VOL. 37, NO. 1 (MARCH 1984) P. 7-22

The Buffalo of the North: Caribou (*Rangifer tarandus*) and Human Developments

A.T. BERGERUD[1], R.D. JAKIMCHUK[2], and D.R. CARRUTHERS[2]

ABSTRACT. The demography, movement, and behaviour patterns of eight caribou populations (Kaminuriak, Nelchina, Central Arctic, Fortymile, Porcupine, British Columbia, Newfoundland, and Snøhetta) exposed to industrial activities or transportation corridors are reviewed. Behaviour patterns of caribou encountering transportation corridors are explainable in terms of adaptive responses to natural environmental features. There is no evidence that disturbance activities or habitat alteration have affected productivity. Transportation corridors have adversely affected caribou numbers by facilitating access by hunters. There are no examples where physical features of corridors or associated disturbances have affected numbers or productivity. Caribou apparently have a high degree of resilience to human disturbance, and seasonal movement patterns and extent of range occupancy appear to be a function of population size rather than of extrinsic disturbance. The carrying capacity of the habitat is based on the space caribou need to interact successfully with their natural predators. Caribou must not be prevented from crossing transportation corridors by the construction of physical barriers, by firing lines created by hunting activity along a corridor, or by intense harassment — a loss in usable space will ultimately result in reduced abundance.

Key words: caribou (*Rangifer tarandus*), disturbance, wolves, predation, overharvest, access

RÉSUMÉ. L'article examine les données ayant trait à la démographie, aux déplacements et au comportement de huit populations de caribous (Kaminuriak, Nelchina, Arctique central, Fortymile, Porcupine, Colombie-Britannique, Terre-Neuve et Snøhetta) exposées aux activités industrielles et aux corridors de transport. Le comportement des caribous ayant contact avec les corridors de transport peut être expliqué comme réaction d'adaptation aux traits naturels du milieu. Les corridors de transport ont affecté de façon défavorable le nombre de caribous en facilitant l'accès aux chasseurs. Il n'existe aucun exemple dans lequel les aspects physiques des corridors ou des problèmes associés ont touché le nombre ou la productivité. Le caribou possède apparemment un niveau élevé de résistance aux interventions humaines, et son déplacement saisonnier et la portée de sa distribution semble varier en fonction des variations en population plutôt que des dérangements extrinsèques. La capacité de soutien de l'habitat est fondée sur l'espace dont a besoin le caribou pour réagir de façon satisfaisante face à ses prédateurs naturels. Le caribou ne doit pas être empêché de traverser les corridors de transport par la construction de barrières physiques, par les lignes de tir créées par la chasse le long du corridor ou par des harcèlements intenses; il en résulterait une perte d'espace qui entraînerait éventuellement une réduction des nombres.

Mots clés: caribou (*Rangifer tarandus*), dérangement, loups, predation, surchasse, l'accès aux chasseurs

Traduit pour le journal par Maurice Guibord.

INTRODUCTION

During the past decade, considerable research has been carried out on disturbance to northern mammals. In particular, various pipeline projects and proposals became the focal point of environmental concerns, debate, and public hearings. The Trans-Alaska Oil Pipeline (TAPS) is now an operating system, and continued research (Cameron and Whitten, 1976, 1980) is providing information on the response of caribou to that development and its ancillary activities. Klein (1971, 1973) examined issues of potential concern involving caribou populations, including obstruction of movements and various types of direct disturbance to populations and their habitats. Natural gas pipeline proposals in Canada and the U.S.A. stimulated baseline research and disturbance studies sponsored by government, industry, and academic institutions. The implications of aircraft disturbance received considerable attention (Miller and Gunn, 1979), supplementing earlier quantitative evaluations of caribou responses to noise (McCourt and Horstman, 1974) and roads (Surrendi and DeBock, 1976).

With increased interest in disturbance as a facet of impact assessment, considerable debate on its significance to wildlife took place within the profession and in public fora (Jakimchuk, 1978). In the early and mid-1970s, bio-energetic impacts were postulated as a concern related to industrial developments (Geist, 1975).

A panel discussion at the First International Reindeer/Caribou Symposium in 1972 was devoted to the implications to caribou of northern development; several papers on disturbance-related topics were presented there and at the Second International Reindeer/Caribou Symposium in 1979. These symposia brought together an enormous amount of research, much which is relevant to evaluating the significance of disturbance to caribou populations. The literature available on human disturbance to northern large mammals is compiled in Shank's (1979) annotated bibliography and review containing over 551 references. Sopuck *et al.* (1979) have also completed a comprehensive review of general wildlife impacts including disturbance to large and small mammals. Klein (1980) expanded his 1971 assessment of the effects of obstructions on caribou.

In a casual examination of the existing literature, one may find evidence to support virtually any conclusion regarding the significance of disturbance to large ungulates (Shank, 1979). This uncertainty is largely a result of the emphasis being placed on individual and group observations which are then extrapolated to the population level, and of the great variation in information ranging from anecdotal notes to quantitative studies. To date, there have been no studies directed specifically at establishing the effect of specific disturbance(s) on the population dynamics of caribou. The difficulties involved in such a study are obvious. However, in a number of

[1]Biology Department, University of Victoria, Victoria, B.C., Canada V8W 2Y2
[2]Renewable Resources Consulting Services Ltd., 9865 West Saanich Road, R.R. #2, Sidney, B.C., Canada V8L 3S1

cases the status of populations has been analyzed in relation to disturbance forces operating within their environment (Klein, 1971, 1980; Bergerud, 1974a; Calef, 1974).

We agree with Shank's (1979:5) comment, "In actuality, there is a potentially infinite universe of manners in which human activity can influence animal populations and merely demonstrating that one factor is not operative does not negate the influence of the remainder of possible factors. In other words, the only way in which population responses can be shown not to be influenced by disturbance is to study population dynamics."

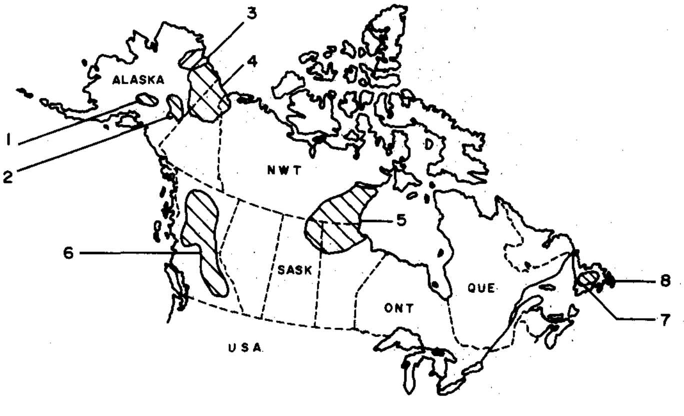

FIG. 1. The location of caribou herds described in this study. 1) Nelchina; 2) Fortymile; 3) Central Arctic; 4) Porcupine; 5) Kaminuriak; 6) British Columbia; 7) Interior; and 8) Avalon.

In this paper we will assess the impact of human disturbance on the demography of eight caribou herds (Fig. 1): the Porcupine, Nelchina, Central Arctic, Fortymile, and Kaminuriak herds; herds in British Columbia and Newfoundland; and the Snøhetta herd in Norway. We have conducted field studies of five of these herds. We have selected these particular herds because they have been mentioned as possibly being adversely affected by human impacts and some demographic statistics are available to evaluate those assertions. In our assessment of human impacts we go beyond simple correlation reasoning which links a response to a coincident event. Instead, we examine data on reproduction and mortality rates, the underlying causes of the observed rates, changes in population size, herd movements, and range use. Our objective is to show how simple correlation reasoning on the effects of human disturbance on caribou obscures alternative explanations and may lead to untestable generalizations and insupportable conclusions.

We define human disturbance very broadly to include hunting impacts, manipulation of predator populations, development disturbance (transportation corridors and physical structures), and habitat modifications such as logging and flooding.

DEMOGRAPHIC CASE HISTORIES

Porcupine Herd

In 1961 Skoog (1968) estimated 110 000 to 117 000 animals in the Porcupine herd. Lentfer (1965) estimated 140 000 in 1965, and subsequent population estimates fell within the range of 100 000-110 000. In 1972, LeResche (1975) estimated 93 000-103 000, and in the same year Roseneau and Stern (1974) estimated 90 000-107 000. In 1977 Bente and Roseneau (1978) estimated 105 000. Hinman (1981) reported an estimated 110 000 animals in 1980. Over the past 20 years the Porcupine herd has remained stable at 100 000-110 000 animals (Fig. 2).

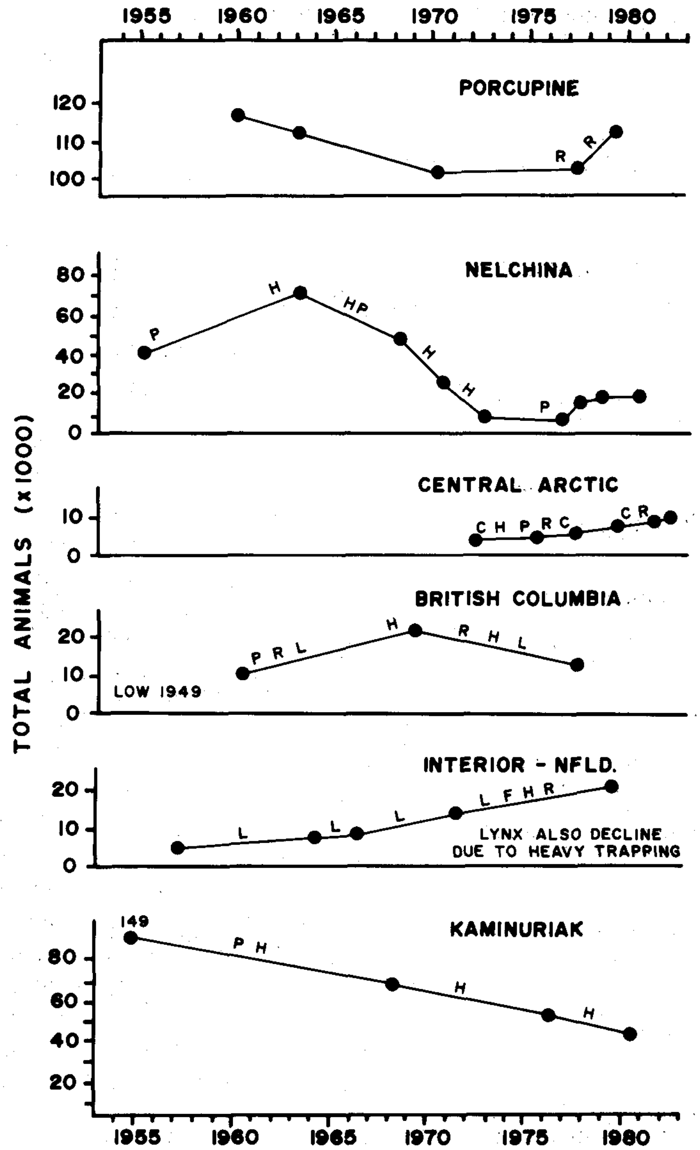

FIG. 2. Trends in population size of (a) Porcupine, (b) Nelchina, (c) Central Arctic, (d) British Columbia, (e) Interior Newfoundland, and (f) Kaminuriak caribou herds, 1949-1981, compared with presence of disturbance features (Skoog, 1968; Bos, 1975; Hawkins and Calef, 1977; Bergerud, 1978; Hinman, 1981; Pitcher, 1982; E. Mercer, pers. comm. 1982; Whitten and Cameron, 1983). Key: P = predator control; H = hunting; C = construction; R = roads; F = flooding; L = logging.

Yearling recruitment has been 10-11% of the total population in July from 1971 to 1980 (Fig. 3) and calves of the year show a similar level of stability at 15-23% of the fall population (Bente and Roseneau, 1978; Hinman, 1981; Jakimchuk *et al.*, 1974; Roseneau and Stern, 1974). In the same period, hunter kill accounted for <3% of the population (Jakimchuk *et al.*, 1974; Calef, 1974, 1975; Hinman, 1981). Since at least 1971, the Porcupine herd has consistently ranged over a 240 000-km² area.

No estimates of wolf (*Canis lupus*) predation rates are available for the Porcupine herd although Jakimchuk *et al.* (1974) observed 131 caribou kills during late winter surveys in 1971. Wolf numbers are thought to be low to moderate over the range. Martell and Russell (1983) estimated 5% annual adult mortality from all sources other than hunting.

Since the late 1960s construction of the Dempster Highway has bisected portions of the winter range of the herd in northern Yukon. In 1976 new construction transected a major spring migration corridor in the northern Richardson Mountains. The highway was completed in 1978, and at that time a five-mile no-hunting corridor was established along the highway. Crossing of the highway by caribou and use of winter ranges south of the highway have continued to the present time.

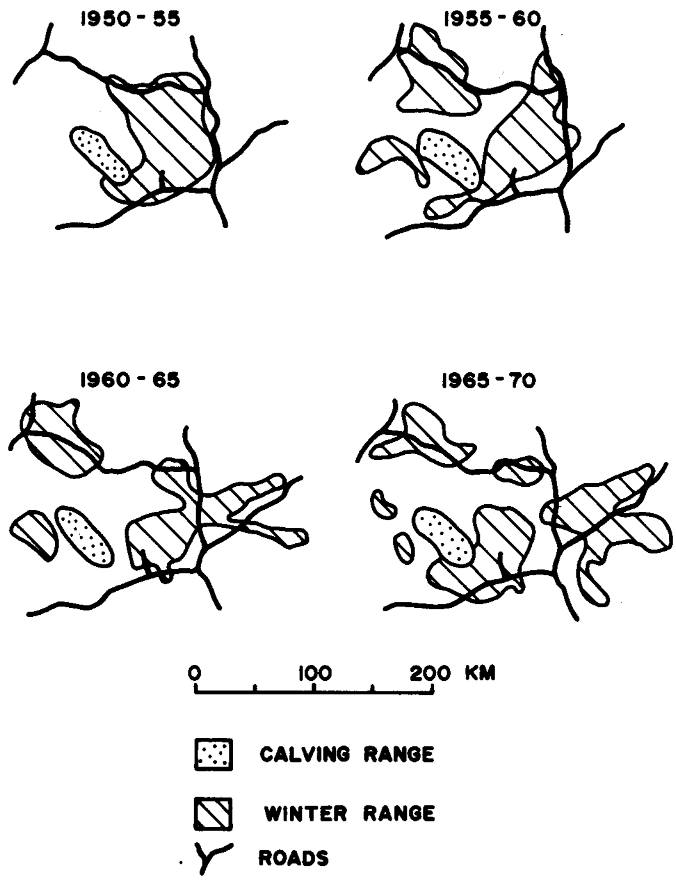

FIG. 4. Increase in extent of winter ranges used by the Nelchina herd, 1950-1970 and in 1973 (adapted from Hemming, 1971 and Bos, 1974).

Nelchina Herd

The Nelchina herd was first estimated at 10 000 animals in 1945 (Skoog, 1968). Estimates from 1948 to 1954 varied from 5000 to 13 200 animals (Skoog, 1968; Bos, 1975). Calf percentage averaged near 15% (range = 13-17%) in 1951 and 1952 (Alaska Dept. Fish and Game Files). In the period 1948-1954, 200+ wolves were removed from the Nelchina range and by 1953 only 12 wolves were estimated to be present; these increased to possibly 425 animals by 1965 (Rausch, 1967). Wolves were again reduced and McIlroy (1976) estimated 300 in 1966-67.

The first systematic caribou census was conducted in February 1955 and estimated 40 000 caribou (Fig. 2; Watson and Scott, 1956). Clearly the early counts were too low. Now a unique opportunity was available: the status of both prey (caribou) and predator (wolves) was established and the interactions of the two could be documented. Skoog (1968) began his intensive studies of the herd in the presence of increasing, known, and unmanaged wolf populations.

Following wolf removal, calf survival was high and calves soon exceeded 20% of the herd (Fig. 3). The herd increased, reaching 71 000 in the winter of 1962-63 (Fig. 2; Skoog, 1968). The increase in numbers was followed by increased movement (Skoog, 1968:649) and range expansion (Fig. 4) across the Richardson Highway.

The herd declined rapidly from 48 000 in 1967-68 to 10 000 by 1972-73 (Fig. 2; Bos, 1975), coincident with an increase in wolf numbers (Rausch, 1967), a decrease in calf survival, and heavy incidence of hunting as the herd crossed the Richardson Highway. The survival of the 1964, 1965, and 1966 cohorts

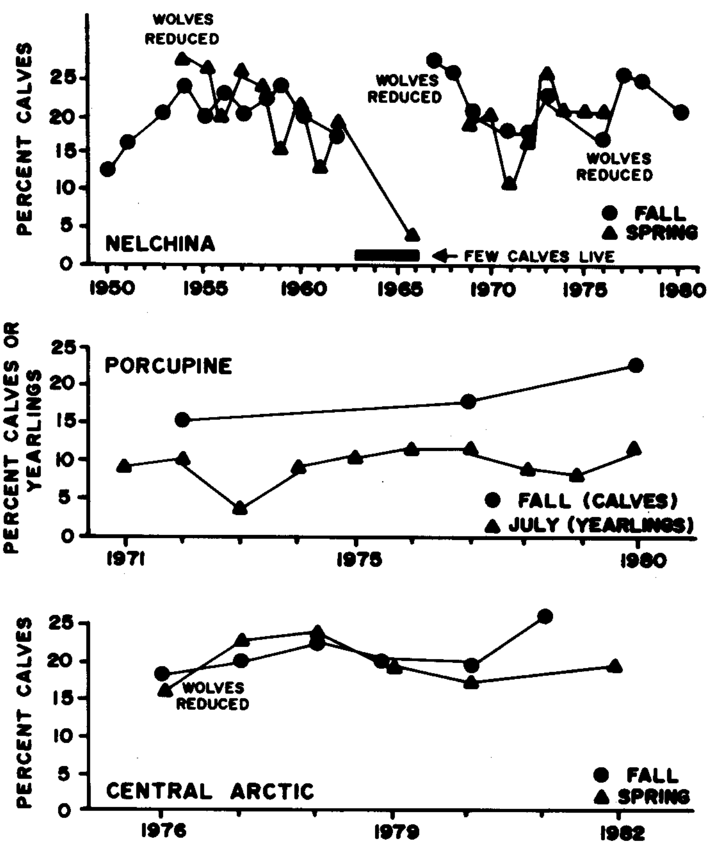

FIG. 3. Trends in calf production and recruitment for the (a) Nelchina, (b) Porcupine, and (c) Central Arctic caribou herds, 1952-1981 (Skoog, 1968; Bos, 1975; Bente and Roseneau, 1978; Doerr, 1980; Hinman, 1981; D. Russell, pers. comm. 1982; Whitten and Cameron, 1983).

was extremely low (Fig. 3; Bos, 1975). This low survival coincided with high wolf numbers, but when wolves were reduced in 1966-67 calf survival improved (Fig. 3). Coincident with a lack of recruitment, harvests of > 10% of the herd apparently occurred in many years between 1961 and 1971 (calculated from Bos, 1975). This heavy harvest was the major cause of the decline (Doerr, 1980).

The herd continued to migrate across the Richardson Highway as it declined, even in the presence of intense human disturbance from hunting. As the herd increased between 1955 and 1962, it expanded its range to include the same area it had ranged in the 1880s prior to the construction of most of the surrounding transportation corridors (Fig. 5). As the herd increased it crossed the Denali, Taylor, Glenn, and Richardson highways (Fig. 5). Roads were not a barrier to movement but did permit human access which greatly contributed to overharvest and subsequent decline.

The herd continued to decline after 1972 (Hinman, 1981), and in 1976 protective measures (a hunting closure in 1976 and permit-only hunting since 1977, and a wolf control program) were implemented by the Alaska Department of Fish and Game. By 1981 the herd had increased to a fall population of 20 730 and was considered to be increasing (Pitcher, 1982). Fall calf percentages have varied from 18% in 1976 to >20% in subsequent years. Construction of the Trans-Alaska oil pipeline, generally parallel to the Richardson Highway, was underway during the mid-1970s. The pipeline, which bisects herd migration routes, was completed in 1977 during the period of the arrested decline of the Nelchina herd (Fig. 2). The increase in numbers and productivity of the herd which has continued to the present commenced during the actual construction period.

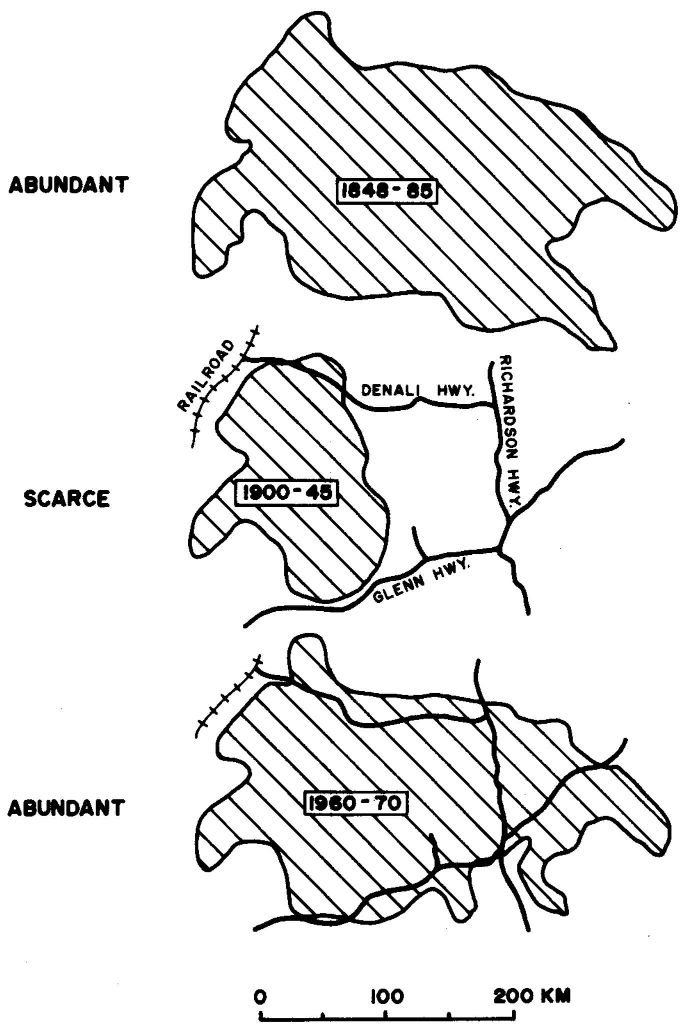

FIG. 5. Comparison of the range used by the Nelchina herd when it was abundant (1848-1885 and 1960-1970) and when it was scarce (1900-1945) (adapted from Hemming, 1975).

TABLE 1. Trends in population size for the Fortymile caribou herd

Year	Population	Source
1920s	500 000	Murie (1935)
1940s	10 000	Skoog (1956)
1950s	50 000	Davis *et al.* (1978)
1960s	Decreasing	Davis *et al.* (1978)
1968	30 000 - 40 000	Skoog (1968)
1972	15 000	LeResche (1975)
1975	4000	Davis *et al.* (1978)
1981	12 000	Hinman (1981)

Fortymile Herd

Davis *et al.* (1978) have provided a comprehensive review of the population dynamics of the Fortymile herd that is not reviewed here. The herd's numbers have fluctuated greatly in the twentieth century (Table 1). Some authors have implied that hunting along the Steese Highway may have resulted in range abandonment for the Fortymile herd in Alaska (Calef, 1974; LeResche, 1975).

As the herd has increased or decreased, its range has also expanded or contracted (Fig. 6). When the herd declined in the

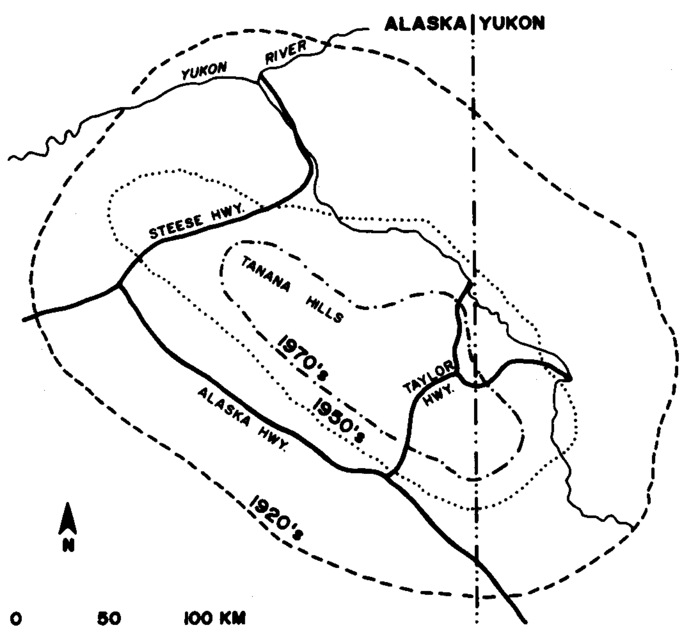

FIG. 6. Distribution of the Fortymile herd between the 1920s and 1970s (adapted from Davis *et al.*, 1978).

1960s and 1970s it stopped crossing the Steese Highway, but continued to cross the Taylor Highway (Davis *et al.*, 1978). The size of overall range of the herd has been positively correlated with abundance (Hemming, 1971; LeResche, 1975; Skoog, 1956; Davis *et al.*, 1978).

Davis *et al.* (1978:ii) concluded their review on limiting factors by stating: "From 1970 through 1972 harvests greatly exceeded the yearling recruitment rate and contributed greatly to the population decline...and...circumstantial evidence... strongly suggest[s] that predation is likely the major factor responsible for the continuous caribou decline since 1960..." We believe that the major impact of the Steese and Taylor highways has been to allow access by hunters, thereby contributing to the overharvest and decline of the herd; no barrier effect or range abandonment has been documented.

Central Arctic Herd

Skoog (1968) described caribou in Alaska's central arctic region prior to 1950 as the "Central Brooks Range herd". Thereafter the herd was thought to have merged with the Western Arctic herd. Child (1973) reviewed available information on caribou in the region and concluded that approximately 3000 caribou summered in the area around Prudhoe Bay in the early 1970s. Roseneau *et al.* (1974) believed that these caribou calved in the region, and referred to them as the Central Arctic herd. Cameron and Whitten (1976) considered these caribou a discrete subpopulation of 4000-6000 animals, characterized by synchronous and uniform north-south movements and fidelity to a calving ground on Alaska's North Slope. Recent calving grounds were subsequently described by Cameron *et al.* (1981). By 1982 the herd had increased to 9000 animals (Whitten and Cameron, 1983) (Fig. 2).

During the early period of development of the Prudhoe Bay oil field and before construction of the Trans-Alaska Pipeline System (TAPS), there were at least 30 000 caribou occupying the current range of the Central Arctic herd (Child, 1973). With the decline of the Western Arctic herd in the early 1970s, the number of caribou in the area declined to 5000 (Cameron and Whitten, 1976). We believe that the Central Arctic herd is a remnant of the Western Arctic herd that roamed the North Slope west of the Canning River in the recent and historic past (Skoog, 1968; Roby, 1978). Continued growth of both herds is likely to result in their integration, and the creation of new patterns of distribution and movement. Since 1976, increased numbers (1200-15 000) of Western Arctic caribou have been observed wintering in the range of the Central Arctic herd (Carruthers, 1983).

Studies of caribou response to the TAPS corridor in this region commenced in 1974 (Cameron and Whitten, 1976; Roby, 1978). The objectives of these studies centered on the postulated barrier and disturbance created by the TAPS and associated haul road and the implications to caribou range use and herd viability and integrity. These studies were initiated along the TAPS corridor (Sagavanirktok River valley) at a time when understanding of overall range use and movements was incomplete and affinities with adjacent herds were not recognized as important considerations.

Roby (1978), Cameron *et al.* (1979), and Cameron and Whitten (1980) have reported local "abnormalities" in caribou distribution and group composition along the TAPS corridor, which they interpret as avoidance of the corridor. They conclude that this behaviour potentially can reduce the productivity of the herd and may result in "fracturing" of the herd. These effects have not been demonstrated during eight years of research and the consequences appear to be absent based on available demographic data which indicate a healthy, expanding population (Figs. 2, 3; Hinman, 1981; Whitten and Cameron, 1983).

The natural mortality rate is unknown but is considered to be low in view of the low wolf population after 1977 (Cameron and Whitten, 1979). Prior to 1977 wolves were "common" on the range of the Central Arctic herd (Roby, 1978; Cameron and Whitten, 1979). Between 1977 and 1979 "at least three active packs" were reduced to "two to three individuals" by legal and illegal hunting (Cameron and Whitten, 1979:34). Short-yearling recruitment between 1976 and 1978 increased from 16 to 24%, and averaged 22% after 1978 (Fig. 3; Cameron and Whitten, 1983).

Mortality from hunting appears to have been low (<2%) since 1976 (Cameron and Whitten, 1979; Hinman, 1981). Prior to 1976 there were no controls on hunting of the Central Arctic herd and the pre-1976 harvest is unknown (Cameron and Whitten, 1979).

The construction of the Dalton Highway (North Slope Haul Road) began in April 1974 and was completed in September 1974. The 122-cm-diameter Trans-Alaska Pipeline System was constructed parallel to the road and the Sagavanirktok River in 1975 and 1976. A small-diameter natural gas pipeline (buried) was constructed beside the Dalton Highway in 1976 and 1977. During this period hunting was restricted within 8 km of the Dalton Highway.

The Central Arctic herd continued to migrate north and south, parallel to the TAPS and the Dalton Highway, during and after this construction period. Between 1973 and 1982 the herd had increased at an average annual rate of 13%. Productivity in June was high (85 calves/100 cows) (Banfield *et al.*, 1981). Mortality rates probably decreased after 1976 because of legal and illegal wolf hunting, and hunter harvest of caribou is believed to have declined as a result of implementation of controls. The construction and operation of two pipelines and the Dalton Highway through the center of the range of the Central Arctic herd and the proliferation of oil field facilities in the Prudhoe Bay area were not correlated with a negative demographic response by the herd between 1974 and 1982.

At this time the Western Arctic herd, adjacent to the Central Arctic herd, is increasing (Davis and Valkenburg, 1983; Davis *et al.*, 1980). We predict that, as the Western Arctic herd increases, it will expand into the range now occupied by the Central Arctic herd. If that happens it could merge with the Central Arctic herd, with the result that behaviour of the latter herd will no longer be distinct and its current range use may change. We make this prediction now because, if the Central Arctic herd should abandon or alter its range, it would surely be attributed to human disturbance rather than to the natural spacing shift of a large, mobile population.

British Columbia Herds

Caribou were common in the 1930s in B.C. but declined to low numbers in the 1940s and early 1950s (Bergerud, 1978). This decline coincided with an expansion in numbers and distribution of moose (*Alces alces*) and wolves (Hatter, 1950). Poisoning programs between 1940 and 1963 caused a decline in the wolf population. The caribou population then increased and reached at least 20 000 animals by 1968-1970 (Fig. 2; Bergerud, 1978). The population then declined again; by 1977-78, when many of the herds were censused, the population was down to 10 000 animals. A census of many of these herds in October 1982 indicated a further decline of approximately 50% (Bergerud, unpubl.).

The decline of caribou north of Prince George has been attributed to heavy predation on calves and to overharvest of adults resulting from increased hunter access along new transportation routes (Bergerud, 1978). In 1979 and 1980 young caribou calves were radio-tagged and followed for several months. Predation by wolves and bears was the major cause of mortality (R. Page, pers. comm. 1982).

Several herds were overharvested during the period of declining numbers. For example, the Pink Mountain-Prophet River herd declined from at least 3500 animals in 1969 to possibly only 300-400 animals in 1978. The increased harvest occurred because the Alaska Highway provided hunter access to caribou that came unusually far east, and because hunters travelled seismic lines via snowmobile to reach the animals. Other herds that were obviously overharvested because of increased hunter access included the Telkwa herd, the Tweedsmuir herd, and the Atlin herd (Bergerud, 1978). Helicopters were used to reach the Telkwa herd; the Tweedsmuir herd was accessible from boats travelling up a reservoir created by damming, and access to the Atlin herd was provided primarily by mining roads.

The decline of caribou in central B.C. south of Prince George (Yellowhead herd) was attributed to overhunting and to habitat destruction from logging (Bloomfield, 1980). He included as secondary adverse effects of development: (1) road and habitat barriers to movement; (2) herd displacement; (3) loss of range continuity; (4) increased access; and (5) harassment of caribou. Bloomfield (1980) provided little demographic evidence in support of his view that habitat destruction and harassment *per se* were major factors in the decline. He did not measure reproductive or adult mortality rates, nor did he record animals in poor condition or find starved animals. He found one animal illegally killed.

The Yellowhead Highway and nearby railroad (in the Fraser River valley) are not barriers to caribou movement. The caribou seek both the road and railroad corridors in periods of deep snow. There has been a number of collisions of caribou with trains (K. Child, pers. comm. 1982). The caribou also risk death on the paved highway, which they seek out to escape adjacent deep snow and possibly also to lick salt. The animals are habituated to the heavy traffic and remain on the paved surface in the presence of traffic (K. Child, pers. comm. 1982). At Kootenay Pass, B.C., animals cross the main highway and use the corridor under the adjacent power line (Johnson and Todd, 1977). Several animals have been killed by vehicles. The animals commonly remain on the side of the road unless approached by people on foot.

Bloomfield (1980:713) also believed harassment was a factor in the decline of the Yellowhead herds: "Harassment can result in diminished growth and reproduction, avoidance or abandonment of critical areas, injury or death." His reference for this generalization was his thesis (Bloomfield, 1979). But during his study he did not measure growth or birth rates, nor did he document avoidance or abandonment of range, or harassment. Such undocumented generalizations, we believe, confound our understanding of caribou behaviour and demography.

The caribou in central and southern B.C. did not decline because of habitat destruction or harassment *per se*. Calf survival is higher for caribou in disturbed central and southern B.C. than in northern B.C. where habitats have not been logged (Figs. 7, 8). In southern and central B.C. the animals commonly make use of arboreal lichens on the branches of freshly cut trees. Ritcey (1980:4), speaking of the decline in central B.C. south of the Yellowhead area, said, "Since productivity has remained high we can only assume that mortality factors not related to nutritional deficiencies are responsible for any possible reduction in numbers."

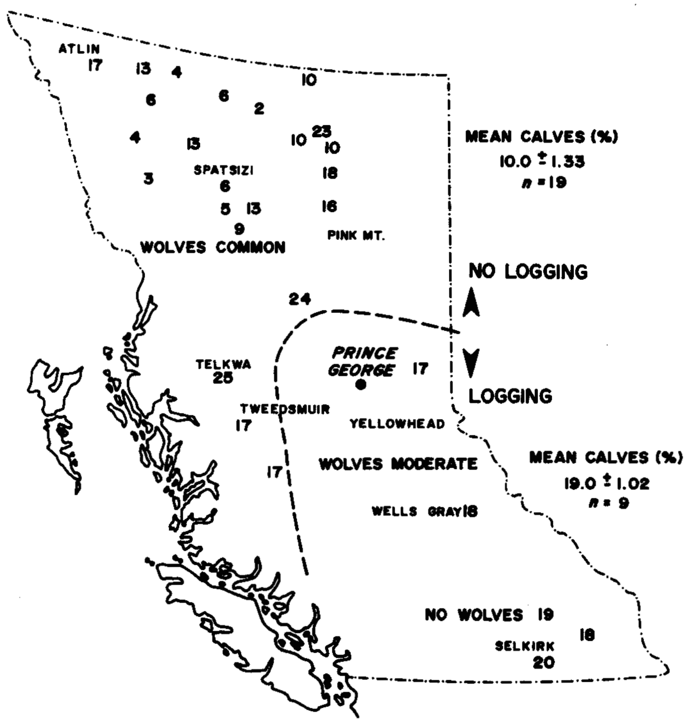

FIG. 7. The location of B.C. caribou herds and the percentage of calves in 1976 and 1977; comparison is between herds in northern British Columbia, where wolves were common and the forest was not logged, *vs.* those in southern British Columbia, where there were few wolves and much of the forest has been logged (Bergerud, 1978).

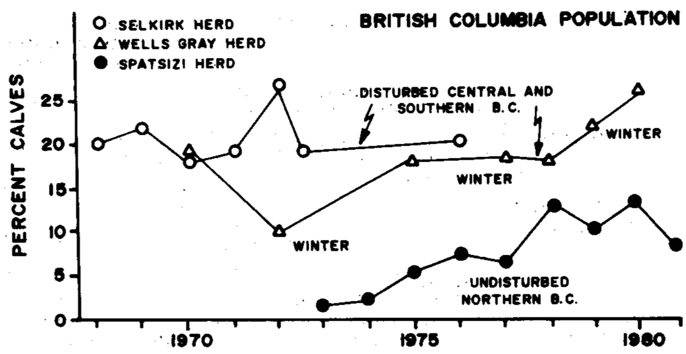

FIG. 8. Percent calves in composition counts: two herds in disturbed central and southern British Columbia *vs.* one in undisturbed northern British Columbia (Freddy, 1974; Bergerud, 1978).

The mortality factor that precipitated the decline of herds in southern and central B.C. was increased hunting, facilitated by increased access from an expanding network of public and private roads. The decline of the Yellowhead herds was a direct result of hunting and poaching (Fig. 9). Loss of food and cover habitat were not causative factors in the decline.

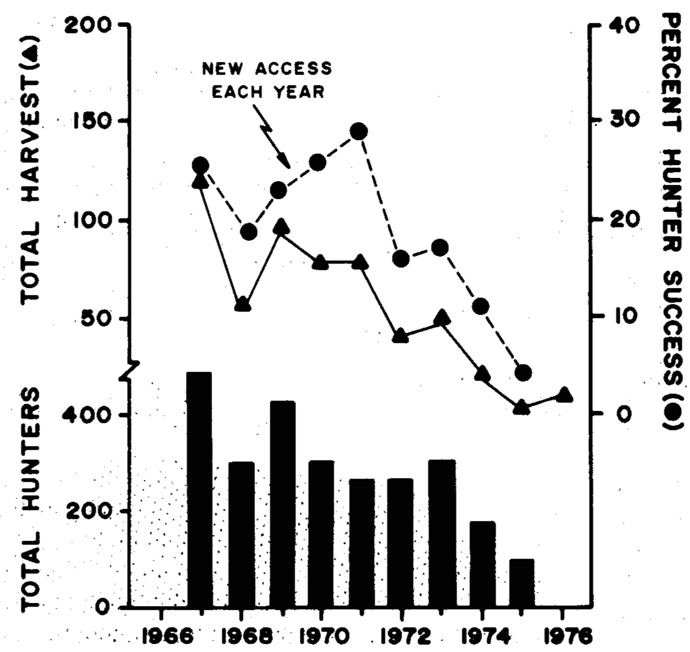

FIG. 9. Decline of the Yellowhead herds based on hunting statistics (Bergerud, 1978).

Newfoundland Herds

The Interior herd of Newfoundland has been exposed to considerable human disturbance. Large areas of former winter range have been flooded since 1970, coincident with the construction of roads and canals. Over 75% of the original forest has been logged (Bergerud, 1971), and the range has been bisected by logging roads and two public highways (Fig. 10). The herd is also the most intensively monitored in North America. Calf percentages are determined in spring, and the herd is counted at intervals. Demographic statistics now span

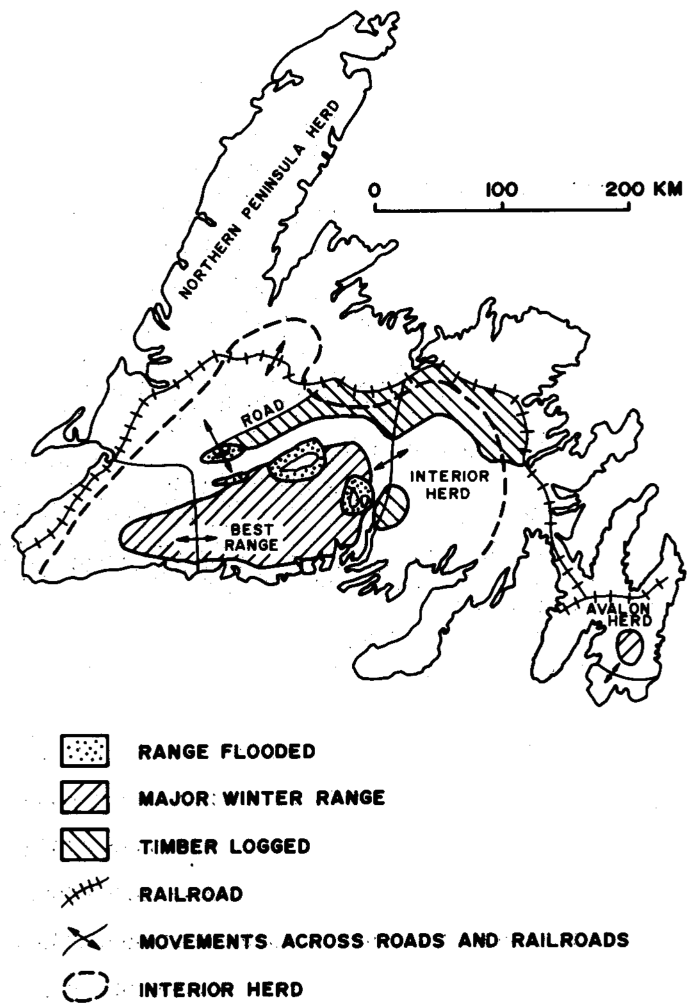

FIG. 10. Distribution and movements of Newfoundland caribou herds (Interior and Avalon) in relation to roads, logging, and flooding.

25 years, from 1956 to 1981, embracing the interval of extensive development.

The caribou in Newfoundland may have numbered 40 000 animals around 1900 (Bergerud, 1971). The Newfoundland railroad was built across the caribou range between 1890 and 1897 (Dugmore, 1913). Caribou from the Northern Peninsula, White Bay Downs, and the White and South Hills historically migrated south to the east of Grand Lake. These herds intersected the railroad near Howley, the Gaff Topsails, and Millertown Junction (Fig. 11). More than 400 hunters (Millais, 1907) massed at these crossings each fall to slaughter the animals. The estimated 15 000 animals in these herds were eliminated by hunting in a period of about 15 years (Bergerud, 1971). Even though these animals met a firing line of hunters (Millais, 1907:102), they continued to cross the railroad until the herd was nearly destroyed.

A Newfoundland herd not discussed in Bergerud (1971), the Topsails herd, now ranges on both sides of the railroad in the area where the Northern Peninsula herd used to migrate south (Fig. 11). This herd numbered less than 300 animals in the

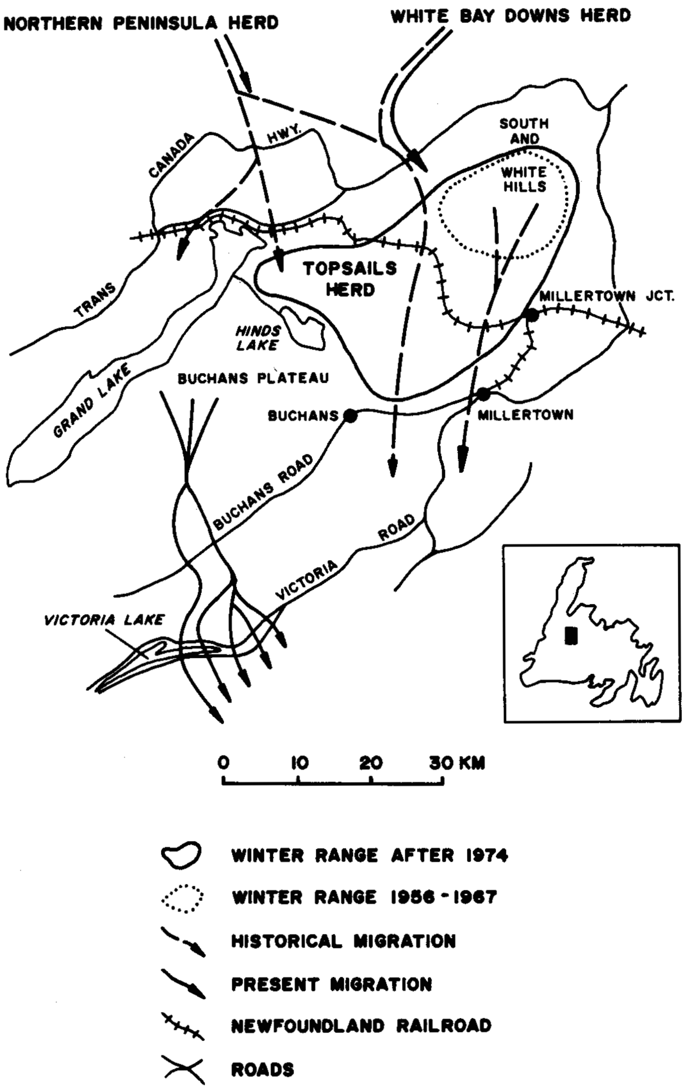

FIG. 11. Migration and distribution of caribou in central Newfoundland in relation to transportation corridors.

1950s and wintered in the White and South Hills. The herd presently consists of 2000 caribou, which freely cross the railroad that bisects their range. The area is open flat tundra and the trains can be seen and heard at great distances.

There are now over 20 000 caribou in the Interior herd (E. Mercer, pers. comm. 1982; Fig. 2), though their numbers are currently limited by illegal hunting (E. Mercer, pers. comm. 1982), which is more prevalent because of the expanded road network and the advent of the snowmachine. Nevertheless, the Interior herd has increased at r = 0.06 for the past 15 years (Fig. 2). Calf survival has been high and percent parous females has consistently been >80% (Fig. 12). The herd has remained productive, even as its size has tripled and as development has resulted in destruction of lichen ranges, the removal of much of the original timber, and the bridging of the range by public and private roads, hydro lines, and canals.

The Avalon herd of Newfoundland provides a second example of caribou crossing a road as range expansion accompanied a growing population. As the herd increased, from 125 animals in 1956 to 3000 animals in 1979 (Bergerud, 1971; E.

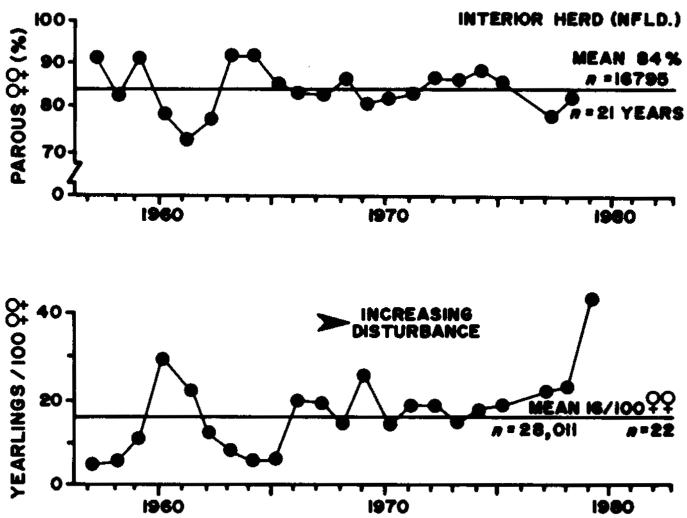

FIG. 12. Counts of yearlings/100 females and percent parous females in June in the Interior herd, Newfoundland (Bergerud, 1971; Fong and Mercer, 1975; Newfoundland Wildlife Files).

Mercer, pers. comm. 1979), it expanded its range south until it encountered a road across the south end of the peninsula (Fig. 10). In July 1978 Bergerud observed hundreds of caribou, mostly females and calves, just north of the road within sight of the fast-moving traffic and accompanying clouds of dust. The animals had habituated to the traffic and could be approached to within 100 m. In the summer of 1980, 500 animals crossed the road and again in 1981 several hundred crossed. The animals in this herd had no tradition of crossing this road and had no experience with other roads.

Kaminuriak Herd

Our intent is to evaluate the impact on the Kaminuriak herd of the Hudson Bay Railroad to Churchill, Manitoba. The railroad was constructed between 1925 and 1931 south of the Churchill River (Fig. 13). Banfield (1980) believed that the Kaminuriak herd increased throughout its range in the early 1940s. Subsequently the herd showed a continuous decline, from 145 000-149 000 animals in the period 1949-1955 to 63 000 animals in 1968 (Fig. 2); Banfield, 1954, 1980; Loughrey, 1955; Parker, 1972). Berger (1977) felt that the barrier effect of the railroad might have contributed to the decline in the herd's population.

The southward movement of the herd has varied through time. Parker (1972), in his review of historical records, concluded that barren-ground caribou were seldom south of the Churchill River before 1900. The distribution observed by Hanbury in 1904 (Parker, 1972) was similar to that documented by Parker in 1966-1968. In both periods the animals were north of the Churchill River.

Two southward penetrations across the Churchill River occurred in the twentieth century, one around 1900 and the other starting about 1935 (Parker, 1972). Lawrie (1948, in Parker, 1972) stated that the first heavy migration along the railroad began in 1935, and that caribou were even more plentiful in 1942. In 1945-46 extended movements brought caribou for the first time in 40 years to God's Lake, Cross Lake, and Oxford

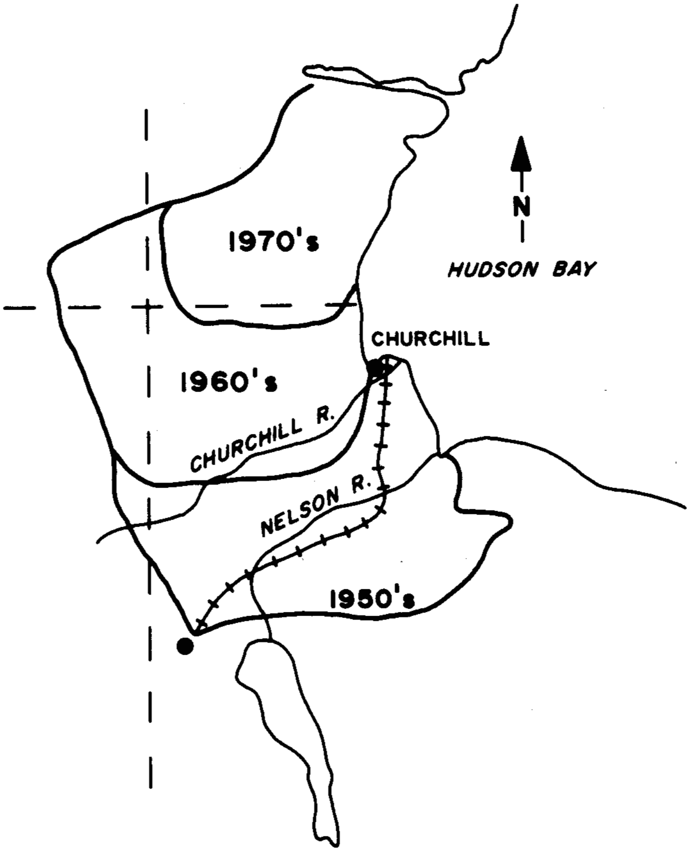

FIG. 13. Distribution of the Kaminuriak caribou herd between the 1950s and 1970s (Simmons *et al.*, 1979).

House. Banfield (1973) documented crossings of the railroad between 1947 and 1953; the migrations ceased after the winter of 1957-58.

Additionally, Parker (1972) concluded that the population increases in the late 1940s resulted in greater penetration southwards. Simmons *et al.* (1979) have provided a distribution map of the herd by decades (Fig. 13). They show that the herd was as far south as the railroad in the 1950s (Fig. 13) and had more northerly range in the 1960s and 1970s. This expansion and contraction of range according to fluctuations in numbers is comparable to that discussed for the Nelchina and Fortymile herds.

In summary, historically the Kaminuriak herd seldom came as far south as the Churchill and Nelson rivers, making only one known crossing prior to 1935. The herd first started crossing the railroad four years after its construction, and the animals continued to cross the corridor as long as the herd was abundant in the 1940s and early 1950s. As the population declined, the herd no longer came as far south as the railroad. The railroad did not act as a barrier; however, it did provide access to the herd in some years, thereby indirectly contributing to a greater kill than would have occurred in its absence. Banfield (1954), who was actually at the crossings in the 1950s, described the crossing as a normal occurrence for many years. The decline of the Kaminuriak herd has resulted from excessive harvests (Banfield, 1954, 1980) coincident with low calf survival due to wolf predation (Parker, 1972; Miller and Broughton, 1974), and possible shifting of part of the herd (Heard *et al.*, 1981; Donaldson, 1981).

Snøhetta Herd

Klein (1971) reported that construction of a railroad across the wild reindeer range between Knutsho (eastern) and Snøhetta (western) range in Dovrefjell National Park in Norway was a barrier to reindeer migrating between the ranges, and this resulted in extensive deterioration of vegetation on the Snøhetta range. This is the most widely quoted example of a transportation corridor acting as a barrier.

Two of us (RDJ and ATB) visited the Doverfjell crossing in 1979. We examined the crossing site and discussed it with E. Gaare and T. Skogland who have studied this population over 10 years. They estimated that the herd had contained about 1000 animals in 1900; it had been depleted by overhunting. The herd was subsequently protected, and increased. Most of the animals wintered on the Snøhetta range but a portion of the herd (250) wintered across the valley on the Knutsho range.

The herd subsequently declined. Skogland and Mølmen (1980:134) stated: "During the period 1920-25 it is believed that the reindeer in the area numbered a few hundred. With such small numbers large scale seasonal migrations ceased. During this period (1921) the railroad across Dovrefjell was completed...after this period...migrations ceased entirely."

During the second world war, hunting was limited and the herd increased until it numbered 15 000 by 1960 (4.4 animals $\cdot km^{-2}$) (Thomson, 1977; Reimers, 1975; Skogland and Mølmen, 1980). In 1956, during a winter with heavy snow, a few hundred animals crossed the railroad and highway and wintered on the Knutsho range. Migration across the railroad has been maintained ever since, with 1/3 of the winter population migrating (Skogland and Mølmen, 1980); these researchers report that most of the crossings take place at night when traffic is lightest. They conclude: "It appears that no type of technical installation poses immediate avoidance reaction as long as it does not physically restrict the animals' presence. The same appears true of access roads. It is the human presence on or nearby the road that induces avoidance reaction" (Skogland and Mølmen, 1980:140).

The obstacles at Dovrefjell include a high board snow-fence with an opening made for the caribou to pass through, a wire fence over which they must jump, the railroad, a major highway used by large trucks, a telephone line, and a river. We have never seen comparable obstacles in North America. Although the migration stopped coincident with railroad construction, now the animals cross not only the railroad but the two fences and the major highway. It is not apparent how the railroad alone could have halted the migration: the supposed cause, the railroad, is still present but the supposed effect of no-migration is absent. The halt in migration was probably a result of a contraction of the range because the herd's numbers were low.

DISTURBANCE THROUGH HARASSMENT

Human harassment of ungulates has been purported to cause death, reduced reproduction, and abandonment of ranges

(Geist, 1978). This hypothesis can be tested for caribou with data from the Interior herd in Newfoundland. In June 1959 and June 1964 ATB severely harassed the females on the Pot Hill calving grounds. Each day females with newly-born calves were hazed by helicopter for prolonged periods to ascertain parous condition and to see if the females would run. All those that did not run had dead calves nearby; those calves that were investigated all had been bitten by lynx (Bergerud, 1971).

TABLE 2. Percent calves (Sept-Oct) and percent parous females at Pot Hill, Newfoundland, compared with percentages for adjacent, undisturbed calving populations. Numbers in parentheses are disturbed populations. (Bergerud, 1971)

Year	Pot Hill % Calves	Pot Hill % Parous Females	Grey River % Calves	Grey River % Parous Females	Sandy Lake % Calves
1958-59	16.0	nd	16.7	92	13.0
1959-60	(20.1)	(77)	nd	80	17.5
1960-61	nd	66	9.9	nd	10.8
1961-62	nd	83	13.0	71	4.4
1962-63	3.3	90	5.7	89	8.5
1963-64	4.3	95	8.9	nd	13.6
1964-65	(6.3)	(96)	9.2	84	12.3
1965-66	nd	93	8.3	79	10.8

This disturbance was severe; the same animals were chased day after day. The calving area of the Pot Hill herd is only 200 km^2 but the animals did not abandon the area. Calf survival of the 1959 and 1964 cohorts was comparable to survival of cohorts born before 1959 and between 1959 and 1964, and similar to that of calves on two adjacent undisturbed calving grounds (Table 2). Also, the females of the Pot Hill herd were highly productive in 1960 and in 1965, one year after harassment (Table 2). The number of females on the Pot Hill calving ground increased in 1965, the year after the disturbance (Bergerud, 1971). Lynx predation was the major cause of death on all three adjacent calving grounds (Bergerud, 1971).

Another example of extreme disturbance of calving females occurred on Brunette Island, Newfoundland, in 1980. On 29 May seven females were chased by helicopter, and darted and drugged with M-99 (Etorphine). One female had a newborn calf; the other six females gave birth 1 June (n = 2), 2-3 June (n = 1), 7 June (n = 1), 9 June (n = 1), and date unknown (n = 1). None of the darted females abandoned their very localized range, and all were repeatedly seen near where they were drugged (H. Butler, pers. comm. 1980). The physical condition of those seven calves from hazed females was compared to that of four calves from non-hazed mothers in the fall (one calf from a non-hazed dam had died between spring and fall). Comparisons were made of calf antler length, physical size, and general activity level. H. Butler noted no difference between experimental and control groups.

At the other extreme of the gestation period, the Newfoundland Wildlife staff captured several hundred swimming female caribou from the Buchans herd in 1962 and 1963, two to five weeks post-conception. Some animals were pulled into boats and hogtied; others were driven into lakeside traps. Animals were held up to several days in tightly crowded corrals. Sixty-two of these females were seen the next spring, and most were accompanied by calves. Pregnancy rates for the herd were higher than in the previous three years (Bergerud, 1971).

In another example, this one in Manitoba in April, Miller *et al.* (1971, 1975) captured migrating gravid females in nets. They reported that 81% (n = 21) of those captured were accompanied by calves in mid-June, compared to 80% (n = 1148) of animals classified on the calving ground at the same time. Similar observations were made in Alaska by Valkenburg *et al.* (1983). They concluded that helicopter chasing, capture, and handling of gravid female caribou in the spring did not affect production or survival. They observed similar calf production between captured (84%, n = 43) and other females (78%, n = 7835) and similar survival rates in the fall (61% for captured *vs.* 64%, n = 354, for others).

We do not suggest that harassment is either unimportant or acceptable; however, there are data to suggest that caribou and other deer species (Hamlin, 1982) can withstand periodic severe disturbance without adverse effects on productivity and survival. This level of resilience has long been noted in large domestic mammals.

CARIBOU RESPONSES TO LINEAR FEATURES

Numerous authors, in discussing factors governing caribou movement and its orientation, have variously referred to caribou following paths of "least topographic resistance" or "most favourable physiographic features" (Banfield, 1954; Kelsall, 1960, 1968; Skoog, 1968; Miller *et al.*, 1972; Bergerud, 1974b; McCourt *et al.*, 1974). Our observations of migratory movements of caribou herds now suggest a broader concept. During spring migrations, the caribou of the Porcupine herd travel up the axis of the rugged Richardson Mountains; on summer movements they ascend steep slopes in the Brooks, British, and Ogilvie ranges where caribou have been observed at higher elevations than Dall's sheep. Such anomalies may be better explained by the concept that caribou move in response to paths of least *energetic* resistance, consistent with their learned directional orientation. Such a concept explains many discrepancies which are not explained by either topographic or orientation factors alone. This principle also has a direct bearing on understanding reported responses to man-made linear features, obstructions, and barriers, and the associated energetic costs of "deflections" of movements.

Parker (1972) and Kelsall (1968) showed how cows of the Kaminuriak and Beverly herds oriented to calving grounds despite the use of divergent winter ranges. Indeed, they followed a path of least topographic resistance. However, the traditional migration routes of other herds include precipitous mountain terrain and dangerous rivers. Movement traditions and behaviour may be evolutionary adaptations involving factors such as insect harassment, predation, range utilization, and the comparative energetic costs of travelling shorter, more difficult routes *vs.* longer, easier ones (Jakimchuk, 1980; Reichman and Aitchison, 1981). Movement behaviour probably has both a phylogenic and an ontogenic origin which enable caribou to respond to a variable extrinsic environment while maintaining traditions such as those described by Bergerud (1974b) and Skoog (1968).

There are numerous well-documented examples of the "least energetic resistance response". Caribou avoid swimming lakes during summer movements, and they travel single-file in deep snow but fan out where travel is unimpeded. They cross rivers and large lakes at narrow points and follow wind-blown ridgetops, despite steeper topography, when valleys are clogged with snow. This principle is observed in the similar responses of caribou to natural and man-made features encountered in their movements, and may account for much of what has been termed deflection, or paralleling man-made objects in response to disturbance.

As early as 1960 Kelsall (1960) noted that caribou would deflect from their course in order to take advantage of frozen lakes providing easier (less energetic) travel, but would abandon the route if it turned many degrees off their course (traditional orientation). The differential use of seismic lines and winter roads documented by McCourt *et al.* (1974) and Decker (1976) is identical to Kelsall's (1960) description. The associated "deflections" were oriented along the caribou's line of travel, and were not followed if they deviated from the intended travel route (McCourt *et al.*, 1974; Kelsall, 1960). The energetic benefits derived from behaviour observed in response to natural and man-made linear features may in fact exceed the energetic costs of deflections as calculated by Geist (1975).

Paralleling behaviour appears to be, at least in part, a natural response to find the path of least energetic resistance. In a study of trail systems in northeastern Alaska, LeResche and Linderman (1975:54) found that: "Caribou follow contours in hilly terrain, use gentle slopes and passes, travel in narrow lines in steep areas; *course natural obstacles* [emphasis ours] before crossing them (see also Skoog, 1968); and follow previous caribou trails."

The foregoing examples of "natural deflections" are useful in explaining caribou responses to berms and other linear features in terms of their potential energetic and dislocation impacts. For example, it has always puzzled us that berms are perceived to represent physical barriers when berm-like features (eskers) and steep mountain ranges are commonly encountered in caribou range and are readily traversed by caribou. Thus the paralleling of "apparent obstacle effects" reported by Urquhart (1971, 1972), Surrendi and DeBock (1976), and Hanson (1980) can be explained in a manner which also accounts for apparently different thresholds of response to obstacles.

Hanson (1980) reported a barrier threshold of 1.2 m; Cameron and Whitten (1976) found that caribou crossed the haul road at a mean height of 1.43 m, selecting significantly lower heights over higher sections. Paralleling and selection for lowest crossing points explain the apparent difference in "barrier" thresholds for the same population. During migrations, Kaminuriak caribou unhesitatingly crossed drift fences 1.0–1.5 m high and jumped fences >2 m high (Miller *et al.*, 1972). The most logical explanation for these observations is that caribou actively seek the path of "least energetic resistance" rather than respond to physical barriers with a fixed threshold height.

That hypothesis, however, does not explain the "retreat behaviour" reported by Surrendi and DeBock (1976) and Hanson (1980). Retreat from berms or roadways may reflect responses to stimuli other than obstacle height (e.g. hunters, or perception of an earlier route). Control data on normal directional variations in movement are not available from those studies.

DISCUSSION

Human Impacts on Caribou Demography

One can draw conclusions about human impacts on population status by correlation reasoning: numbers changing coincident with disturbance. A more precise method is to measure reproductive or mortality rates and, without knowing their cause, correlate these rates with disturbance. One may attain a higher level of confidence by ascertaining reproductive and mortality rates, their causes, and their impacts on population size. The most sophisticated experimental design is to perturb the system (e.g. by removing wolves) and note *predicted* changes using both experimental and control populations.

Many biologists use correlation reasoning and imply cause-and-effect. Bloomfield (1980) noted that caribou declined coincident with habitat change, and he argued cause-and-effect. The Kaminuriak herd had low calf percentages in the 1970s; some Inuit believe that aerial harassment caused this low productivity. But there were few calves also in 1966-1968 (Parker, 1972), prior to extensive exploration in the north. Therefore, the supposed cause is not necessarily an actual one.

The main fallacy in the correlation argument for cause-and-effect is that other possible causes could have occurred simultaneously with the supposed cause. As the forests were logged in British Columbia, logging roads were built. Declines in caribou could have resulted solely from increased mortality from hunting made possible by improved access, and not from the loss of food and cover resources. Correlation evidence is the springboard to hypothesis testing. If habitat destruction is suspected as the cause, there are verifiable test implications. One might suspect low pregnancy percentages, or poor growth, or one might expect to find starved animals. If these test implications cannot be verified against control populations the hypothesis is not sufficient.

We disagree with Klein's (1980:525) statement: "Historically, fractured *Rangifer* ranges through human development activities have led to range abandonment, herd reduction, or extinction...". He has not documented fractured ranges for North American herds, or the demographic statistics of changes in reproductive or mortality rates that could cause such reductions or extinctions. Alternate explanations for caribou declines — unsatisfactory recruitment resulting from predation, and excessive mortality from hunting — are documented (Banfield, 1954; Kelsall, 1968; Bergerud, 1971, 1974a, 1980; Davis *et al.*, 1978).

Caribou probably can be displaced from ranges by complete habitat alienation, e.g. by agriculture or by extreme and persistent harassment. However, current industrial development activities in North America are not of this magnitude. Caribou in the Central Arctic herd have increased despite the extensive accumulation of structures and transportation facilities within their range, and the Western Arctic herd is expanding into this same development area.

Again we question Klein's (1980:523) conclusion: "Roads, railroads, pipelines, power lines, artificial or altered water courses or other man-made linear featurees can, independent of other human activities, block, delay or deflect the movements of caribou and reindeer." Clearly a large-diameter pipeline resting on the ground can be a barrier; however, to date there is no unequivocal example of such effects for a North American caribou herd.

In discussing possible barrier effects, Klein (1980) quoted authorities who lacked firsthand knowledge. For example, he cited Justice Berger (1977) with respect to the possible impacts of the Hudson Bay Railroad on the Kaminuriak herd. Justice Berger had based his opinion on Calef's testimony before the hearing; Calef, in turn, had said he did not know about the barrier effect of the Hudson Bay Railroad but that in Norway a railroad had blocked a migratory crossing. Calef was referring to Klein's (1971) reference to the Dovrefjell crossing.

In this review we have provided a more parsimonious alternative cause for many of the examples of hypothesized effects of barriers presented by Klein (1980). When herds have stopped crossing transportation corridors, it has generally been because numbers have declined and ranges contracted. The evidence shows such contractions to be independent of the presence of transportation corridors. Our explanation depends on the naturally evolved tendency of caribou to alter their movements and range in response to changes in their numbers. It does not require the added assumption and restriction that caribou have evolved behaviour in response to artifacts that were not part of their natural environment. The generalization is that caribou do cross transportation corridors.

We believe that some biologists, in their concern for disturbance at the individual level, may have overlooked the major population regulation factors of hunting and predation. At the First International Reindeer/Caribou Symposium, biologists debated the impacts of pipelines and northern development on caribou, yet the herds in Alaska at the time were declining from predation and overhunting (Davis *et al.*, 1980; Doerr, 1980).

We have reviewed the case histories of eight herds where human impacts on caribou demography have been suspected. One documented impact on caribou was an increase in calf survival following a reduction in wolf populations (also see Davis *et al.*, 1983). Calf survival in the Nelchina, Fortymile (Davis *et al.*, 1978), Central Arctic (Cameron and Whitten, 1979), and British Columbia herds increased following wolf reductions. The second documented impact was increased hunting mortality following improved access from transportation corridors; examples were the Nelchina, Fortymile, and British Columbia herds. The expansion of the Nelchina herd brought it in contact with an already existing road network and resulted in an overharvest. The Kaminuriak herd was little affected by increased access due to roads but was still overharvested.

The Porcupine herd represents a control population, stable in numbers and productivity and little affected by hunting or by predator management. Completion of the Dempster Highway through its range was accompanied by controls of hunting. This "control" population, exposed to a transportation corridor and to other human activities, has not demonstrated any significant demographic changes in response to these developments. There is no convincing evidence from any of the eight herds investigated that habitat loss or disturbance has adversely altered productivity or adult mortality rates, resulting in declines.

There is ample evidence, however, that hunting (much of which is subsistence hunting by native people), and low calf survival due to predation and other factors, are responsible for caribou declines (Simmons *et al.*, 1979; Bergerud, 1980; Davis *et al.*, 1980; Haber and Walters, 1980; Davis and Valkenburg, 1983).

The unsupported belief that human disturbance may adversely affect caribou has had at least one major repercussion. The Canadian Department of Indian and Northern Affairs has enacted "Caribou Protection Measures" which restrict entry and travel in the vicinity of the calving grounds of the Beverly and Kaminuriak herds between 15 May and 31 July. It is now considerably more difficult for biologists to research questions relative to calving — the key to our understanding of caribou demography. The Northwest Territories government requires that researchers obtain a research permit, and is quite prepared to deny access if native communities near the proposed research area do not give consent. Further, native observers are often required to be hired in major research programs.

These are serious restrictions on free movement in Canada and provide the potential for government interference in research by denying access to large areas of northern Canada. We note that ACUNS (1983) also has concerns in this area and has formed a committee to investigate these restrictions on research. The biological justification of these restrictions relative to the dynamics of caribou populations has not been documented.

Predation as a Factor Influencing Sensitivity to Disturbance

Predation is a "prime mover" in the evolution of behaviour patterns in caribou (*sensu* Wilson, 1975). Natural selection acts against those individuals that respond inappropriately. Predation thus reduces the behaviour repertoire of individuals, i.e., animals are more alike than they would be in the absence of predation. This selection results in animals adapted to avoid predation but does not necessarily improve their adaptation to other components of the environment. The reactions and sensitivity of caribou should be evaluated in the context of survival strategies which caribou have perfected in close association and co-evolution with wolves (Bergerud, 1974b).

Male and female caribou have far different parental investments because of polygynous breeding. The male's fitness depends on intrasexual competition for females. His role in propagation ceases upon breeding. The female must continue her care until the calf has a reasonable chance of survival or dies. Because of these investment differences females can be expected to be more wary and select more predator-free habitats than males, even at the expense of optimal foraging. Thus, disturbance reactions are greatest on the calving grounds after the birth of the calves; here selection is the harshest culler.

Human activity can upset predator-prey relations. After caribou have habituated to the presence of humans, they may seek human activities because of reduced predator abundance. The caribou from Lake Nipigon, Ontario, winter around the Armstrong airport, probably because of favourable foraging in the absence of predators. Moose may show the same response on Isle Royale (R. Peterson, pers. comm. 1981). When we modify the habitat we may aid wolves in their searching effort — a trail built through caribou escape habitat in Pukaskwa National Park, Ontario, is an example. Small reduced stands of climax forest may attract caribou and act as traps — predators know where to search. Logging-road networks become travel routes for wolves (Bibikov, 1980). Haul roads may be avoided by caribou because of increased predator presence (Roby, 1978). Wolves followed a snowshoe track made by ATB and found caribou that previously had been secure on a mountain refuge surrounded by soft deep snow. Seismic lines provide opportunities for wolf ambush, as do roads in forest valleys. The examples are many and will become more explicit when we know more about the strategies used by both caribou and wolves in their interactions. Human activities can potentially affect caribou indirectly through their alteration of predator-prey systems.

We believe that the major environmental variable that permits caribou to co-exist with predators is space. Caribou need extensive areas so as to space themselves far from denning wolves. Again, space is needed that will provide habitats where caribou have a slight advantage such as mobility. The greater the space the greater the chance for dispersal of caribou, which increases the searching time for wolves. Huffaker's (1958) complex space for fluctuating predator-prey oscillations applies to caribou.

As herds increase they take up more space. The Nelchina, Fortymile, and Newfoundland herds faced hunters in firing lines along transportation corridors but continued to migrate to meet their spatial requirements. However, there must be a point where harassment is so continuous and severe that animals will no longer pass. Such potential barriers must be prevented if caribou are to maintain their populations in natural environments.

Adaptability of Caribou

Caribou are perceived by many as not adaptable to the presence of humans. Yet caribou are one of the few large mammals man has been able to domesticate. One basis for this misconception is their unwary behaviour. Caribou escape strategies, i.e. detecting motion, grouping up, and standing ground or approaching and verifying, which are successful for natural predators, are ill-adapted to men with firearms.

Caribou are as adapted as other North American ungulates to man's presence. When caribou are captured and placed in holding pens they become calm within hours. Moose captured in Newfoundland remained in a state of panic and many died in captivity (Pimlott and Carberry, 1958). Recently ATB placed wild adult caribou in a game farm and within two weeks they could be approached to within 10 m. Within two months the animals would enter a shed and stand on a scale for weighing. The large herds of caribou feeding along the highway on the Avalon Peninsula, along the TAPS corridor, and along the Dempster Highway are comparable to the herds of habituated pronghorn antelope (*Antilocapra americana*) on the Great Plains, which feed beyond rifle range. Caribou, like pronghorns, also crawl under fences (Miller *et al.*, 1972). Caribou wintering at Armstrong, Ontario, may be avoiding predators as are mule deer (*Odocoileus hemionus hemionus*) that visit downtown Waterton, Alberta (Geist, 1980). Caribou may be found on the highway near McBride, B.C., as are road-wise elk (*Cervus canadensis*) in Banff and Jasper National Parks. Caribou learn that chainsaws signal availability of arboreal lichens, just as black-tailed deer (*Odocoileus hemionus columbianus*) approach felled trees to gain access to browse. The sight of caribou standing on the railroad or stopping the Churchill Express recalls the migration of buffalo (*Bison bison bison*) in the past.

But, adaptable as the caribou is, it still has the same problems as the buffalo — overharvest and the need for space. Our conclusion is that caribou can tolerate and adapt to the presence of man if we will permit them to live by not overharvesting. Caribou will cross major transportation corridors and physical obstructions to maintain their space, but there is probably some upper limit to their tenacity. We must not permit the dissection of caribou populations into small discrete units so that they lose their ultimate adaptation — mobility, to seek space to cope with an ever-changing extrinsic environment.

REFERENCES

ACUNS Report. 1983. Northern research regulation. Northline 3(2):2. Ottawa: Association of Canadian Universities for Northern Studies.

BANFIELD, A.W.F. 1954. Preliminary Investigation of the Barren-Ground Caribou. Part I. Former and present distribution and status. Wildlife Management Bulletin Series 1, No. 10A. Canadian Department of Northern Affairs and National Resources. 79 p.

______. 1973. Effects of a Railroad to the Arctic on Northern Wildlife. Canadian Wildlife Service, Ottawa. 30 p.

______. 1980. Notes on caribou distribution, abundance and use in the Northwest Territories, 1933-1949. In: Banfield, A.W.F. and Jakimchuk, R.D. (eds.). Analyses of the Characteristics and Behaviour of Barren-Ground Caribou in Canada. Polar Gas Project, Toronto. 48 p.

______, JAKIMCHUK, R.D. and CAMERON, R.D. 1981. An Assessment of Issues Concerning Caribou and North Slope Petroleum Development. Caribou Advisory Panel Final Report, ARCO Alaska Inc. 36 p.

BENTE, P.J. and ROSENEAU, D.G. 1978. An Aerial Photo-Estimate of the 1977 Porcupine Caribou Herd Population. Renewable Resources Consulting Services Ltd., Sidney, B.C. 84 p.

BERGER, T.R. 1977. Northern Frontier, Northern Homeland. The Report of the Mackenzie Valley Pipeline Inquiry, Vol. I. Ottawa: Ministry of Supply and Services. 213 p.

BERGERUD, A.T. 1971. The Population Dynamics of Newfoundland Caribou. Wildlife Monograph 25. 55 p.

______. 1974a. Decline of caribou in North America following settlement. Journal of Wildlife Management 38(4):757-770.

______. 1974b. The role of the environment in the aggregation, movement, and disturbance behaviour of caribou. In: Geist, V. and Walther, F. (eds.). The Behaviour of Ungulates and Its Relationship to Management. Morges, Switzerland: IUCN Publications, New Series No. 24. 552-584.

______. 1978. The Status and Management of Caribou in British Columbia. B.C. Fish and Wildlife Branch Report. 150 p.

______. 1980. A review of the population dynamics of caribou and wild reindeer in North America. In: Reimers, E., Gaare, E. and Skjenneberg, S. (eds.). Proceedings, Second Reindeer/Caribou Symposium. Trondheim, Norway: Direktoratet For Vilt Og Ferskvannsfisk. 556-581.

BIBIKOV, D.I. 1980. Wolves in the U.S.S.R. Natural History 89(6):58-62.

BLOOMFIELD, M.I. 1979. The Ecology and Status of Mountain Caribou and Caribou Range in Central British Columbia. M.Sc. thesis, University of Alberta, Edmonton. 318 p.

______. 1980. The impact of development, settlement and associated activities on mountain caribou in Central British Columbia, Canada. In: Reimers, E., Gaare, E. and Skjenneberg, E. (eds.). Proceedings, Second International Reindeer/Caribou Symposium. Trondheim, Norway: Direktoratet For Vilt Og Ferskvannsfisk. 705-715.

BOS, G.N. 1974. Nelchina and Mentasta Caribou Reports. Alaska Department of Fish and Game, Pittmann Robertson Project W-17-5 and W-17-6. 34 p.

______. 1975. A partial analysis of the current population status of the Nelchina caribou herd. In: Luick, J.R., Lent, P.C., Klein, D.R. and White, R.G. (eds.). Proceedings, First International Reindeer and Caribou Symposium. Biological Papers of the University of Alaska, Special Report No. 1. 170-180.

CALEF, G.W. 1974. The predicted impact of the Canadian Arctic Gas pipeline project on the Porcupine caribou herd. In: Environmental Impact Assessment of the Portion of the Mackenzie Gas Pipeline from Alaska to Alberta. Winnipeg, Manitoba: Research Reports, Vol. 4. Environmental Protection Board. 101-120.

______. 1975. Population status of caribou in the Northwest Territories. In: Klein, D.R. and White, R.G. (eds.). Parameters of Caribou Population Ecology in Alaska. Biological Papers of the University of Alaska, Special Report No. 3. 9-16.

CAMERON, R.D. and WHITTEN, K.R. 1976. First Interim Report of the Effects of the Trans-Alaska Pipeline on Caribou Movements. Special Report No. 2, Joint State/Federal Fish & Wildlife Advisory Team, Alaska. 53 p.

______. 1979. Effects of the Trans-Alaska Pipeline on Caribou Movements. Alaska Department of Fish and Game. Pittmann Robertson Project W-17-10 and W-17-11, Progress Report Vol. IV. 36 p.

______. 1980. Influence of the Trans-Alaska Pipeline corridor on the local distribution of caribou. In: Reimers, E., Gaare, E. and Skjenneberg, S. (eds.). Proceedings, Second International Reindeer/Caribou Symposium. Trondheim, Norway: Direktoratet For Vilt Og Ferskvannsfisk. 475-484.

______ and SMITH, W.T. 1981. Distribution and Movements of Caribou in Relation to the Kuparuk Development Area. Alaska Department of Fish and Game, Third Interim Report. 37 p.

______ and ROBY, D.D. 1979. Caribou distribution and group composition associated with construction of the Trans-Alaska Pipeline. Canadian Field-Naturalist 93(2):155-162.

CARRUTHERS, D.R. 1983. Overlap of Central and Western Arctic caribou within the current range of the Central Arctic caribou herd. Prepared for ARCO Alaska Inc. by Renewable Resources Consulting Services Ltd., Sidney, B.C. 20 p.

CHILD, K.N. 1973. The Reactions of Barren-Ground Caribou (*Rangifer tarandus granti*) to Simulated Pipeline and Pipeline Crossing Structures at Prudhoe Bay, Alaska. Completion Report, Alaska Cooperative Wildlife Research Unit, University of Alaska, Fairbanks. 51 p.

DAVIS, J.L., SHIDELER, R. and LeRESCHE, R.E. 1978. Fortymile Caribou Herd Studies. Alaska Department of Fish and Game, Pittman Robertson Projects W-17-6 and W-17-7, Final Report. 153 p.

DAVIS, J.L. and VALKENBURG, P. 1983. Qualitative and Quantitative Aspects of Natural Mortality of the Western Arctic Caribou Herd. Alaska Department of Fish and Game, Pittmann Robertson Project W-22-1, Progress Report. 15 p.

______ and BOERTJE, R.D. 1983. Demography and limiting factors of Alaska's Delta caribou herd, 1954-1981. Proceedings, Third International Reindeer/Caribou Symposium. Acta Zoologica Fennica 175:135-137.

DAVIS, J.L., VALKENBURG, P. and REYNOLDS, H.V. 1980. Population dynamics of Alaska's Western Arctic caribou herd. In: Reimers, E., Gaare, E. and Skjenneberg, S. (eds.). Proceedings, Second International Reindeer/Caribou Symposium. Trondheim, Norway: Direktoratet For Vilt Og Ferskvannsfisk. 595-604.

DECKER, R. 1976. Bluenose Caribou Herd: Aerial Surveillance of the Spring Migration, 1976. Northwest Territories Wildlife Service Report. 27 p.

DOERR, J.G. 1980. Modeling the population decline of two Alaskan caribou herds. In: Reimers, E., Gaare, E. and Skjenneberg, S. (eds.). Proceedings, Second International Reindeer/Caribou Symposium. Trondheim, Norway: Direktoratet For Vilt Og Ferskvannsfisk. 611-623.

DONALDSON, J. 1981. Population and Recruitment Estimates for the Lorillard and Wager Caribou Herds in 1977. Department of Indian and Northern Affairs, Environmental Social Program, ESCOM Report No. AI-43. 50 p.

DUGMORE, A.A.R. 1913. The Romance of the Newfoundland Caribou. Philadelphia, PA: J.P. Lippincott Co. 186 p.

FONG, D. and MERCER, E. 1975. Newfoundland Caribou Classification Data 1964-74. Wildlife Division Report 75C-1A. 47 p.

FREDDY, D.J. 1974. Status and Management of the Selkirk Caribou Herd, 1973. M.Sc. thesis, University of Idaho, Moscow, Idaho. 1132 p.

GEIST, V. 1975. Harassment of large mammals and birds with a critique of the research submitted by Arctic Gas Study Ltd. Report to the Berger Commission, Faculty of Environmental Design, University of Calgary.

______. 1978. Behaviour. In: Schmidt, J.L. and Gilbert, D.L. (eds.). Big Game of North America. Ecology and Management. Harrisburg, PA: Stackpole Press. 283-296.

______. 1980. Downtown deer. Natural History 89(3):56-64.

HABER, G.C. and WALTERS, C.J. 1980. Dynamics of the Alaska-Yukon caribou herds and management implications. In: Reimers, E., Gaare, E. and Skjenneberg, S. (eds.). Proceedings, Second International Reindeer/Caribou Symposium. Trondheim, Norway: Direktoratet For Vilt Og Ferskvannsfisk. 645-663.

HAMLIN, K.L. 1982. Effect of capture and marking on fawn production in deer. Journal of Wildlife Management 46(4):1086-1089.

HANSON, W.C. 1980. Caribou-pipeline encounters in northern Alaska. Draft Report, Ecological Science Department, Battelle Institute, Pacific Northwest Labratory, Richland, WA, U.S.A.

HATTER, J. 1950. The Moose of Central British Columbia. Ph.D. thesis, Washington State College, Pullman, WA. 365 p.

HAWKINS, R. and CALEF, G.W. 1977. A population estimate for the Kaminuriak herd in 1976. Northwest Territories Fish and Wildlife Service. Unpublished report [Available from Wildlife Service, Government of Northwest Territories, Yellowknife, N.W.T., Canada X1A 2L9.]

HEARD, D.C., CALEF, G.W. and COOPER, S. 1981. Numbers, Distribution and Productivity of Caribou in northeastern Keewatin, N.W.T. in 1976. Department of Indian and Northern Affairs, Environmental Social Program, ESCOM Report No. AI-39. 27 p.

HEMMING, J.E. 1971. The Distribution and Movement Patterns of Caribou in Alaska. Alaska Department of Fish and Game, Technical Bulletin No. 1. 60 p.

______. 1975. Population growth and movement patterns of the Nelchina caribou herd. In: Luick, J.R., Lent, P.C., Klein, D.R. and White, R.G. (eds.). Proceedings, First International Reindeer and Caribou Symposium. Biological Papers of the University of Alaska, Special Report No. 1. 162-169.

HINMAN, R.A. (ed.). 1981. Annual Report of Survey — Inventory Activities. Part II. Caribou, moose and mountain goats. Alaska Department of Fish and Game, Pittman Robertson Projects W-19-1 and W-19-2. Vol XII. 224 p.

HUFFAKER, C.B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. Hilgardia 27:343-383.

JAKIMCHUK, R.D. 1978. Biology and public forums: the Mackenzie Valley example. Symposium on Biology, Science Policy and the Public. Alberta Society of Professional Biologists, Edmonton, Alberta. 15 p.

______. 1980. Disturbance to barren-ground caribou: a review of the effects and implications of human developments and activities. In: Banfield, A.W.F. and Jakimchuk, R.D. (eds.). Analyses of the Characteristics and

Behaviour of Barren-Ground Caribou in Canada. Polar Gas Project, Toronto. 140 p.

______, DeBOCK, E.A., RUSSELL, H.J. and SEMENCHUK, G.P. 1974. A Study of the Porcupine Caribou Herd. Renewable Resources Consulting Services Ltd. Canadian Arctic Gas Study Ltd. Biological Report Series, Vol. 4:1-111.

JOHNSON, D.R. and TODD, M.C. 1977. Summer use of a highway crossing by mountain caribou. Canadian Field-Naturalist 91(3):312-314.

KELSALL, J.P. 1960. Co-operative Studies of Barren-Ground Caribou 1957-1958. Wildlife Management Bulletin Series 1, No. 15. 145 p.

______. 1968. The Migratory Barren-Ground Caribou in Canada. Canadian Wildlife Service Monograph No. 3. Ottawa: Queen's Printer. 340 p.

KLEIN, D.R. 1971. Reaction of reindeer to obstructions and disturbance. Science 173:343-398.

______. 1973. Reaction of Wildlife to Aircraft Disturbance. Alaska Cooperative Wildlife Research Unit, University of Alaska, Fairbanks. Quarterly Report 25(1):18-23.

______. 1980. Reaction of caribou and reindeer to obstructions — a reassessment. In: Reimers, E., Gaare, E. and Skjenneberg, S. (eds.). Proceedings, Second International Reindeer/Caribou Symposium. Trondheim, Norway: Direktoratet For Vilt Og Ferskvannsfisk. 519-527.

LAWRIE, A.H. 1948. Cited in Parker, G.R. 1972. Barren-Ground Caribou Survey, Keewatin. Canadian Wildlife Service Report C.873. Unpublished manuscript.

LENTFER, J. 1965. Caribou Report. Alaska Department of Fish and Game, Pittmann Robertson Projects W-6-R-5 and W-6-R-6, Juneau. 20 p.

LeRESCHE, R.E. 1975. The international herds: present knowledge of the Forty-mile and Porcupine caribou herds. In: Luick, J.R., Lent, P.C., Klein, D.R. and White, R.G. (eds.). Proceedings, First International Reindeer and Caribou Symposium. Biological Papers of the University of Alaska, Special Report No. 1. 127-139.

______ and LINDERMAN, S.A. 1975. Caribou trail systems in northeast Alaska. Arctic 28(1):54-61.

LOUGHREY, A.G. 1955. Manitoba and Keewatin Barren-Ground Resurvey, 1955. Canadian Wildlife Service Report C.52. Unpublished manuscript. 51 p.

MARTELL, A.M. and RUSSELL, D.E. 1983. Mortality rate in the Porcupine caribou herd. Proceedings, Third International Reindeer/Caribou Symposium. Acta Zoologica Fennica 175:139-140.

McCOURT, K.H. and HORSTMAN, L.P. 1974. The reaction of barren-ground caribou to aircraft. In: Jakimchuk, R.D. (ed.). The Reaction of Some Mammals to Aircraft and Compressor Station Noise Disturbance. Renewable Resources Consulting Services Ltd. Canadian Arctic Gas Study Ltd. Biological Report Series, Vol. 23:1-36.

McCOURT, K.H., FEIST, J.D., DOLL, D. and RUSSELL, J.J. 1974. Disturbance Studies of Caribou and Other Mammals in the Yukon and Alaska, 1972. Renewable Resources Consulting Services Ltd. Canadian Arctic Gas Study Ltd. Biological Report Series, Vol. 5:1-245.

McILROY, C. 1976. Moose survey — inventory progress report — 1974. Game management units 11 and 13. In: McKnight, D.E. (ed.). Annual Report of Survey — Inventory Activities. Part II. Moose. Alaska Department of Fish and Game, Pittmann Robertson Project W-17-7. 187 p.

MILLAIS, J.G. 1907. Newfoundland and Its Untrodden Ways. London: Longmans, Green and Co. 340 p.

MILLER, F.L., ANDERKA, F.W., VITHAYAS, C. and McCLURE, R.L. 1975. Distribution, movements and socialization of barren-ground caribou radio tracked on their calving and post-calving areas. In: Luick, J.R., Lent, P.C., Klein, D.R. and White, R.G. (eds.). Proceedings, First International Reindeer and Caribou Symposium. Biological Papers of the University of Alaska, Special Report No. 1. 423-435.

MILLER, F.L., BEHRAND, D.F. and TESSIER, G.D. 1971. Live capture of barren-ground caribou with tangle nets. Transactions of the Northeastern Section of the Wildlife Society 28:83-90.

MILLER, F.L. and BROUGHTON, E. 1974. Calf Mortality on the Calving Ground of Kaminuriak Caribou. Canadian Wildlife Service Report Series No. 26. 25 p.

MILLER, F.L. and GUNN, A. 1979. Responses of Peary Caribou and Muskoxen to Helicopter Harassment. Canadian Wildlife Service Occasional Paper No. 40. 88 p.

MILLER, F.L., JONKEL, C.J. and TESSIER, G.D. 1972. Group cohesion and leadership responses by barren-ground caribou to man-made barriers. Arctic 25:193-202.

MURIE, O.J. 1935. Alaska-Yukon Caribou. North American Fauna Series No. 54. Washington, D.C.: U.S. Department of Agriculture. 93 p.

PARKER, G.R. 1972. Biology of the Kaminuriak Population of Barren-Ground Caribou. Part I. Total numbers, mortality, recruitment and seasonal distribution. Canadian Wildlife Service Report Series No. 20. 95 p.

PIMLOTT, D.H. and CARBERRY, W.J. 1958. North American moose transplantations and handling techniques. Journal of Wildlife Management 22(1):51-62.

PITCHER, K.W. 1982. Big Game Studies. Volume IV. Caribou. Alaska Department of Fish and Game, Susitna Hydro-Electric Project, Phase I, Final Report. 101 p.

RAUSCH, R.A. 1967. Some aspects of the population ecology of wolves. American Zoologist 7:253-265.

REICHMAN, O.J. and AITCHISON, S. 1981. Mammal trails on mountain slopes: optimal paths in relation to slope angle and body weight. American Naturalist 117:416-420.

REIMERS, E. 1975. Age and sex structure in a hunted population of reindeer in Norway. In: Luick, J.R., Lent, P.C., Klein, D.R. and White, R.G. (eds.). Proceedings, First International Reindeer and Caribou Symposium. Biological Papers of the University of Alaska, Special Report No. 1. 181-188.

RITCEY, R.W. 1980. Summer caribou census. Fish and Wildlife Branch, Kamloops, B.C. Unpublished report. 7 p. [Available from B.C. Fish and Wildlife Branch.]

ROBY, D.D. 1978. Behavioral Patterns of Barren-Ground Caribou of the Central Arctic Herd Adjacent to the Trans-Alaska Oil Pipeline. M.Sc. thesis, University of Alaska, Fairbanks. 250 p.

ROSENEAU, D.G. and STERN, P.M. 1974. Distribution and Movements of the Porcupine Caribou Herd in Northeastern Alaska, 1972. Renewable Resources Consulting Services Ltd. Canadian Arctic Gas Study Ltd. Biological Report Series, Vol. 7:1-209.

______ and WARBELOW, C. 1974. Distribution and movements of the Porcupine caribou herd in northeastern Alaska. In: McCourt, K.H. and Horstman, L.P. (eds.). Studies of Large Mammal Populations in Northern Alaska, Yukon and Northwest Territories, 1973. Renewable Resources Consulting Services Ltd. Canadian Arctic Gas Study Ltd. Biological Report Series Vol. 22:1-197.

SHANK, C.C. 1979. Human-Related Disturbance to Northern Large Mammals: A Bibliography and Review. Foothills Pipe Lines (South Yukon) Ltd. 254 p.

SIMMONS, N.M., HEARD, D.C. and CALEF, G.W. 1979. Inter-jurisdictional management problems: Kaminuriak caribou herd. Transactions of the North American Wildlife Conference 44:102-113.

SKOGLAND, T. and MØLMEN, Ø. 1980. Prehistoric and present habitat distribution of wild mountain reindeer at Dovrefjell. In: Reimers, E., Gaare, E. and Skjenneberg, S. (eds.). Proceedings, Second International Reindeer/Caribou Symposium. Trondheim, Norway: Direktoratet For Vilt Og Ferskvannsfisk. 130-141.

SKOOG, R.O. 1956. Range, Movements, Population and Food Habits of the Steese-Fortymile Caribou Herd. M.Sc. thesis, University of Alaska, Fairbanks. 145 p.

______. 1968. Ecology of the Caribou (*Rangifer tarandus granti*) in Alaska. Ph.D. thesis, University of California, Berkeley. 699 p.

SOPUCK, L.G., TULL, C.E., GREEN, J.E. and SALTER, R.E. 1979. Impacts of Development on Wildlife: A Review from the Perspective of the Cold Lake Project. Prepared by LGL Ltd., Calgary, for Esso Resources Canada Ltd. 40 p.

SURRENDI, D.C. and DeBOCK, E.A. 1976. Seasonal Distribution, Population Status and Behaviour of the Porcupine Caribou Herd. Canadian Wildlife Service Report to Mackenzie Valley Pipeline investigation. 145 p.

THOMSON, B.R. 1977. The Behaviour of Wild Reindeer in Norway. Ph.D. thesis, University of Edinburgh, Edinburgh, Scotland. 428 p.

URQUHART, D.R. 1971. Caribou Distribution and Behaviour in Relation to a Seismic Grid. Game Management Division, Northwest Territories Government, Progress Report No. 2. 15 p.

______. 1972. Oil Exploration and Banks Island Wildlife. Game Management Division, Northwest Territories Government. 105 p.

VALKENBURG, P., BOERTJE, R.D. and DAVIS, J.L. 1983. Effects of darting and netting on caribou in Alaska. Journal of Wildlife Management 47(4):1233-1237.

WATSON, G.W. and SCOTT, R.F. 1956. Aerial censusing of the Nelchina caribou herd. Transactions of the North American Wildlife Conference 21:499-510.

WHITTEN, K.R. and CAMERON, R.D. 1983. Population dynamics of the Central Arctic Herd, 1975-1981. Proceedings, Third International Reindeer/Caribou Symposium. Acta Zoologica Fennica 175:159-161.

WILSON, E.O. 1975. Sociobiology. Cambridge, MA: Belknap Press of Harvard University. 697 p.