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

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SUMMARY

Satellite transmitters were placed on 65 adult females of the Porcupine and Central Arctic Caribou (Rangifer tarandus) Herds from 1985 to 1990. Satellite collars were reliable and cost effective. Caribou movements and activities followed similar annual patterns in both herds, with highest rates in midsummer and lowest in midwinter. Seasonal migrations were directional rather than maximal. Migratory routes followed high ground in the boreal forest zone and valleys, troughs, or plateaus through high mountains. Spring routes were more constricted than fall routes because of the effects of snowcover. Movements onto the calving grounds tended to follow the receding snowline. Calving caribou preferentially selected the coastal plain of the Arctic National Wildlife Refuge between the Hulahula and Aichilik Rivers, except when delayed by late-melting snow. Predator avoidance was probably the primary factor in calving-site selection, and calf mortality was lower in the preferred calving area than elsewhere. Forage characteristics were also more favorable in the area between the Hulahula and Aichilik Rivers.

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

CONTENTS

BACKGROUND

The Porcupine Caribou (Rangifer tarandus) Herd (PCH; n = 178,000 in July 1989) migrates seasonally between wintering areas in the boreal forests of northwestern Canada and northeastern Alaska and calving grounds on the arctic coast of the Yukon Territory and Alaska. Large-scale development of nonrenewable resources is planned throughout this resource-rich area. Concerns about the impact of development on the PCH have been expressed by numerous governmental agencies, environmental groups, and subsistence users. International concern is exemplified by the establishment of an agreement between the U.S. and Canadian governments to protect the PCH and its habitat.

Geological and seismic explorations for oil and gas have already been conducted on the traditional calving grounds of the PCH. It is likely that some sort of development will occur in the near future. The PCH wintering areas in the Ogilvie and Richardson Mountains in Canada and on some lands in Alaska are also subject to intensive oil and mineral exploration. The Dempster Highway, completed in 1979, provides access to much of the herd's winter range in Canada. Protection of habitats on calving grounds and key winter ranges and mitigation of the impacts of development require detailed knowledge of habitat use, movement patterns, and travel corridors.

The large size, remote location, and international movements of the PCH make it difficult and costly to study. Monitoring movements and habitat use through direct observation or by relocating caribou equipped with conventional radio collars has proven difficult. The feasibility of using satellite radio collars to monitor daily movements of caribou in the PCH was tested in 1984. The prototype satellite radio collars (i.e., PTT's for "platform transmitter terminals") provided accurate and reliable data at a reasonable cost. Second-generation satellite transmitters were developed and deployed in 1985, and results have demonstrated a capability for describing migrational routes and movement patterns in greater detail than had been previously possible. In particular, we have noted extensive mid- and late-summer movements not previously reported. Also, mercury tip switches within the PTT's have provided data on daily activity patterns of caribou. Third-generation transmitters with greater accuracy and programming capabilities became available in 1986 and have been deployed on some caribou. PTT's have also been deployed on Central Arctic Herd (CAH; $\underline{n}$ = 16,000 in 1986) females to compare movements of the highly migratory PCH with the more sedentary CAH and also to describe reactions of caribou to existing oil field development.

This study is one component of a cooperative program between the Alaska Fish and Wildlife Research Center (U.S. Fish and Wildlife Service) and the Alaska Department of Fish and Game. The overall goals of this cooperative study are 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.

OBJECTIVES

To identify migration routes between summer and winter ranges.

To determine movement patterns on the arctic coastal plain in relation to topographic features, broad habitat types, and existing or potential petroleum production and transportation facilities.

STUDY AREA

The overall study area encompassed the entire ranges of the PCH and CAH in northern Alaska and in the Yukon and Northwest Territories in Canada. The CAH lives all year north of the arctic divide, and it is relatively sedentary, compared with the PCH, which migrates long distances between summer ranges in arctic tundra habitats and winter ranges in the boreal forest zone.

METHODS

Satellite Telemetry

Details of collar design, the satellite telemetry system, location determination, and data acquisition and retrieval have been reported by Fancy et al. (1989a, 1989b, 1990c) and Harris et al. (1990). Up to 20 adult female caribou at a time from the PCH and 10 from the CAH were equipped with collars bearing both PTT and standard transmitters. Each PTT transmitted 6 hrs/day, provided 2-5 locations daily, and functioned for approximately 1 year. Collared caribou were monitored until they died or could no longer be located because of failure of both the PTT and standard transmitters. Caribou were recaptured and fitted with new collars as PTT's failed or neared the end of projected battery life. When a collared caribou died, the collar was retrieved, refurbished as necessary, and placed on a different caribou. In addition to location data, each PTT transmitted data on internal canister temperature (an approximation of ambient temperature). Caribou activity was monitored by a microprocessor that measured the amount of time (i.e., s/min) a mercury tip switch had been activated. A short-term activity index, with a maximum value of 60, was recorded during the minute prior to each transmission. Long-term activity was computed as the sum of 60-second counts for a 24-hour period. The activity counters, in conjunction with location data, could also function as "mortality sensors." The date a caribou died could usually be determined from a combination of location data and activity counts near zero.

Location and sensor data were processed through a series of programs for entry into the ARC/INFO and MOSS/MAP Geographic Information Systems. Travel routes and distances were calculated from the straight-line distances between successive relocations.

Migrational Routes

During the fall (September, October) and spring (April, May), migrational routes for the PCH were determined by plotting the cumulative movements of all satellite-collared caribou. Because detailed digitized terrain and habitat maps are unavailable for much of the winter range and for nearly all of Canada, migratory movements can only be compared with very broad terrain and habitat features discernible from topographic maps; therefore, analysis is necessarily more qualitative than quantitative. Satellite location data were also supplemented by fixed-wing tracking of caribou with standard radio collars. Trail systems were noted during tracking flights as well as during general reconnaissance surveys of the migrations. Trails were clearly visible in snow, and fresh trails could also be distinguished along river bars and in tundra vegetation during the summer and fall. In this way, data from satellite relocations could be compared with routes used by other members of the herd; however, because of shortfalls in anticipated funding from USFWS cooperators, supplementary data were collected only for limited time periods and geographical areas.

Calving Site Selection

Data from satellite-collared caribou were used in conjunction with conventional radiotelemetry data; habitat and terrain maps; estimates of forage quantity, quality, and digestibility; snow cover maps; and information on predator distribution to determine factors involved in calving-site selection. Findings (Fancy and Whitten 1991) have been prepared for publication and appear in Appendix A.

Insect Relief Habitat

Although the analysis of PTT location data in relation to insect relief habitat has been delayed because of funding constraints, it has recently been initiated by USFWS personnel. Because no direct data on insect abundance were collected, the analysis will concentrate on habitat use and movements in relation to weather data, including PTT internal canister temperatures, Kaktovik weather station data, and ANWR field camp data. General relationships between weather patterns and insect activity are available from previous studies in the Prudhoe Bay area (White et al. 1975; Cameron and Whitten 1979, 1980, 1981; Dau 1986).

RESULTS AND DISCUSSION

General Findings

Capture-recapture dates and current (Apr 1990) status of satellite-collared caribou are summarized in Tables 1 and 2. PTT's in the CAH have been deployed so that some collared caribou are likely to frequently encounter oilfield facilities (i.e., captured in or near the Prudhoe Bay and Kuparuk oilfields), while others are likely to encounter development only infrequently (i.e., captured in the Canning River-Sadlerochit Mountains area east of the oilfield).

Findings on system capability and cost effectiveness of satellite telemetry and on basic seasonal movements and activity patterns for satellite-collared caribou of the PCH and CAH were reported in Fancy et al. (1989a, 1989b, 1990c) and Harris et al. (1990). Satellite transmitters proved to be reliable and accurate. Transmitters that operated 6 hrs/d were located a mean of 3.5 times daily and transmitters operating 12 hrs/d were located a mean of 8.0 times daily. Mean location error of second-generation transmitters used from 1985 to 1990 was 763 m; whereas, the mean error for third-generation transmitters used after 1986 was 483 m. The high frequency and accuracy of locations allowed very detailed determination of movement patterns. For studies requiring frequent locations, satellite telemetry was cost-effective, compared with the conventional radio telemetry method using airplanes (Table 3). Satellite telemetry also functioned during adverse weather conditions that would have precluded any conventional tracking.

Seasonal movement and activity patterns determined by satellite were similar in both the highly migratory PCH and the more sedentary CAH (Figs. 1 and 2). Both herds showed peak daily movements and activity during July; the lows occurred during January through April. The mean annual distance traveled by PCH cows (4,355 ± 150 [SE] km) exceeded that for CAH cows (3,031 ± 97 [SE] km), probably reflecting increased directional movement during spring and fall migrations. Nevertheless, some CAH cows that never moved more than 100 km from their capture sites had larger annual movements than some PCH cows that moved up to 300 km between seasonal ranges. Thus even apparently sedentary caribou moved great distances during the course of a year. Maximum movements for PCH cows (up to 5,055 km/yr) were the longest documented for any terrestrial animal.

Movements and activity documented during this study are consistent with the hypothesis that caribou have evolved extremely efficient locomotion (highest efficiency of walking reported for any terrestrial mammal; Fancy and White 1987), such that the energetic costs of moving long distances are usually small, relative to the potential gains of finding more abundant or higher-quality forage. Daily movements are greatest during midsummer, when high levels of harassment from insects drive caribou away from preferred feeding sites, to which they return whenever insect levels abate. From an energetic standpoint, extensive movements both within and between seasonal ranges are adaptive, if they result in even small increases in daily eating time, eating rates, or forage digestibility.

Satellite telemetry data have been used in conjunction with standard telemetry data and general survey observations to prepare a number of technical reports on the PCH and CAH (excluding P-R Annual Progress Reports for the current project), including Fancy et al. (1989c, 1990a, 1990b) and Whitten et al. (1989, 1990). More detailed analyses of CAH PTT's in relation to oilfield structures will continue to be reported under the Federal Aid in Wildlife Restoration Project (Cameron et al. 1989b, 1990a). Findings on the CAH also appear in Cameron et al. (1989a, 1990b) and Smith and Cameron (1990).

Migrational Routes

Satellite telemetry data indicated that caribou are highly mobile at all times of year, except during midwinter and a brief period at calving for parturient cows. Our data do not support the traditional notion that long and arduous migrations separate seasonal ranges on which caribou remain sedentary. Daily movements in summer far exceed those during spring and fall. The seasonal shift-pause theory (Skoog 1968) more nearly describes the continuous wanderings of caribou, although it still implies a more sporadic or episodic annual movement pattern than indicated by satellite telemetry. What distinguishes spring and fall migrations is the more consistently directional net movement, and they generally end up far from where they were at the beginning of the period, having travelled between predominantly taiga or alpine habitats and arctic tundra. Fall and spring migrations occur during the September-October and May-June periods, respectively. Most of the long-distance shifts in herd distribution occur during these periods, although some directional movement also occurs before and after them.

Cumulative plots of satellite-collared caribou movements indicate that neither fall nor spring movements are random, rather they follow definite and rather narrow corridors (Figs. 3 and 4); however, there are many corridors, and the number of caribou using particular ones vary widely both within and between years. For the most part, corridors occur at higher elevations with relatively gentle terrain, avoiding extensive spruce woodlands, wet lowlands, and precipitous mountains. Thus migrational paths tend to be in hilly country over much of the taiga and tundra zone and valleys, troughs, or plateau areas through high mountains.

During autumn (mainly September) most Porcupine caribou follow a circular path around the Old Crow Flats in the Yukon Territory (Fig. 3). Movement is generally clockwise, and most caribou cross portions of all of the herd's 3 major wintering areas (i.e., the Ogilvie Mountains in the Yukon, the Richardson Mountains along the Yukon/NWT border, and the Chandalar area in Alaska south of the Brooks Range). Caribou crossing the Porcupine River upstream from Old Crow during September may appear to be heading toward the Ogilvie wintering area; however, they are just as likely (and in recent years more likely) to winter in either the Chandalar or Richardson areas. Use of particular wintering areas may be a function of proximal cues (e.g., weather, forage phenology, and photoperiod) along the route and where caribou are when these cues occur. Timing of events may also be a factor; e.g., a sudden snowstorm in early September may not elicit the same response as one in mid-October. Caribou may not react to proximal cues uniformly. Thus much of the PCH may be "staged" along the international border northwest of Old Crow Flats around the 1st of October each year, when sudden movements to the winter areas begin; however, they may follow numerous routes out of the area to different wintering grounds.

During spring deep snow in lowland and wooded areas and occasionally mountain passes can delay the onset of migration as well as greatly constrict the movement corridors (Fig. 4). This is in contrast to the relatively diffuse fall migrational corridors that are used before snow accumulation hinders movements. The apparent constriction of migrational routes in spring may result, in part, from caribou generally following windswept, low-snow terrain; i.e., hilly country and valleys to the south and north of the Arctic Divide, respectively. Constriction of routes probably also results from caribou following each others tracks through deep snow. Few caribou appear to break trail across deep snow--most follow other caribou tracks, and eventually the spring migration trails become well-trodden, well-packed "highways" across areas that otherwise would be difficult to negotiate.

Whereas fall migration paths generally diverge from a broad staging area around Old Crow Flats (Fig. 3), spring trails tend to converge north of the Arctic Divide in the windswept British and Barn Mountains (Fig. 4). This area, as well as the coastal plain south of Herschel Island, normally has little snow accumulation. Further westward movement toward the core calving area south of Barter Island proceeds along the foothills at the southern edge of the coastal plain and only spills out onto the plain in Alaska as the snow melts.

Movement toward the eastern coastal plain in the Yukon Territory is probably an innate response, although learned tradition cannot be ruled out. Caribou moving out of the Chandalar wintering area generally still move across the border into the British Mountains, ignoring the proximal cues or "paths of least resistance" down the windswept Aichilik or Kongakut River valleys that would greatly shorten the route to the core calving area south of Barter Island. During some years, however, such a shortcut would result in caribou encountering a snowbound core area, forcing them to calve in mountains or foothills with high densities of predators (see Appendix A). The more traditional but longer movement takes them to a predictably windswept area of the coastal plain that has low snow accumulation. While the core area may offer better conditions for calving in most years, initial movement to the eastern coastal plain keeps all options open for those years when the core area is unavailable or unsuitable because of snow.

Major shifts in distribution also occur during midsummer, late summer, and early winter. July and August movements commonly take caribou into both the Chandalar and Richardson wintering areas, but they do not remain there long. Extensive movements within the traditional winter areas occur in November and December. Early winter shifts are common between the Ogilvie and Richardson areas, such that some reports have treated these as a single large wintering area. Note, for instance that more satellite-collared caribou entered the Ogilvie area in October than came out in April (Figs. 3 and 4), primarily because of early winter shifts to the Richardson Mountains.

Calving Site Selection

Variation in use of the traditional calving area of the PCH could be explained by variation in snow cover on the calving grounds and along the spring migration routes. Thus individual females did not show fidelity to specific calving sites. Nevertheless, when not hindered by snow, cows preferentially selected the coastal plain in ANWR between the Hulahula and Aichilik Rivers. Selection of this area was primarily for predator avoidance, although forage quality and quantity may also have been involved.

calves that were born in the preferred calving area or spent time there after birth survived better than calves that remained elsewhere. Use of the calving grounds is discussed more thoroughly in Appendix A.

MANAGEMENT RECOMMENDATIONS

Satellite Telemetry as a Management Tool

Satellite telemetry has proven to be an accurate, reliable method for obtaining detailed movement and activity data for caribou in the Arctic environment. Satellite transmitters, in spite of relatively high purchase and data access costs, are nevertheless cost effective whenever large numbers of locations from individual animals in remote areas are necessary. In the PCH, for instance, even small numbers of working PTT's (< 10) would be adequate to indicate major wintering, calving, and postcalving areas. Additional tracking of conventional transmitters or general aerial surveys would be required to define boundaries or locate other caribou in the general area, but the satellite collars would greatly reduce the search area or, at least, direct search effort to areas certain to have caribou. Thus even 5-10 PTT's in large migratory caribou herds would probably prove cost-effective in facilitating many standard S&I activities.

Remotely sensed data from PTT's will never replace data obtained by direct observation, and they cannot provide data such as group size, parturition status, proximity to predators, or exact distance from fixed features such as pipelines. Because of their high costs, PTT's will likely also never replace standard transmitters in studies requiring a large sample of individuals but only a few locations (e.g., mortality and productivity studies). Nevertheless, satellite telemetry should have a definite and expanding role in the future of wildlife research and management.

Conservation of the Porcupine Caribou Herd

Results of the current project confirmed earlier findings on the importance of the coastal plain between the Hulahula and Aichilik Rivers for calving. Efforts to afford special protection for this area should continue. At the very least, the Department should continue to urge further studies on possible mitigation of disturbance to calving caribou and/or special status (e.g., moratorium on leasing) for the southeastern part of the 1002 Area. The 242,000 acres designated as the "core calving area" in the draft LEIS to Congress (Clough et al. 1986) would probably be an adequate portion of the overall core (or traditional high-density calving area) to protect.

Satellite and conventional telemetry data indicate that all portions of the 1002 Area are used by the PCH during the post-calving period and the area west of the Sadlerochit River is used by CAH caribou to varying degrees all year. Therefore, any petroleum development in ANWR will impact caribou to some extent. At the present time, no information on size or location of potential developments is available. Extensive inventories of caribou distribution, habitat use, and mortality risk exist and will be available for estimating impacts or planning for mitigation should specific developments be proposed.

ACKNOWLEDGMENTS

Valuable assistance to this project was provided by Cathy Curby, Gerald Garner, Jim Greslin, Richard Harris, and Larry Pank of the U.S. Fish and Wildlife Service and Wayne Regelin and Dan Reed of the Alaska Department of Fish and Game.

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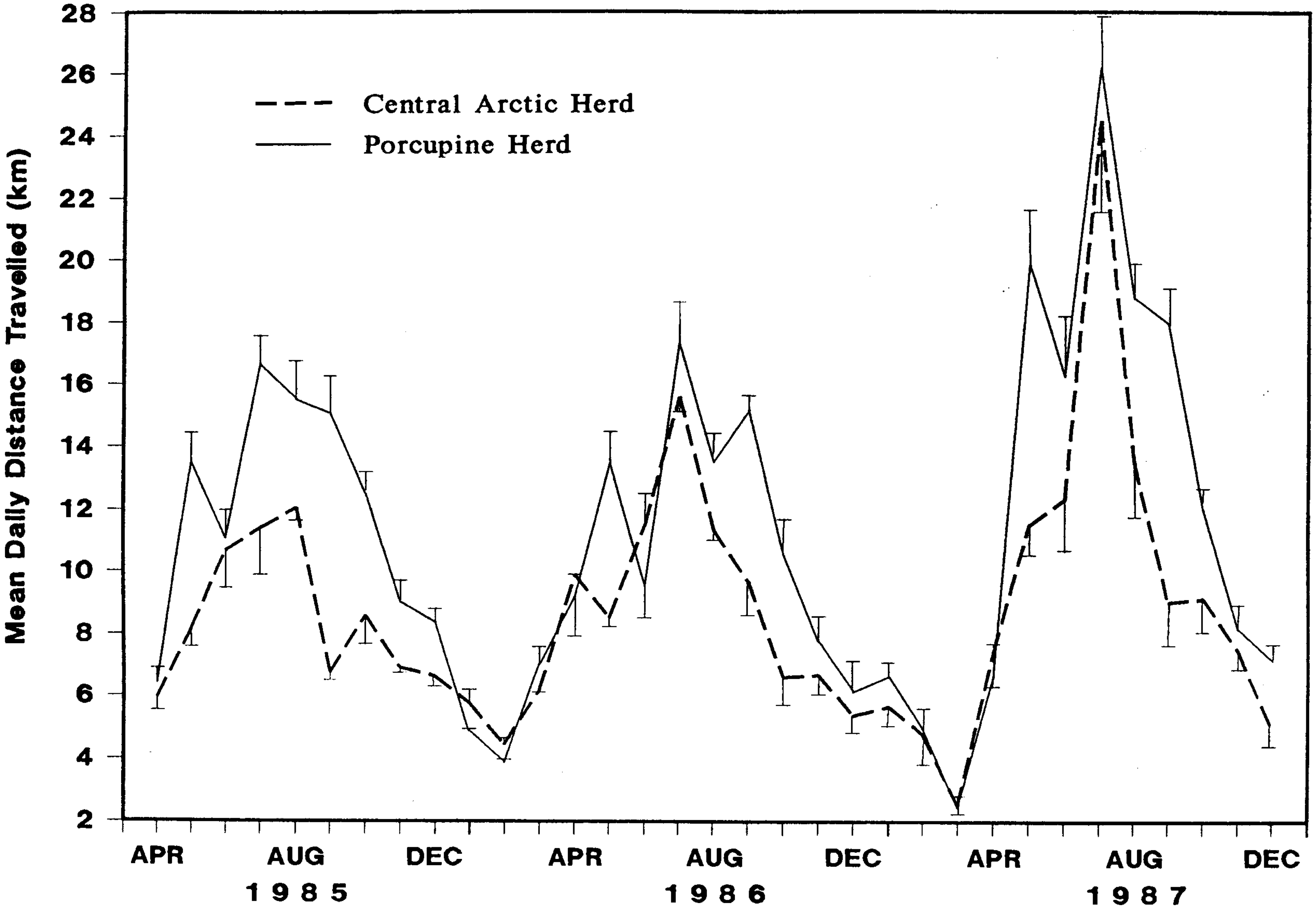

Figure 1. Movement rates of (means ± 1 SE) of Porcupine and Central Arctic herd cows between 1985 and 1987.

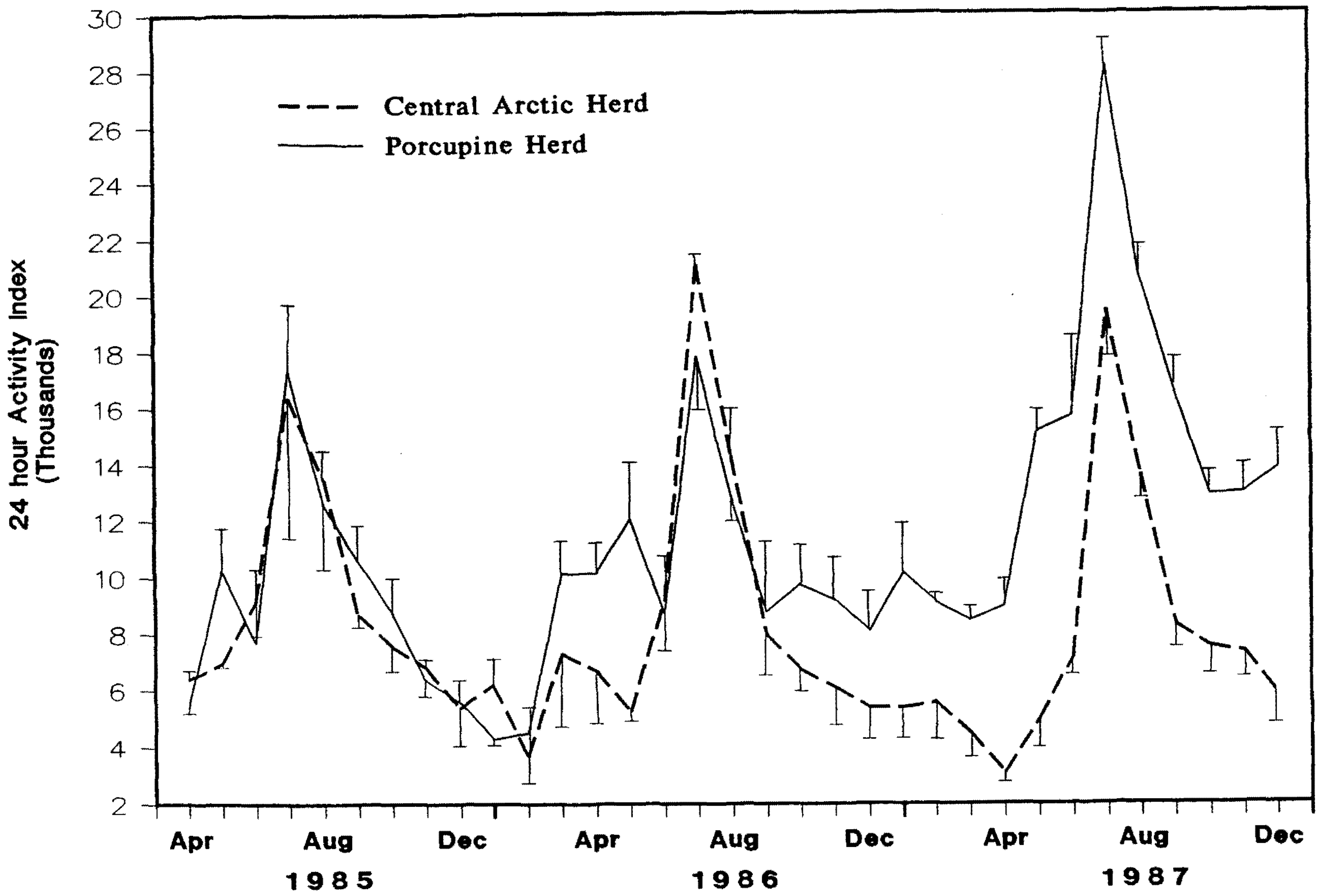

Figure 2. Mean long-term activity index (± 1 SE) for Porcupine and Central Arctic Caribou Herd cows between 1985 and 1987. The index represents the number of seconds each day during which a mercury switch was activated.

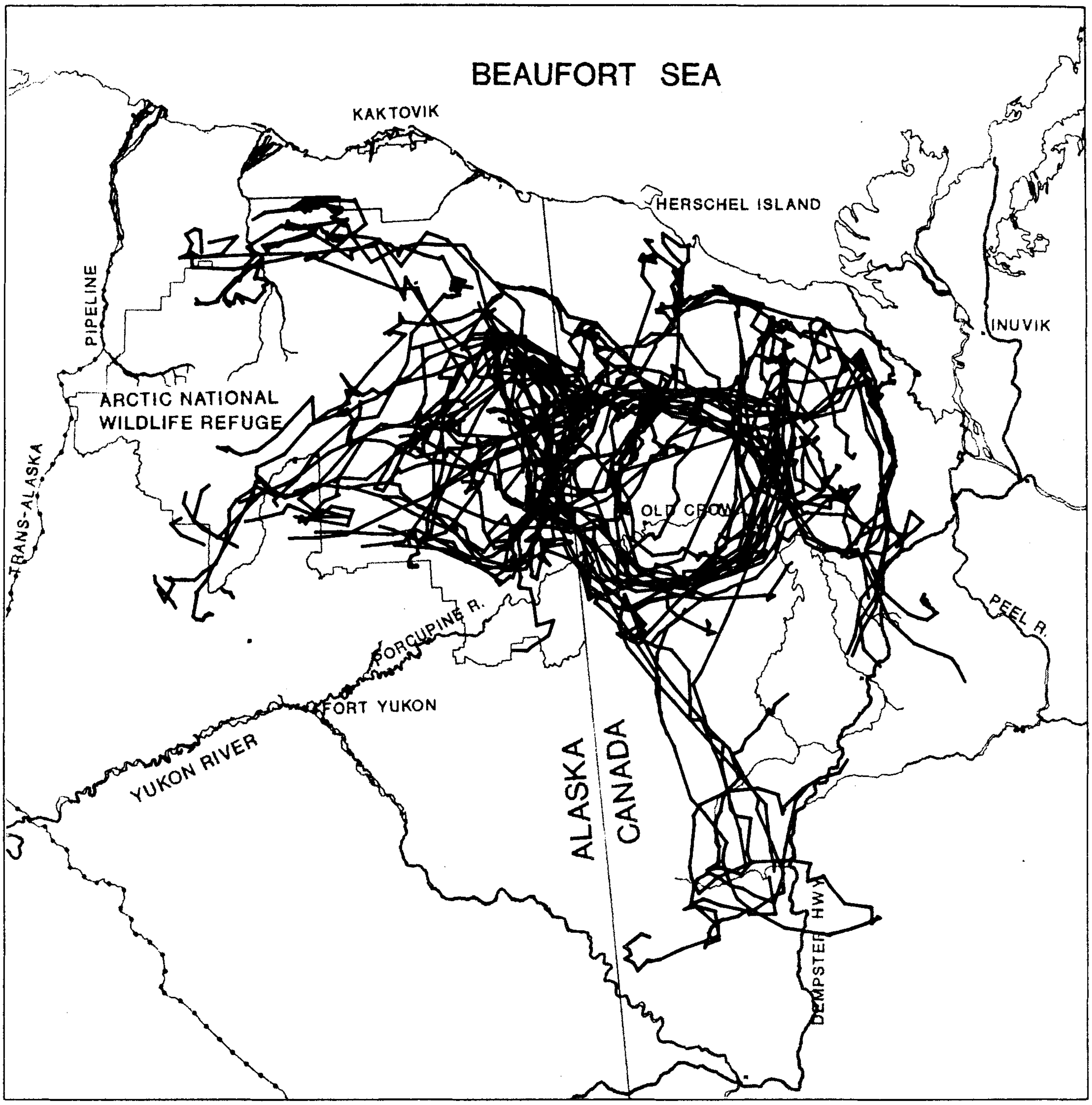

Figure 3. Cumulative movements of satellite-collared cows of the Porcupine Caribou Herd during fall, migration (September and October) 1985-89.

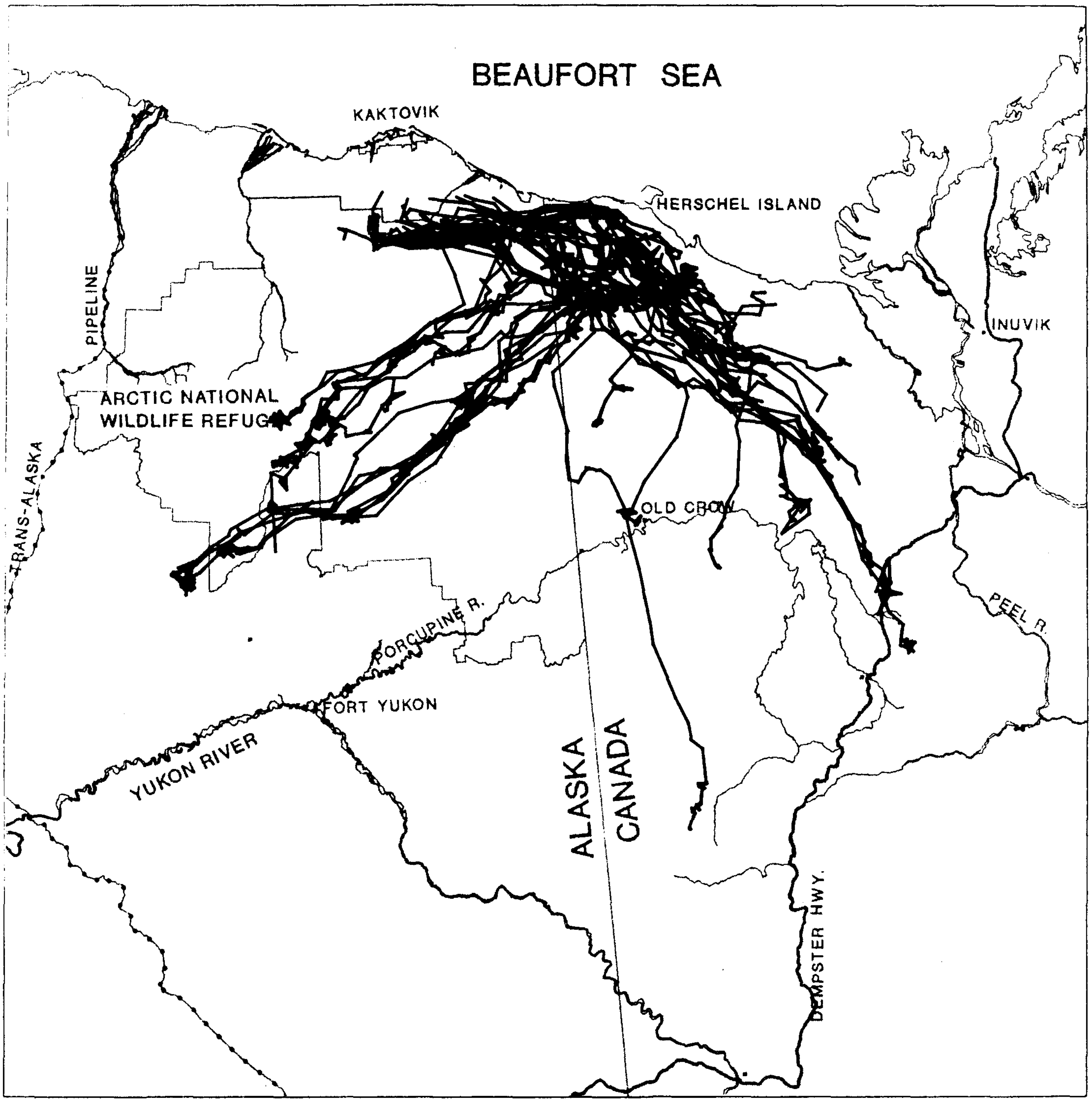

Figure 4. Cumulative movements of satellite-collared cows of the Porcupine Caribou Herd during spring migration (April and May) 1985-89.

Table 1. Deployment data and current status of satellite radiocollars (PTT's) on female caribou from the Porcupine Caribou Herd.

I.D. No.	Capture date	Recapture for collar replacement	Comments and current status (April 1990)
S8	4/85	3/86, 10/86, 10/87	Died of unknown causes 7/88; PTT retrieved
S9	4/85	3/86, 6/86	PTT failed 5/86; recollared with conventional transmitter 6/86; died of unknown causes 12/86
S10	4/85	3/86, 3/87, 4/88, 4/89, 4/90	Died 4/90, capture mortality; PTT not retrieved
S11	4/85	3/86, 3/87, 7/87, 10/87, 4/88	Died of unknown causes 7/88; PTT retrieved
S12	4/85	3/86	Died of unknown causes 8/86; PTT retrieved
S13	4/85	3/86, 10/86, 10/87, 9/88, 6/89, 4/90	Still alive; PTT transmitting
S14	4/85	3/86, 10/86, 3/87, 4/88, 4/89, 9/89, 4/90	Still alive; PTT transmitting
S15	4/85		Killed by bear (along with calf) 6/85; PTT retrieved
S16	6/85		Killed by wolves 11/85; PTT retrieved
S17	3/86		Died of unknown causes 5/86; PTT retrieved
S18	10/86		Killed by wolves 1/87; PTT retrieved
S19	10/86	10/87	Killed by wolves 6/88; PTT retrieved
S20	10/86	10/87, 9/88, 9/89	Still alive; PTT transmitting
S29	3/87		Died of unknown causes 3/88; PTT retrieved
S30	3/87	4/87	Died 4/87, apparent capture mortality; PTT retrieved
S31	3/87	4/88, 4/89	Died 1/90; PTT retrieved

Table 1. Continued.

I.D. No.	Capture date	Recapture for collar replacement	Comments and current status (April 1990)
S32	3/87	6/88	Died of unknown causes 11/88; PTT retrieved
S35	10/87		Killed by bear 6/88; PTT retrieved
S36	10/87	9/88, 9/89	Still alive; PTT transmitting
S37	10/87	9/88, 4/90	Still alive; PTT transmitting
S40	10/87		Died of unknown causes 7/88; PTT retrieved
S42	4/88	4/89, 4/90	Died of unknown causes 5/90; PTT not retrieved
S43	4/88	4/89, 4/90	Still alive; PTT transmitting
S44	4/88		Died of unknown causes 4/88; PTT retrieved
S45	4/88		Died 4/88, apparent capture mortality; PTT retrieved
S46	4/88	6/88	Died 6/88, capture mortality; PTT retrieved
S47	4/88	4/89, 4/90	Died 4/90, capture mortality; PTT not retrieved
S48	4/88		Killed by wolves 4/88; PTT retrieved
S49	4/88		Died of unknown causes 4/88; PTT retrieved
S50	4/88	4/89	Died of unknown causes 4/89; PTT retrieved
S51	6/88	4/89, 4/90	Still alive; PTT replaced with VHF transmitter 4/90
S53	4/89	9/89	Died 3/90; PTT retrieved
S54	4/89		Died 4/89, apparent capture mortality; PTT retrieved

Table 1. Continued.

I.D. No.	Capture date	Recapture for collar replacement	Comments and current status (April 1990)
S55	4/89		Still alive; PTT failed 11/89
S56	4/89	4/90	Still alive; PTT transmitting
S57	4/89		Shot 11/89; PTT retrieved
S58	4/89		Still alive; PTT transmitting
S59	4/89	4/90	Still alive; PTT transmitting
S60	4/89	4/90	Still alive; PTT replaced with VHF transmitter 4/90
S61	4/89	4/90	Died 4/90, capture mortality; PTT not retrieved
S68	9/89		Still alive; PTT transmitting

Table 2. Deployment data and current status of satellite radiocollars (PTT's) on female caribou from the Central Arctic Caribou Herd.

I.D. No.	Capture date	Recapture for collar replacement	Comments and current status (April 1990)
S5	4/85	3/86	Status unknown; PTT batteries exhausted 3/87 and standard transmitter failed. No longer trackable; collar not retrieved.
S6	4/85	3/86, 3/87	Died of unknown causes 6/87; PTT retrieved
S21	10/86	10/87	Died of unknown causes 10/88; PTT retrieved
S22	10/86	10/87	Died of unknown causes 2/88; PTT retrieved
S23	10/86	11/86, 3/87, 10/87, 9/88, 10/89	Still alive; PTT transmitting
S24	10/86	10/87, 10/88	Died of unknown causes 1/89; PTT retrieved
S25	10/86	10/87, 10/88	Died of unknown causes 11/88; PTT retrieved
S26	10/86	7/88, 7/89	Still alive; PTT transmitting
S27	10/86	8/87	Died of unknown causes 10/87; PTT retrieved
S28	10/86	10/87, 10/88	Status unknown; PTT failed and standard transmitter batteries exhausted
S33	5/87	4/88	Killed by wolves at capture site 4/88; PTT retrieved
S34	7/87	7/88, 4/89, 4/90	Died 4/90, capture mortality
S38	10/87		Died of unknown causes 1/88; PTT retrieved
S39	10/87	10/88	Died of unknown causes 12/88; PTT retrieved
S41	10/87	9/88, 9/89	Still alive; PTT transmitting
S52	10/88	10/89	Still alive; PTT transmitting

Table 2. Continued.

I.D. No.	Capture date	Recapture for collar replacement	Comments and current status (April 1990)
S62	4/89		Still alive; PTT transmitting
63	4/89	9/89	Still alive; PTT transmitting
64	4/89	5/90	Still alive; PTT replaced with VHF transmitter 5/90
65	7/89		Still alive; PTT transmitting
66	7/89	4/90	Still alive; PTT replaced with standard transmitter 4/90
67	7/89		Still alive; PTT failed 10/89
69	10/89		Still alive; PTT transmitting
70	10/89		Still alive; PTT transmitting

Table 3. Comparative cost per animal to locate 10 caribou using satellite-vs. radio-telemetry techniques in northern Alaska. Calculations are based on a 5-year study using satellite transmitters with a 1-year battery life or radio-transmitters with a 3-4 year battery life. An additional set of collars is included to replace used collars when the caribou is recaptured. Radio-telemetry study costs includes $3500 for radio-tracking equipment. Labor costs are not included.

Satellite-telemetry	Per collar cost	Cost per location (Locations per year)		
Initial cost per collar (includes backup VHF transmitter)	$3300.00	n=10	n=52	n=365
Additional collar	3300.00			
Refurbishment costs ($750 x 4)	3000.00	$350	$ 74	$ 18
Capture costs ($1500 x 5)				
Argos processing ($8.22/d)	7500.00			
Radio-telemetry				
Initial cost per collar	$ 330.00	$893	$778	$754
Additional Collar	330.00			
Capture costs ($1500 x 2)	3000.00			
Radio-tracking flight	750.00[a]			

[a] Assumes that each caribou is located visually to get an accurate location. Full coverage of study area requires 30 H @ $250/hr air charter cost.

APPENDIX A

Selection of Calving Sites by Porcupine Herd Caribou

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Fancy, S. G. and Whitten, K. R. 1991. Selection of calving sites by Porcupine Herd caribou. Canadian Journal of Zoology 69:000-000.

Abstract: Characteristics of 305 calving sites used by 131 different radio-collared caribou (*Rangifer tarandus*) cows from the Porcupine herd in northeastern Alaska and the northern Yukon Territory were investigated between 1983 and 1990 to determine the factors influencing calving site selection. Cows selected areas north of the foothills primarily to reduce exposure of calves to predators. Sites dominated by *Eriophorum* tussocks were selected secondarily for access to newly-emerging vegetation. Highest calf mortality occurred in years when snow melt was relatively late and calving occurred closer to the foothills and in Canada. Industrial development of the coastal plain of the Arctic National Wildlife Refuge could increase calf mortality if calving were displaced south and east of potential development areas.

INTRODUCTION

The U. S. Congress directed the U. S. Department of the Interior in 1980 to conduct biological and geological studies on the coastal plain of the Arctic National Wildlife Refuge (ANWR) in northeastern Alaska to provide information necessary for future management of the area. The "1002 area" of the coastal plain contains important fish and wildlife habitats, including the most frequently used calving and post-calving habitats for the Porcupine Caribou Herd (PCH; _Rangifer tarandus granti_). Unfortunately, the coastal plain is also generally considered the most promising onshore petroleum exploration area in the United States (Clough _et al_. 1987). After completing a 5-yr baseline study program, the Department of the Interior concluded that major impacts to the PCH could occur if a major oil discovery is located and developed in the 1002 area (Clough _et al_. 1987).

The U. S. Fish and Wildlife Service and the Alaska Department of Fish and Game have conducted cooperative studies since 1982 on the PCH (n = 178 000, 1989) and the adjacent Central Arctic Herd (CAH, n = 13 000, 1983) to assess the potential effects of petroleum exploration and development on caribou. A major concern based on studies of the CAH (e.g., Whitten and Cameron 1983, Dau and Cameron 1986) is that development of the 1002 area can displace parturient cows from traditional calving areas, thereby increasing mortality on calves or reducing foraging opportunities for cows and calves. The purpose of this study was to determine why PCH caribou select certain areas for calving, and thereby provide information for assessing and mitigating potential effects of oil development on the PCH during the calving period.

METHODS

The PCH annually migrates between winter ranges in northeastern Alaska and northwestern Canada and its calving grounds along the Beaufort Sea coast. Detailed descriptions of the range and seasonal movement patterns of the PCH can be found in Garner and Reynolds (1986) and Fancy _et al_. (1989).

Caribou Capture and Radio-tracking Flights

Beginning in 1981, standard VHF radio-collars were deployed on adult and yearling female caribou using methods described by Fancy _et al_. (1989). Beginning in April 1988, however, all adult caribou were immobilized, using a mixture of 3 mg carfentanil citrate (Wildlife Labs, Fort Collins, CO) and 7.5 mg acepromazine maleate with Naloxone (450 mg, Wildlife Laboratories) as the antagonist. Individuals were recaptured as needed every 3-5 yr to replace transmitters before batteries were exhausted.

Mortality-sensing transmitters were deployed on 118 calves on 2-3 June 1988, using methods described by Garner _et al_. (1985). Previous experience with capturing calves (Whitten _et al_., unpubl. manuscript) indicated that calves that were abandoned at the time of capture subsequently died within 48 h. Because we could not distinguish between natural and capture-induced abandonment, and inclement weather precluded observations of collared calves for 2 d following capture, we excluded the 14 calves that died within 48 h of capture from further analysis.

Satellite transmitters compatible with the Argos Data Collection and Location System (Fancy et al. 1988, 1989) were deployed on 33 PCH cows between April 1985 and August 1990. Data were received monthly from Service Argos (Landover, Md) and processed as described by Fancy et al. (1988, 1989). The satellite transmitter package (Telonics, Inc.; Mesa, Ariz) weighed 1.6 kg (including a VHF radio transmitter to locate the caribou from an aircraft) and had a 1-yr battery life. Individual caribou were monitored for ≤ 5 yr by replacing their transmitters annually. Transmitters were programmed to operate 6 $h \cdot d^{-1}$ or 6 $h \cdot 2d^{-1}$, and provided 3-4 locations per day of operation. Mean location errors were 760 m for Generation-2 transmitters (68% of locations used in this study) and 480 m for the newer Generation-3 transmitters (32% of locations, Fancy et al. 1989).

Radio-collared cows (n = 131, including those also monitored by satellite) were observed from fixed-wing aircraft at 1-3 d intervals between ca. 28 May and 30 June each year to determine date and location of calving and the fate of their calves. Calving dates and neonatal survival for calves of collared cows were determined from a combination of criteria, including presence of a calf at heel, presence or absence of hard antlers, udder distention, or observations of cows standing over dead calves (Whitten, in press). Cows not showing any overt signs of pregnancy, but not obviously barren (e.g, already possessing velvet antlers), were relocated at least weekly until 30 June to ensure that no births were missed. Each cow that had apparently lost her calf was observed at least one additional time during the calving period to confirm that no calf was present.

We conducted radio-tracking flights covering the entire range of the PCH using fixed-wing aircraft to relocate collared caribou, ca. 2-5 times each year between October and early May. Locations during the period between early January and early April, when cows were most sedentary (Fancy et al. 1989; unpubl. data) were classified into 1 of 3 categories (Alaska, Richardson Mountains, or Ogilvie Mountains) to determine relationships between wintering areas and calving sites. For the purpose of this analysis, all wintering locations in the Yukon that were south and west of the Porcupine and Eagle rivers were included in the Ogilvie Mountains category, whereas locations east of the Eagle River and along the axis of the Richardson Mountains were included in the Richardson Mountains category.

Calving Distribution

Locations where radio-collared cows were first observed with a calf during intensive monitoring flights each year were used as calving sites. Calving sites were digitized and entered into the ARC/INFO geographic information system (GIS) for analysis of calving distribution and calving site selection. Calving sites for 54 cows that calved in widely scattered locations in the mountains or west of the Katakturuk River were excluded from analysis. We tested the hypothesis that the distribution of calving sites on the coastal plain was random by arbitrarily partitioning the coastal plain into six blocks of similar area (Fig. 1: A-F) to determine the number of calving sites · km^{-2} expected within each block, if sites were evenly distributed. Blocks were delineated on the east and west by major rivers or the Alaska-Yukon border, and on the north by the coastline. The southern boundaries of the blocks were drawn where the coastal plains and foothills give rise to the mountains of the Brooks and British ranges. The area within each block was determined using the ARC/INFO geographic information system.

Calving Site Selection

Factors influencing calving site selection were determined by comparing attributes of calving sites for 1983-90 with those of randomly-selected sites within the area bounded by the outermost calving sites (including those in the mountains, but excluding 2 cows that calved with the CAH, see Fig. 1). We excluded sites where 16 cows were first observed with their calves because each calf was estimated to be >5 d old (based on their size and behavior) and might have been born several kilometers from the location. (These 16 cows were used in the calving distribution analysis above because they were located within the same block before and after calving). Logistic regression analyses (McDonald, in press) were conducted to determine which attributes best discriminated between 305 sites selected for calving and 305 randomly-selected sites on the calving grounds.

We determined the elevation, percent slope, and landcover type for each calving site and random site using digital maps with a resolution (i.e., pixel size) of 50 x 50 m in Alaska (U.S.G.S. Eros Data Center, Anchorage, AK; Garner and Reynolds 1987:60) or 100 x 100 m in Canada (Nixon et al., in press). Landcover maps in both Alaska and Canada were based on LANDSAT multispectral scanner data; however, the use of different classification algorithms for each map precluded direct comparisons. Snow cover at each site on 1 June each year (i.e., <25%, 25-75%, >75% snow cover) was determined from TIROS-N AVHRR imagery (Eastland et al. 1989). For each site, we also recorded latitude and longitude (in UTM coordinates), shortest distance to the coast, shortest distance to a major river, shortest distance to the foothills (i.e., the southern boundary of the blocks in Figure 1), proportion of area within a 1-km radius that was dominated by tussock tundra, and proportion of area within a 1-km radius that contained landcover types dominated by *Dryas* vegetation types. Distance to the foothills was negative for sites south of the foothills line. *Dryas* vegetation types included dry prostrate dwarf scrub and moist prostrate dwarf scrub types in Alaska, and the *Dryas* sedge type in Canada.

Calving Site Fidelity

We determined whether individual cows showed fidelity to calving sites in different years by comparing distances between all calving sites for each radio-collared cow between 1983-1990 with a distribution of distances for random sites obtained through computer simulation. The number of calving sites for each cow varied from 1-7 (mean $\pm$ SD = 2.24 $\pm$ 1.45, n = 131); separate analyses were required depending on the number of calving sites included. We calculated the shortest distance between any two calving sites, and the shortest distance connecting all calving sites, for each cow. Then, we generated 8000 sets (i.e., 2-7 locations) of random sites from an area delineated by the outermost calving sites (Fig. 1), and calculated the above distance parameters for each simulation. Differences between cumulative frequency distributions of observed and simulated distances were compared using the Kolmogorov-Smirnov test for goodness of fit (Sokal and Rohlf 1969:573).

Calf Mortality

Relationships between habitat and mortality risk were investigated by comparing attributes of sites where radio-collared cows were observed with live calves with attributes of sites where cows lost calves. The site where a cow lost a calf was considered to be the site where she was first observed without a calf. We excluded all locations in Canada from this analysis because (1) if displacement occurred, it would most likely be to areas immediately south and east of the 1002 boundary; (2) different landcover classification schemes were used in Alaska and Canada, precluding direct comparisons of landcover data; (3) no landcover data were available in Canada for the area north and west of the Malcolm River; and (4) digital elevation and slope data were not available for the northern Yukon, and obtaining these data directly from maps for all locations in Canada would be a very time-consuming process. We randomly selected only one location each year during late May through June 1983-1990 where each cow was first observed with a calf, because serial observations of individual cows with calves may not be independent.

RESULTS

Calving Distribution

The distribution of calving sites among the six designated blocks (Fig. 1) on the coastal plain in 1983-90 was nonrandom (Table 1, X^2 = 77.0, 5 df, P < 0.0001). The area between the Hulahula River and the international border (Blocks B, C, and D; Fig. 1) contained 1.5 times as many calving sites $\cdot$ km^{-2} as expected, whereas the coastal plain east of the international border contained only 0.7 times as many sites as expected. Selection for areas west of the Aichilik River in Blocks B and C, where much of the area is at higher latitude, appears strong even though complete snow cover remains near the coast in most years. A greater proportion of the coastal plain east of the Aichilik River is snow-free or has mottled snow during the early calving period (Eastland et al. 1989, unpubl. data).

The east-west distribution of calving sites was related to the herd's winter distribution. Cows that wintered in the

Richardson Mountains calved further west than those that wintered in Alaska or the Ogilvie Mountains (Fig. 2). In most years, the windswept ridges of the Richardson Mountains allow caribou to begin spring migration and arrive on the calving grounds earlier than cows wintering in other areas with deeper snow (Thompson 1978). We found a significant correlation between date of arrival on the calving grounds and longitude of calving sites (early-arriving cows calved further west) for cows tracked by satellite (Spearman's rank correlation; $n = 39$, $r = 0.646$, $\underline{P} < 0.001$). However, we found no relationship between arrival date on the calving grounds and date of calving (Spearman's rank correlation; $n = 39$, $r = 0.25$, $\underline{P} > 0.20$).

Calving Site Selection

The movements of pregnant cows tracked by satellite between 1985 and 1989 averaged >10 $km \cdot d^{-1}$ in a northwest direction during the 12-d period before calving (Table 2). During the 6-d period beginning at calving, cows moved <5 $km \cdot d^{-1}$ and movement direction was random. Daily relocations of radio-collared cows indicated that most cows selected a calving site on or 1-3 d before their calving date, and remained in that general area for 1-2 weeks. The 24-h activity index, an independent measure of caribou movement (Fancy et al. 1989), followed a pattern similar to rates of movement (Table 2).

Selection for landcover types characterized by Eriophorum tussock tundra was apparent in both Alaska and Canada (Table 3). In Alaska, 55% of calving sites were located in Moist Graminoid Tundra or Mesic Erect Dwarf Scrub types characterized by E. vaginatum (Garner and Reynolds 1987:60), whereas only 40% of the randomly-selected sites were located in these types. In Canada, 54% of calving sites were located in tussock tundra types, compared to 30% for randomly-selected sites. When landcover types in both Alaska and Canada were reclassified as tussock versus non-tussock types and combined, we found a highly significant selection for tussock types at calving (Fisher's exact test, $\underline{P} < 0.0001$).

Logistic regression was used to determine the set of attributes that best discriminated between sites selected for calving and randomly-selected sites. Attributes were included in the model if their regression coefficient was significantly different from zero at the 95% confidence level (X^2 test with 1 degree of freedom; BMDP 1988). The analysis yielded the model ($X^2 = 53.84$, 3 df, $\underline{P} < 0.0001$):

$$w(x_1,x_2,x_3) = \exp(1.571x_1 + 0.015x_2 - 2.830x_3)$$

where x_1 is the proportion of area within 1 km of a site dominated by Eriophorum tussocks, x_2 is the distance between a site and the foothills, and x_3 is the percent slope. This selection function can be solved for any site to determine the relative probability of that site being selected for calving (McDonald, in press). For example, a site 20 km north of the foothills characterized by 100% tussock tundra within 1 km and a slope of 2% is 29 times more likely to be selected for calving than a site 20 km south of the foothills line which has no tussocks and a slope of 45%. Compared to randomly-selected sites, calving sites were significantly further west, further north, at lower elevations on gentler slopes, closer to major rivers, further from the foothills, and had more snow and tussock tundra (Table 4).

Fidelity to Calving Sites

Although PCH cows showed a high fidelity to the calving grounds between the Katakturuk and Babbage rivers, they did not return to the same sites on the calving grounds each year to calve (Table 5). None of the cumulative frequency distributions of distances between calving sites were different (Kolmogorov-Smirnov test; $\underline{P} > 0.20$) from the distributions for randomly-selected sites. Thus, although cows select areas with certain characteristics (e.g., away from the foothills, tussock tundra) for calving, annual variation in wintering areas and migration routes used by individual cows, and variation in snow cover during migration and on the calving grounds, make it unlikely that a cow will calve near the same exact location each year.

Calf Mortality

Fourteen (13.5%) of 104 calves collared in 1988 that survived >48 h after capture died by 30 June (Table 6). As in previous years, June mortality for calves of radio-collared cows in 1988 was higher than that for collared calves. This result is expected as calf mortality is greatest within 48 h of birth, and many calves are stillborn or die before they can be collared. After adjusting for perinatal mortalities (i.e., excluding deaths that occurred <48 h after birth), similar rates of death were obtained for collared calves and calves of collared cows (Table 6).

In our 1988 study of collared calves, no significant difference ($X^2 = 0.85$; $\underline{P} > 0.10$) was found between mortality of calves originally collared within the 1002 area (9 of 55) and those collared south and southeast of the 1002 area (5 of 49). Snow melt on the coastal plain in 1988 was the latest on record (Eastland _et al_. 1989, unpubl. data), and a relatively high proportion of calves present within the snow-covered 1002 area were captured compared to those captured outside the 1002 area.

Locations where cows that lost calves were first observed without a calf were significantly further south and closer to the foothills than locations where cows were observed with live calves (Table 7).

DISCUSSION

Concentrations of cows have used the coastal plain between the Hulahula and Aichilik rivers for calving in 17 of the past 19 years, but the location of areas having the highest concentration of caribou during calving varies annually. We believe that most of this annual variation can be explained by variation in snow cover, both on the calving grounds and on winter range. In years of relatively early snow melt, the highest concentration of calving sites has consistently been located in Alaska west of the Aichilik River and close to the coast, whereas in all years when snow melt was relatively late, calving sites were concentrated east of the Aichilik River or in the foothills.

Primary wintering areas for the PCH occur in areas of relatively shallow snow, and snow has been shown to influence the initiation and progress of spring migration (Thompson and Roseneau 1978; Garner and Reynolds 1986; Russell et al., unpubl. data). Cows wintering on wind-blown ridges of the Richardson Mountains are least likely to encounter deep snow that may delay arrival on the calving grounds; these cows tend to calve further west than cows wintering in Alaska or the Ogilvie Mountains. Cows delayed by deep snow depths during spring migration may calve before they reach an area with the combination of factors (e.g., greater distance from foothills, tussock tundra, lower elevations, gentler slopes) associated with most calving sites.

Once they reach the coastal plain, parturient cows continue to travel 10-12 km $\cdot$ d^{-1} until they bear their calf. In most years, they appear to follow a band of advancing partial snow melt towards the north and west, and we believe that the apparent selection for areas dominated by tussock tundra during calving is an artifact of their association with this band of mottled snow. The microtopography of Eriophorum tussocks promotes melting, evaporative loss of snow cover, and early growth of vegetation (Lent 1980), and in most years when cows arrive on the coastal plain, the northernmost patches of bare ground are associated with tussock tundra landcover types (Eastland et al. 1990). Areas north of the melt line are probably not used because foraging is difficult through the heavy, wet snow, and green vegetation and dry sites for calving are lacking.

Our results are consistent with the hypothesis that within the constraints of snow cover and the timing of their arrival on the calving grounds, cows select calving sites primarily to reduce exposure of calves to predators. There is a secondary benefit in being able to take advantage of the first green vegetation (primarily Eriophorum vaginatum) and bare patches available on the coastal plain. Bears (Ursus arctos), wolves (Canis lupus) and golden eagles (Aquila chrysaetos) appear to be more abundant in the foothills and mountains than on the coastal plain during the calving season (pers. observ.), and radio-tracking studies of predators have confirmed that most predators remain south of the coastal plain during calving (Young et al. 1990). Our results and those of an earlier calf mortality study (Whitten et al., unpubl. manuscript) indicate that mortality risk (i.e., the probability of a calf dying) for calves during June is higher for calves that spend time closer to foothills or mountains than for those further north on the coastal plain.

The rate of calf deaths is greatest within 48 h of birth (Whitten et al., unpubl. manuscript; this study). This perinatal mortality appears to be influenced more by maternal or fetal condition and behavior than location of the calving site. Roffe (1990) found that 78% (43/55) of PCH calves (<48 h old) for which he determined cause of death were stillborn or died of emaciation or malnutrition. However, his results may underestimate predation as a mortality factor during the perinatal period because only carcasses that were largely intact were necropsied, and all carcasses were collected from a relatively predator-free calving concentration area on the coastal plain. The association of perinatal and other calf mortalities with the foothills that we found may be partly explained if cows in poor condition or with poor maternal instincts tended to calve on the periphery of the main calving concentration. However, very young calves are particularly vulnerable to predators (Miller et al. 1988), and perinatal deaths in the foothills and mountains could also have been due to predation. Following the perinatal period, predation is involved in the majority of calf mortalities in the PCH. Whitten et al. (unpubl. manuscript) reported that predation was involved in 13 of 18 collared calf mortalities, and mortality sites where predators were involved were at higher elevations than sites where calves died for other reasons (e.g., disease, drowning, malnutrition).

Our contention that cows select calving sites primarily to reduce exposure of calves to predators and secondarily for their nutritional value is based on several factors. During calving, barren cows and bulls occur closer to the foothills and mountains where plant phenology is more advanced and foraging opportunities are presumably superior (Whitten and Cameron 1980). Furthermore, in years of relatively early snow melt, as in 1990, many cows calve north of areas dominated by tussock tundra, thereby decreasing foraging opportunities but increasing the distance from predators. Finally, simulation studies indicate that cows have an energy deficit during early calving because the biomass of Eriophorum and other forage species is low (Fancy 1986).

However, tussock tundra may provide the best foraging opportunity among vegetation types available on the coastal plain. Flower buds of E. vaginatum are highly digestible and may be an important source of nitrogen and minerals for parturient cows (Kuropat and Bryant 1980; Fancy et al. 1989; Russell et al., unpubl. data). The biomass and digestibility of Eriophorum within the 1002 area are higher than in peripheral areas to the south and east (Felix et al. 1989, White et al. 1989, Christensen et al. 1990).

The selective advantage of calving in the northwestern portion of the calving grounds is reflected in annual rates of calf death. Snow melt on the Alaskan portion of the calving grounds in 1988 and 1987 was the latest and second latest, respectively, recorded in 20 yr. In 1987, >67% of calves were born in Canada, and calves born in Alaska were born relatively close to the foothills. In 1988, the majority of calving occurred in the foothills and mountains south of the 1002 area boundary. In contrast, calving in 1989 and 1990 was concentrated north of the foothills and west of the Aichilik River. Snow melt in 1990 was the earliest ever recorded; by 28 May, the entire coastal plain was >95% snow free. Overall and adjusted rates of death for calves during 1987 and 1988 were greater than in 1989 and 1990, when calving was concentrated further from the foothills (Table 6).

Our results suggest that displacement of calving caribou from the 1002 area towards areas of higher predator abundance could result in increased calf mortality. However, if the PCH continues to increase without a proportional increase in predator numbers, the proportion of calves killed by predators could decrease even if calving were displaced closer to areas of higher predator abundance. Additional studies are needed on the relationship between caribou distribution during calving and the potential numerical and functional response of predator populations. Results will be used in simulation models of PCH population dynamics to estimate the potential effects of an oil and gas leasing program in ANWR on the PCH.

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Table 1. Distribution of 267 calving sites in 1983-1990 on the coastal plain of northeastern Alaska and northern Yukon. Blocks A-F refer to areas shown in Figure 1.

Block	% of Area	Sites Observed	Sites Expected	Ratio Obs:Exp	Selection[a] Prob.
A	21.37	11	57.1	0.19	0.032
B	15.61	66	41.7	1.58	0.259
C	19.26	70	51.4	1.36	0.223
D	16.03	65	42.8	1.52	0.249
E	12.49	18	33.3	0.54	0.088
F	15.24	37	40.7	0.91	0.149

[a] Relative probability that block will be selected as a calving site.

Table 2. Movement and activity of parturient cows during 3-d intervals relative to their date of calving. Data collected between 1985 and 1989 using the Argos Data Collection and Location System (Fancy et al. 1989).

Days Relative to Calving Date	n	Distance Travelled (km/d)		24-h Activity Index		Mean Direction ( )	
		Mean ±	SE	Mean ±	SE	Azimuth	P
-12 to -10	42	12.8	1.7	13713	1270	339	***
-9 to -7	42	13.0	1.5	13508	1338	326	***
-6 to -4	42	11.9	1.1	13469	1298	303	***
-3 to -1	42	10.3	1.0	11917	1098	289	***
0 to +2	40	4.7	0.5	8316	882	290	ns
+3 to +5	41	4.2	0.6	7524	839	111	ns
+6 to +8	41	6.9	2.3	10037	1179	244	ns
+9 to +11	39	5.4	0.5	11382	1223	212	ns
+12 to +14	38	7.0	0.7	12700	1347	233	ns
+15 to +17	35	9.0	1.2	14443	1533	261	ns
+18 to +20	34	9.3	0.9	15634	1552	270	ns
+21 to +23	33	10.9	1.0	16994	1924	308	**
+24 to +26	30	13.9	1.2	19624	1999	317	ns

ns = direction not significant; Rayleigh test (Batschelet 1981:54).
** $P < 0.005$.
*** $P < 0.001$.

Table 3. Percent occurrence of landcover types at calving sites (n = 284) and randomly-selected sites (n = 277) in Alaska and Canada. No landcover data were available for the area in Canada west of the Malcolm River.

Location	Randomly-Selected Sites	Calving Sites
Alaska		
Barren Floodplain	1.7	0.4
Barren Scree	1.7	0.4
Dry Prostrate Dwarf Scrub	6.9	3.0
Moist Prostrate Dwarf Scrub	22.4	20.4
Mesic Erect Dwarf Scrub[a]	18.4	24.3
Moist Graminoid Tundra[a]	21.3	30.9
Moist/Wet Tundra Complex	13.8	10.9
Wet Graminoid	10.3	8.3
Very Wet Graminoid	0.0	0.9
Scarcely Vegetated	3.5	0.5
Canada		
Dryas/Sedge	5.8	3.7
Dense Shrub Slope	2.9	1.9
Open Shrub Heath	12.6	20.4
Low Shrub Tundra	1.0	0.0
Lichen/Barren	30.1	9.3
Tussock Tundra w/ 0-15% Shrubs[a]	10.7	22.2
Tussock Tundra w/ 16-25% Shrubs[a]	12.6	24.1
Tussock Tundra w/ 26-35% Shrubs[a]	6.8	7.4
Unvegetated	16.5	7.4
Alluvial	1.0	3.6

[a] Landcover types dominated by tussock tundra.

Table 4. Characteristics of 305 calving sites and 305 randomly-selected sites within the calving grounds, 1983-1990. No vegetation data were available for 21 calving sites and 28 randomly-selected sites.

	Random Sites		Calving Sites		
Variable	Mean	+SE	Mean	+SE	P[a]
Longitude (UTM)	706393	4065	682689	3805	0.0001
Latitude (UTM)	7717719	1505	7725461	1252	0.0001
Elevation (m)	365	18	260	14	0.0001
Slope (%)	9.0	0.7	4.9	0.4	0.0001
Snow cover (class)	2.3	0.1	2.1	0.1	0.0017
Dist. to Coast (km)	30.2	1.0	30.5	1.1	0.817
Dist. to River (km)	4.1	0.3	2.9	0.2	0.002
Dist. to Foothills (km)	7.4	1.2	14.7	1.0	0.0001
Tussocks < 1 km (%)	35.0	1.9	48.6	2.0	0.0001
Dryas < 1 km (%)	20.5	1.2	20.7	1.1	0.899

[a] t-test for difference between means.

Table 5. Comparisons of distances (Mean ± SE, km) between calving sites of radio-collared cows located in 2-7 different years with distances between randomly-selected sites. Cumulative frequency distributions of distances between calving sites and 8000 sets of randomly-selected sites were compared using the Kolmogorov-Smirnov test (Sokal and Rohlf 1969:573).

No. Years	n	Shortest Distance Between Two Sites					Shortest Distance Connecting All Sites				
		Observed		Random		Dmax[a]	Observed		Random		Dmax[a]
		Mean	+SE	Mean	+SE		Mean	+SE	Mean	+SE	
2	43	67.1	49.1	93.6	59.7	0.097					
3	19	27.9	12.0	38.9	21.7	0.266	125.0	58.7	145.3	55.1	0.111
4	7	26.2	10.0	26.2	14.3	0.202	192.8	27.4	179.2	48.5	0.184
5	6	17.6	8.6	19.8	10.7	0.145	179.6	47.9	206.7	43.8	0.201
6	5	7.2	2.7	15.7	8.4	0.297	176.3	28.5	229.7	41.6	0.373
7	2	5.9	1.4	13.2	7.1	0.424	229.1	105.3	250.6	42.2	0.498

[a] All values nonsignificant ($\underline{P} > 0.10$); Kolmogorov-Smirnov test statistic.

Table 6. Percent mortality of collared calves or calves of collared cows during late May and June, 1983-1990. Data for 1983-1985 obtained from Whitten et al. (unpubl. manuscript). Relocations in 1986 were too infrequent to calculate death rates. Numbers in parenthesis are sample sizes.

	Calves of collared cows		Collared Calves
Year	Overall	Adjusted[a]	Adjusted[a]
1983	35 (20)	7 (14)	9 (59)
1984	16 (25)	10 (21)	7 (60)
1985	35 (43)	10 (30)	15 (60)
1986	--	--	--
1987	34 (41)	18 (33)	--
1988	31 (71)	12 (51)	13 (104)
1989	26 (58)	9 (47)	--
1990	9 (54)	0 (52)	--

[a] Adjusted mortality includes only those calves known to have been >48 h old when last observed alive. Perinatal and possible perinatal mortalities are excluded.

Table 7. Characteristics of sites within Alaska where calves of radio-collared cows were observed alive (n = 263) and sites where cows that lost calves (including perinatal mortalities) were first observed without their calf (n = 42) during late May and June 1983-90.

	Cows with Calves		Lost Calves		
Variable	Mean	+SE	Mean	+SE	P[a]
Longitude (UTM)	648849	2442	655658	4800	0.211
Latitude (UTM)	7732351	1160	7725792	2513	0.034
Elevation (m)	272	15	316	35	0.292
Slope (%)	6.6	0.8	4.8	1.2	0.194
Dist. to Coast (km)	31.9	1.2	38.0	3.0	0.065
Dist. to River (km)	2.5	0.1	2.0	0.3	0.129
Dist. to Foothills (km)	18.4	1.1	10.4	2.1	0.001
Tussocks <1 km (%)	45.0	2.2	45.9	5.3	0.881
Dryas <1 km (%)	26.1	1.2	19.7	2.5	0.041
Wet/Very Wet Graminoid <1 km (%)	23.8	1.8	26.2	4.2	0.618
Barrens <1 km (%)	5.0	0.6	8.2	1.7	0.068

[a] t-test for difference between means.

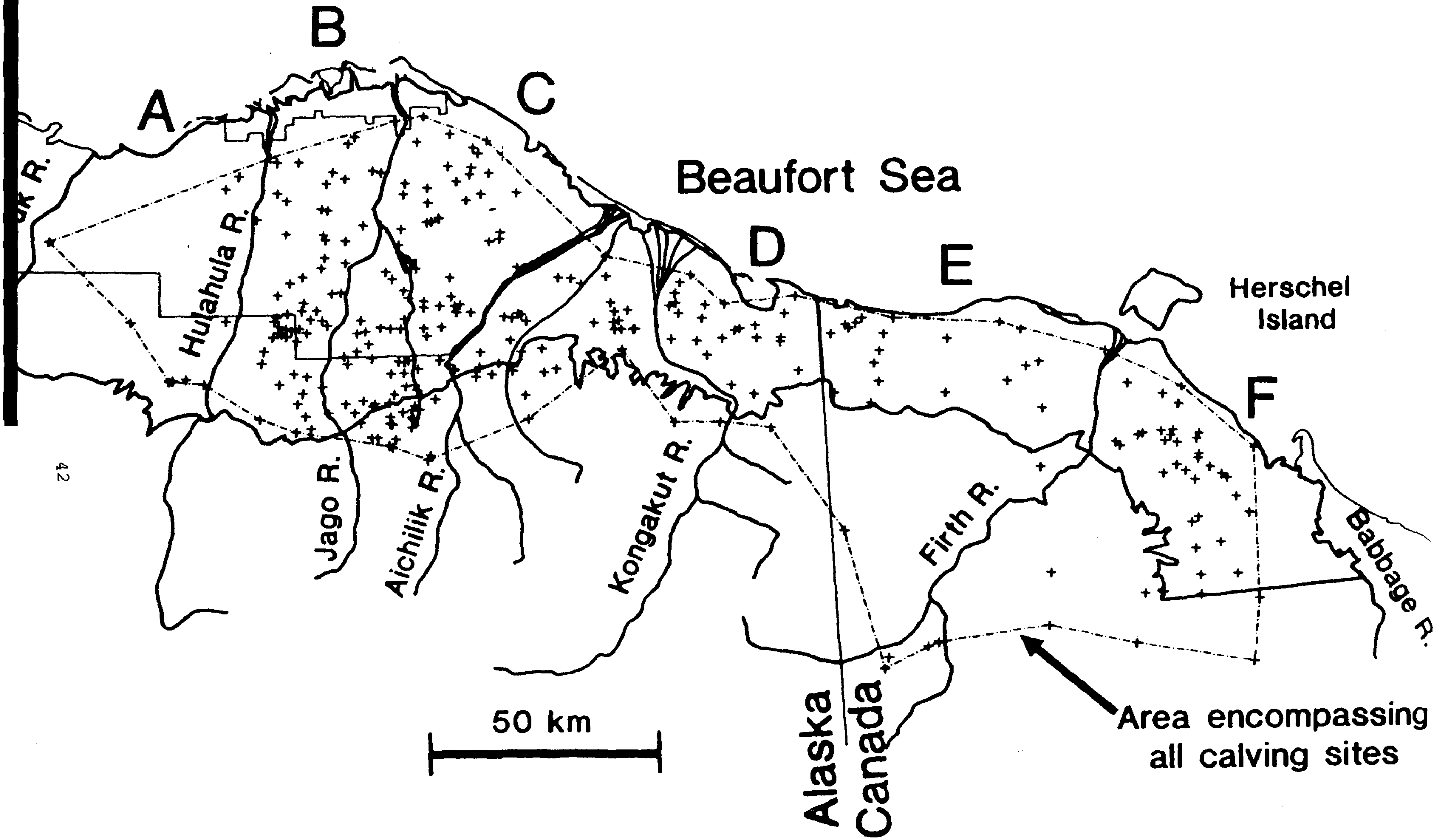

Fig. 1. Calving grounds of the Porcupine Herd, showing areas used in analyses of calving distribution, calving site selection, and fidelity. Blocks A-F were used to test for random distribution of calving sites on the coastal plain. The area encompassing all sites where radio-collared cows were first observed with a calf in 1983-1990 (sites marked by crosses; area delineated by a dash-dot line) was used in analyses of calving site selection and fidelity.

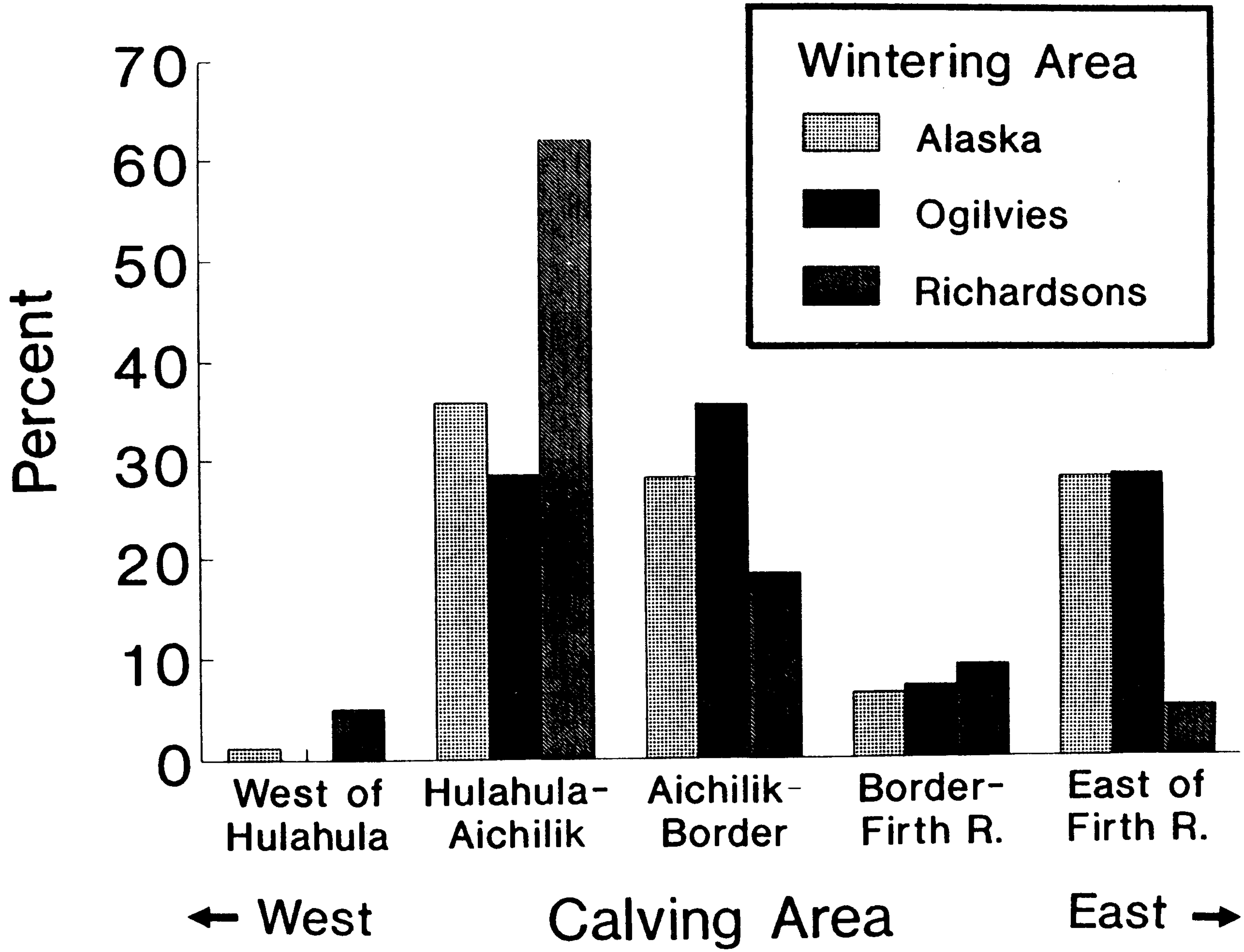

Fig. 2. Relationship between locations of calving sites for 131 individual cows and their previous wintering areas.