from the sales of handguns, sporting rifles, shotguns, ammunition, and archery equipment. The Federal Aid program then allots the funds back to states through a formula based on each state's geographic area and the number of paid hunting license holders in the state. Alaska receives 5% of the revenues collected each year, the maximum allowed. The Alaska Department of Fish and Game uses the funds to help restore, conserve, manage, and enhance wild birds and mammals for the public benefit. These funds are also used to educate hunters to develop the skills, knowledge, and attitudes necessary to be reponsible hunters. Seventy-five percent of the funds for this project are from Federal Aid.