Seasonal movements of caribou in arctic Alaska as determined by satellite

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Between 1985 and 1987, 49 283 locations and 79 101 sets of activity data were obtained for 34 adult female caribou (*Rangifer tarandus granti*) of the Porcupine and Central Arctic herds using satellite telemetry. Daily movement rates of female caribou from the two herds, which differ greatly in size and separation of seasonal ranges, were similar except during the spring and fall migration periods. Movement rates in July exceeded those during migration in both herds. The minimum annual distances travelled by caribou cows, ranging to 5055 km, were the longest movements documented for any terrestrial mammal.

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La télémétrie par satellite a été utilisée de 1985 à 1987 pour suivre 34 caribous femelles adultes (*Rangifer tarandus garanti*) du centre de l'Arctique et de la vallée de la Porcupine. Cette méthode a permis de déterminer la position des caribous 49 283 fois et d'obtenir 79 101 groupes de données sur leurs activités. Les taux quotidiens de déplacement des femelles des deux troupeaux, qui diffèrent considérablement par leur importance et par la distance entre leurs territoires saisonniers, étaient semblables sauf au cours des périodes de migration du printemps et de l'automne. Les taux de déplacement enregistrés en juillet dépassaient ceux des périodes de migration chez les deux troupeaux. Les distances annuelles minimales parcourues par les caribous femalles peuvent atteindre 5055 km et constituent les déplacements les plus importants jamais enregistrés chez un mammifère terrestre.

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Introduction

The extensive movements and migrations of barren-ground caribou (*Rangifer tarandus granti* and *Rangifer tarandus groenlandicus*) are among the most notable characteristics of the species. Each year, most caribou herds in the northern regions of continental North America migrate between winter ranges south of treeline and tundra-dominated calving grounds in the Arctic (Kelsall 1968; Skoog 1968; Hemming 1971; Parker 1972; Miller 1982). The spring migration in April and May is led by pregnant females that commonly travel 7–24 km/day (Parker 1972; Thompson 1978; Fancy 1986; Duquette and Klein 1987). If the onset of migration is delayed by deep snow, rates of movement may exceed 40 km/day (Thompson 1978). After calving, cows and calves form increasingly larger groups that include some bulls and yearlings. During July and early August, caribou are periodically harassed by mosquitos (Cuculidae), bot and warble flies (Oestridae), and black flies (Simuliidae). Large groups of caribou of both sexes and all ages may form and travel extensively to habitats providing relief from insects. By mid-August, caribou disperse in small groups, but continue to travel long distances before beginning the return migration in September and October to winter ranges in the taiga (Kelsall 1968; Skoog 1968; Hemming 1971; Parker 1972).

The seasonal movement pattern summarized above is based primarily on observations of herd distribution made by aerial surveys at several times of the year. Several recent studies using radio-collared individuals have confirmed this general seasonal movement pattern (e.g., Valkenberg et al. 1983; Whitten et al. 1985; Cameron et al. 1986). However, because of the high cost of relocating radio-collared caribou by aircraft in remote areas of the Arctic, prolonged darkness in winter, and unpredictable weather, most of our knowledge about seasonal movements of marked individuals is based on small and sometimes incomplete data sets.

Since 1984, the U.S. Fish and Wildlife Service and the Alaska Department of Fish and Game have been developing and evaluating satellite telemetry as an alternative means of monitoring caribou movements. We have found satellite telemetry to be a cost-effective, accurate, and reliable means of systematically obtaining locational and activity data for caribou in an arctic environment. We present here some of our findings based on this technology, from studies on the Porcupine Caribou Herd (PCH), which migrates between separate winter and summer ranges in Canada and Alaska, and the much smaller Central Arctic Herd (CAH), with less distinctive migration patterns between overlapping seasonal ranges.

Study area

The range of the PCH, estimated to contain ca. 170 000 caribou in 1987 (unpublished data), includes tundra habitats on the arctic coastal plain, and mountainous and forested habitats in northeastern Alaska, northern Yukon Territory, and northwestern Northwest Territories (Fig. 1). The vegetation, geomorphology, and climate of the study area have been described by Spetzman (1959), Wiken et al. (1981), and Garner and Reynolds (1986). Winter distribution varies considerably among years, but the primary wintering areas include the Ogilvie and Richardson mountains in the Yukon, and the Chandalar, Sheenjek, and Coleen river drainages of northeastern Alaska. Spring migration occurs within three broad corridors referred to as the Old Crow, Richardson, and Chandalar migration routes. Calving occurs pri-

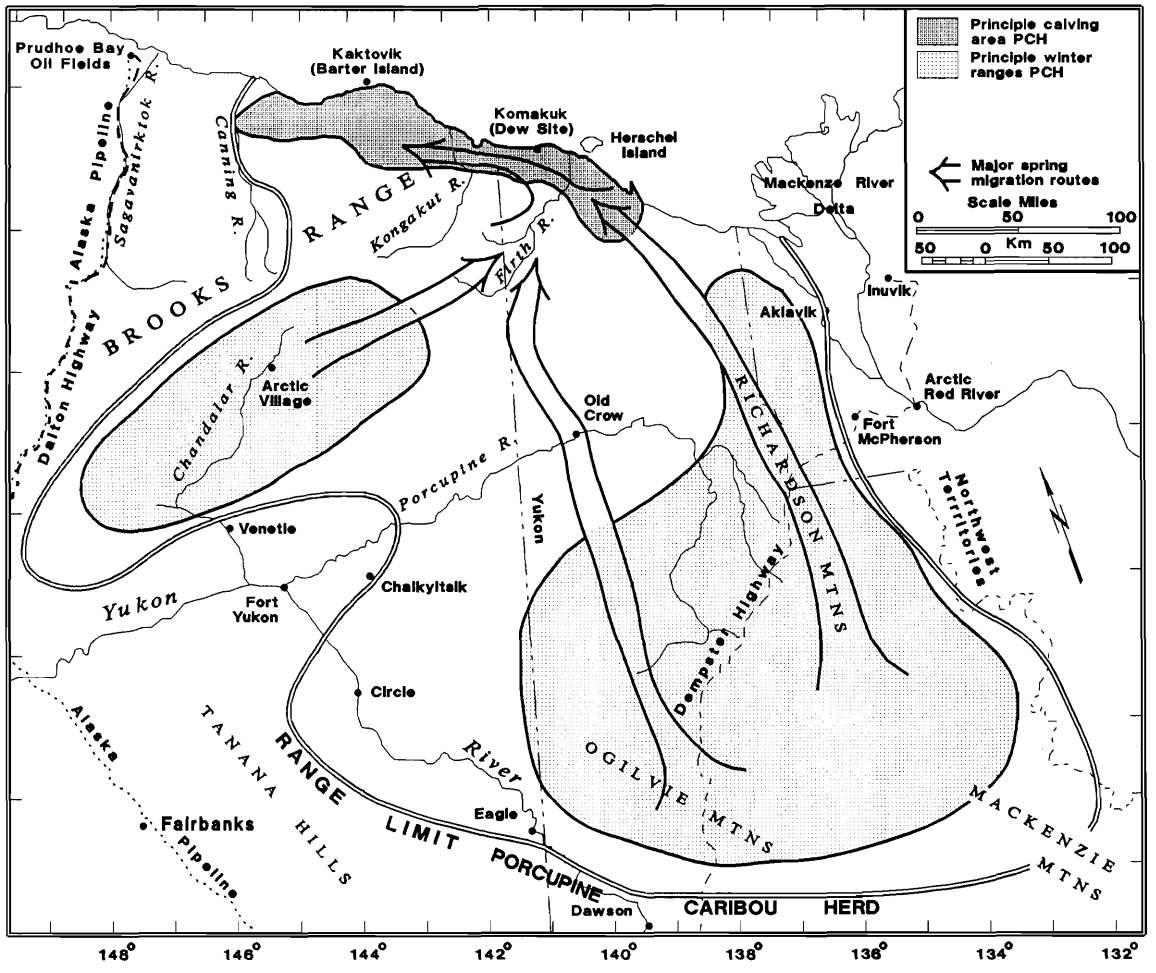

FIG. 1. Annual range of the Porcupine caribou herd.

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marily during the 1st week of June on the coastal plain between the Canning River in Alaska and the Blow River in the Yukon (Thompson 1978; Whitten and Cameron 1983; Garner and Reynolds 1986).

The CAH, estimated at 16 000 caribou in 1986 (R. Cameron, personal communication), ranges north of the crest of the Brooks Range primarily between the Colville and Canning rivers (Cameron and Whitten 1979). The distribution of the CAH in winter is generally south of that in summer (Cameron and Whitten 1979), but considerable overlap of summer and winter distributions occurs, and caribou use of areas within 40 km of the coast during winter is not uncommon. Walker (1985) provided a detailed description of the vegetation and climate of the Central Arctic region.

Methods

Between 10 April 1985 and 31 December 1987, we obtained daily movement and activity data on 34 adult female caribou of the PCH and CAH using the Argos Data Collection and Location System (Argos 1984; Fancy et al. 1988). The Argos system is a cooperative project of the National Oceanic and Atmospheric Administration (NOAA), the National Aeronautics and Space Administration (NASA), and the Centre national d'Études spatiales (CNES) of France. The system consists of two polar-orbiting weather satellites (currently NOAA-10 and NOAA-11), three ground tracking stations, and processing centers in France and Maryland. Fancy et al. (1988) provided a detailed description of the Argos system and potential applications for wildlife research and management.

Caribou were captured on winter range and fitted with a neck collar equipped with an Argos-compatible transmitter and a conventional VHF transmitter that was used to relocate the caribou by aircraft. Adult female caribou were located opportunistically and darted from a helicopter with Cap-Chur equipment and a mixture of M99 (6.25 mg etorphine hydrochloride) and 7.5 mg acepromazine maleate. The antagonist M50-50 (14 mg diprenorphine hydrochloride) was administered to effect recovery. The canister housing the satellite transmitter measured approximately 7 × 11 × 6 cm. The complete package weighed 1.5–1.6 kg and was built by Telonics, Inc. (Mesa, AZ). To prolong battery life, generation 2 satellite transmitters (i.e., transmitters manufactured before September 1986) were programmed to transmit for 6 h each day, giving a theoretical battery life of 1 year. More advanced generation 3 units (n = 13) deployed after September 1986 were programmed to transmit for 12 h each day between 1 May and 30 September, and for 6 h on alternate days between 1 October and 30 April. Each signal included a unique identification number, synchronization and error-checking information, and 32 bits of sensor data, and was transmitted at ca. 60-s intervals on a frequency of 401.650 MHz. Location was calculated from the Doppler shift in the carrier frequency of the transmitted signal as the satellite approached and then moved away from the transmitter (Argos 1984; Fancy et al. 1988).

Transmitters also contained sensors for monitoring the internal temperature of the canister (an approximation of ambient temperature; Pank et al. 1985; unpublished data) and the caribou's activity. For activity monitoring, a microprocessor determined the number of seconds each minute during which a mercury tip switch calibrated for caribou (Pank et al. 1989) was activated. The resulting short-term activity index, having a maximum value of 60, was a reflection of activity (i.e., lying, feeding, walking, running) during the minute

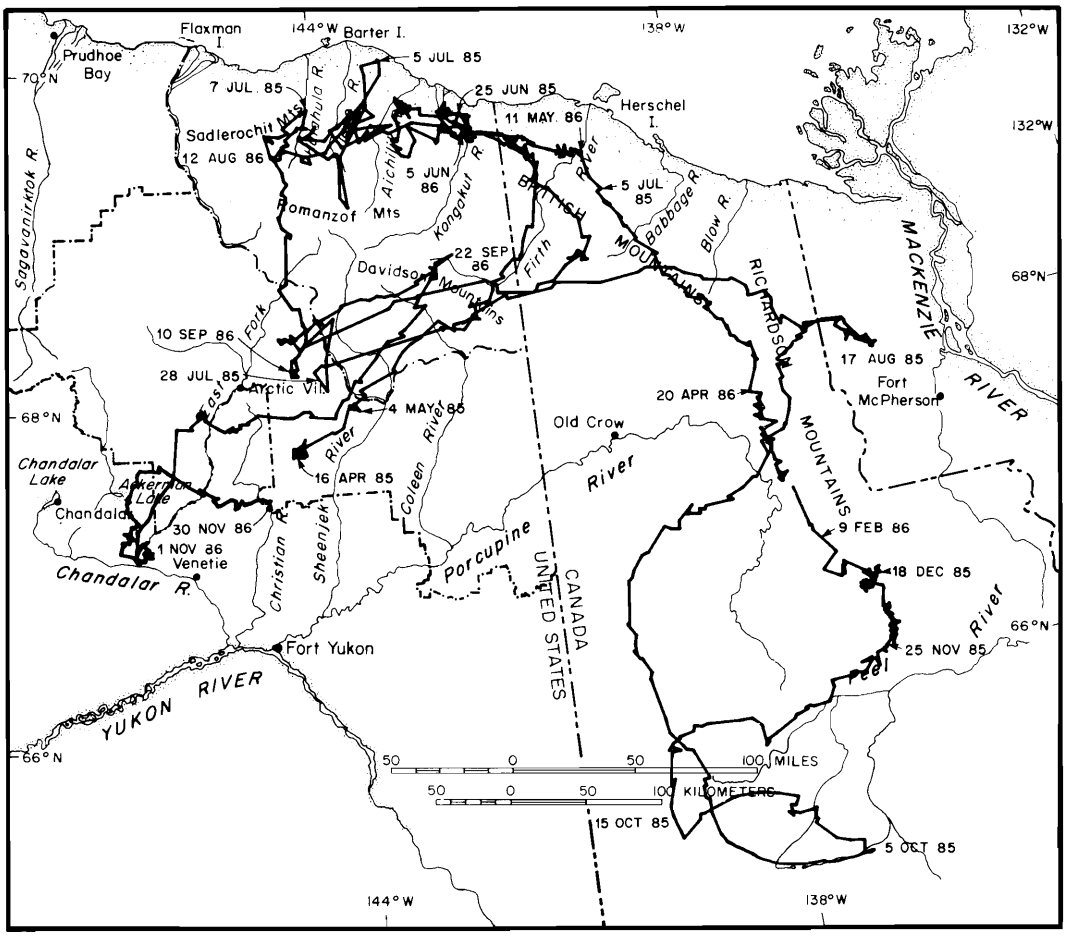

FIG. 2. Movements by adult female caribou S10 between 16 April 1985 and 1 December 1986 as determined by the Argos Data Collection and Location System.

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before transmission. In addition, a long-term activity index was computed as the sum of 60-s counts for a 24-h period (Pank et al. 1989; Fancy et al. 1988).

Location and sensor data were obtained monthly from the Argos processing center on nine-track computer tapes and processed through a series of programs for entry into the ARC/INFO and MOSS/MAPS Geographic Information Systems as described by Fancy et al. (1988). The minimum distance travelled by each caribou between two successive locations was calculated by connecting locations with straight lines. For each month, we calculated the mean daily movement rate for each caribou by summing the lengths of line segments and dividing by the corresponding time interval. Differences in monthly movement rates between herds and years were tested by two-way analysis of variance using the General Linear Model (GLM) procedure (SAS Institute Inc. 1985). Statistical comparisons were evaluated at the 95% confidence level.

Results

System reliability and location accuracy

During 1985–1987, we received 79 101 sets of sensor data and 49 283 locations for satellite-collared caribou of the PCH and CAH. Only 5 of the 42 transmitters attached to caribou before October 1986 failed within 6 months of deployment. A mean of 3.5 locations/d was obtained for caribou with generation 2 transmitters. Caribou with generation 3 transmitters that operated 12 h/d in summer were located a mean of 8.0 times daily. The mean location error for generation 2 transmitters placed at known locations (as described in Fancy et al. 1988) was 760 m (n = 2711 locations). Newer generation 3 transmitters had a mean error of 480 m (n = 403), and 90% of the calculated locations were within 900 m of the true transmitter location. The high frequency and accuracy of locations allowed us to determine very detailed movement patterns for each caribou (Fig. 2).

Seasonal movement patterns

The PCH and CAH exhibited similar annual patterns in their daily rates of movement, with highest values in July and lowest values in February or March (Fig. 3). Differences in mean movement rates between herds and among years were compared for midwinter (February), spring migration (May), midsummer (July), and fall migration (September). We found no significant differences between movement rates for the two herds in February or July (two-way ANOVA; February F = 0.08, $p > 0.75$; July $F = 0.14$, $p > 0.70$). In contrast, differences in movement rates between herds were highly significant during migration periods (May $F = 16.27$, $p < 0.001$; September $F = 49.20$, $p < 0.0001$). Significant between-year differences in movement rates were found for May (two-way ANOVA; $F = 5.69$, $p < 0.01$) and July ($F = 6.67$, $p < 0.005$). Movement rates during May and July in 1985 and 1986 were similar, but were significantly lower than those in 1987 (Duncan's multiple range test; SAS Institute Inc. 1985; Fig. 3).

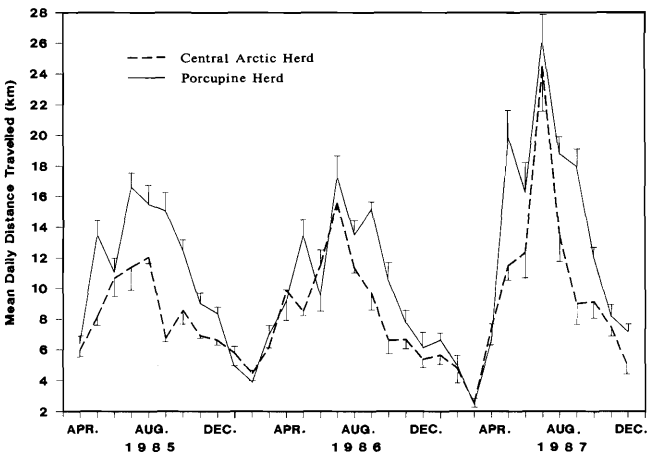

FIG. 3. Movement rates of the Porcupine (means + 1 SE) and Central Arctic (means − 1 SE) caribou herds between 1985 and 1987.

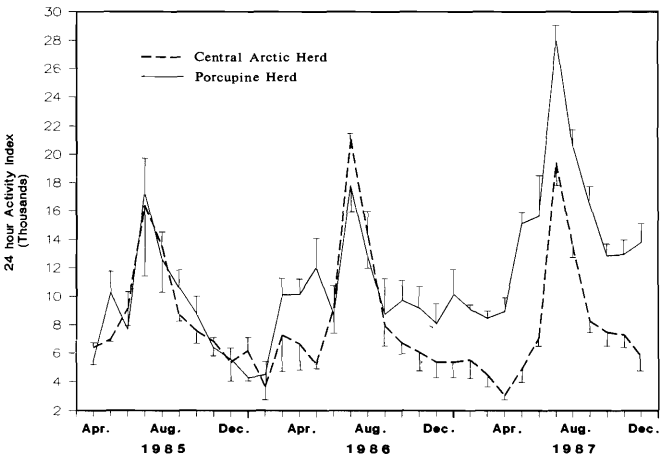

FIG. 4. Mean long-term activity index (+ or − 1 SE) for adult female caribou of the Porcupine and Central Arctic caribou herds between 1985 and 1987. The index represents the number of seconds each day during which a mercury switch calibrated for caribou was activated.

A potential seasonal bias in movement rates exists because we assumed that each caribou moved in a straight line between successive locations. This assumption obviously leads to an underestimate, but less so when movements tend to be rapid and directional, such as during spring migration or insect-induced movements (Skoog 1968; Thompson 1978). However, when movements are relatively localized, during calving and midwinter, a substantial underestimate is possible. We do not believe that the seasonal bias in movement rates is serious enough to affect our interpretation of study findings, however, because the annual pattern in the long-term activity index, an independent measure of mobility (Pank et al. 1985, 1989; Fancy et al. 1988), follows a pattern similar to that of the movement rates (Fig. 4). In work with captive caribou, we have found that high activity counts are associated with walking and running (Pank et al. 1985, 1989; Fancy et al. 1988), and we have found a highly significant linear relationship between the mean monthly long-term activity index and caribou movement rates for the PCH and CAH (regression; $r^2 = 0.21$, df = 388, $p < 0.0001$).

Annual distance travelled

For each caribou, we summed the distances between successive locations to obtain an estimate of the minimum distance travelled per year. We included only those caribou that were tracked over a period of 10 months or longer. The mean annual distance travelled for 10 PCH cows (4355 ± 150 (SE) km) was significantly greater than that for 10 CAH cows (3031 ± 97 (SE) km; ANOVA; $F = 55.01$, $p < 0.0001$). To our knowledge, the movements made by caribou in this study, ranging to 5055 km/year, are the longest documented movements by any terrestrial animal.

Discussion

Gregarious behavior and seasonal migrations are common to many ungulate species living in open environments. Examples include the wildebeest (*Connochaetes taurinus*), Thomson's gazelle (*Gazella thomsonii*), and several species of antelopes in Africa (Bell 1971; Estes 1974), alpine sheep and goats (Lawson and Johnson 1982; Wigal and Coggins 1982), and caribou and reindeer in North America, Scandinavia, and northern Asia (Kelsall 1968; Gaare and Skogland 1975; Geller and Borzhanov 1984). In each case, migrations are related to seasonal changes in weather patterns that affect forage availability and quality.

The search for adequate food in a seasonal and often harsh environment is a primary factor influencing caribou movements (Murie 1935; Banfield 1954; Skoog 1968; Bergerud 1974). Bergerud (1974) hypothesized that gregarious behavior by caribou was incompatible with "a sedentary life in an environment dominated by slow growing plants whose availability in space and time varied with snow conditions. Thus, mobility had selective value and caribou developed their characteristically restless mode of life." We believe that the characteristic migrations of barren-ground caribou between winter ranges and calving grounds are consistent with an optional range use strategy governed by energy and nutrient availability, and risk of predation on calves. Caribou winter ranges are characterized by a relatively high biomass of highly digestible lichens, and relatively soft or shallow snow. However, lichens are deficient in protein and minerals, and caribou cannot sustain rapid growth and milk production on a predominantly lichen diet (Jacobsen and Skjenneberg 1974; Holleman et al. 1979; Rognmo et al. 1983). The optimal range use strategy during the summer period of lactation and rapid growth therefore involves movements to areas where highly digestible forages in the early stages of growth and containing high amounts of nitrogen and minerals can be obtained (Klein 1970; Whitten and Cameron 1980). In addition to their high latitude and often varied topography, factors that prolong the availability of vegetation in the early stages of growth (Fleck and Gunn 1982), the calving grounds of the barren-ground herds are usually characterized by reduced predation risk on calves, delayed insect emergence, and frequent periods of cool, windy weather when insect activity is reduced (Kelsall 1968; Skoog 1968; Bergerud 1974).

Towards the end of the plant growing season in August and September, following the period of intense insect activity, the gross latitudinal trends in plant phenology found in early summer become less pronounced, and caribou disperse throughout a large portion of their annual range to take advantage of localized foraging opportunities (Klein 1970; Whitten and Cameron 1980). When the digestibility and nutrient content of summer forage species declines at the end of the grow-

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TABLE 1. Comparative cost per animal (in U.S. dollars) to locate 10 caribou using satellite- vs. radio-telemetry techniques in northern Alaska

		Cost per location		
		10/year	52/year	365/year
Satellite telemetry				
Initial cost per collar (includes backup VHF transmitter)	$3300.00	$350	$ 74	$ 18
Additonal set of collars	3300.00			
Refurbishment costs ($750 × 4)	3000.00			
Capture costs ($1500 × 5)	7500.00			
Argos processing	8.22/d			
Radio telemetry				
Initial cost per collar	$ 330.00	$893	$778	$754
Additional set of collars	330.00			
Radio-tracking equipment	3500.00			
Capture costs ($1500 × 2)	3000.00			
Radio-tracking flight	7500.00*			

NOTE: Calculations are based on a 5-year study using satellite transmitters with a 1-year battery life or radio-transmitters with a 3- to 4-year battery life. An additional set of collars is included to replace used collars when the caribou are recaptured. Labor costs are not included.

*Full coverage of study area requires 30 h at $250/h air charter cost.

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ing season, lichens again become the most digestible forage and most available source of energy, and movements to areas of high lichen biomass and suitable snow conditions are adaptive.

Caribou have evolved the highest efficiency of walking of any terrestrial mammal (Fancy and White 1987). Because of the multiplier effect (White 1983) of factors associated with energy intake, and the relatively low cost of locomotion, caribou can compensate for the energy cost of extensive movements and can take advantage of foraging opportunities limited in space and time. Thus, from an energetic standpoint, extensive movements between and within seasonal ranges are adaptive if they result in even small increases in daily eating time, eating rates, or forage digestibility (Fancy 1986).

Differences in the extent of area covered by cows of the PCH and CAH may be largely a function of herd size. As herds decrease in size, the size of their range also decreases (Banfield 1951; Skoog 1968). Conversely, as herd size increases, caribou expand their range, and movements become more unpredictable. Skoog (1968) believed that there are social limits on population density that can be sustained by free-ranging caribou herds. Apparently, caribou of the CAH are able to obtain adequate forage throughout the year within a relatively small area, whereas at a higher density, the caribou would presumably consume and trample the forage in an area and would have to abandon it. Factors selecting for a highly migratory pattern are absent in the CAH; nevertheless, CAH cows exhibit the same "restlessness" as PCH cows and move almost as far during a year.

We cannot fully explain the significantly greater movements by satellite-collared caribou in May and July of 1987 compared with 1985 and 1986. Almost the entire PCH wintered in Alaska in the vicinity of Arctic Village in 1986–1987, and the length of the spring migration route in 1987 was similar to those used in 1985 and 1986. April snow depths in 1987, and the timing of migration, were also similar to those of the previous 2 years. Approximately two-thirds of the PCH cows calved in Canada in 1987, further east than usual, and movements by postcalving aggregations in July tended to be further west than in preceding years, accounting for increased movements in July 1987. The number of days in 1987 when weather conditions were conducive to moderate or severe insect activity (calculated from Barter Island weather records using the methods of White et al., 1975) was twice that in 1985, but only slightly higher (11 vs. 9 days) than in 1986. The distribution of CAH caribou and insect activity in July 1987 was not noticeably different from that in preceding years, yet CAH cows moved as far as those in the PCH.

In our study area, satellite telemetry is the only feasible means of systematically acquiring location or sensor data for free-ranging large animals. Fixed observation sites or radio-tracking stations cannot be used because of terrain and the mobility of the animals, and radio-tracking flights frequently cannot be conducted because of darkness or poor weather. Even if it were possible to systematically locate radio-collared caribou from aircraft, the cost per location would be much higher than that for locations determined by satellite (Table 1). For example, in a 5-year study using 10 caribou, the cost to obtain 1 location/d using conventional radiotelemetry would be 43 times that using satellite telemetry. If only 1 location/week were required to meet study objectives, the cost per location using conventional radiotelemetry would be 10 times higher than that using satellite telemetry. In this example, satellite telemetry would be cost effective if 3 or more locations/year were needed for each caribou. In a study involving 50 caribou, the cost to relocate each animal from an aircraft would be reduced, yet satellite telemetry would still be cost effective if more than 13 locations/year were needed to address study objectives.

Satellite telemetry has proven to be an accurate, reliable, and cost-effective approach for monitoring caribou movements and activity in an arctic environment. Improved equipment and software are continually being developed, and smaller, lighter, and more durable transmitters with the capability of monitoring animal behavior, physiology, and physical environment are becoming available. The very detailed data sets we have

obtained for caribou using this technology will further our ability to conduct in-depth analyses on the many puzzling questions about caribou ecology and physiology.

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