Traditional behaviour and fidelity to caribou calving grounds by barren-ground caribou

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Abstract: Evidence for the fidelity of female barren-ground caribou (Rangifer tarandus spp.) of each herd to specific calving grounds is convincing. Involvement of learned behaviour in the annual return of those cows to the same calving grounds implies such actions are a form of «traditional» behaviour. Even wide variations in population size have not yet knowingly led to marked changes in size or location of calving grounds or prolonged abandonment of established ones. Rarely is the adoption of new calving grounds reported and emigration to another herd's calving ground or interchange between calving grounds has not yet been unequivocally documented. The calving experience of individual caribou and environmental pressures may modify the cow's use patterns of her calving grounds. The current definition of herds based on traditional calving grounds may require modification, if increasing caribou numbers result in changes in traditions. However, current data do not contradict either the fidelity to traditional calving grounds or the concept of herd identity based on that fidelity.

Key words: barren-ground caribou, calving grounds, learned behaviour, management, Northwest Territories

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Rangifer, Special Issue No. 1, 1986: 151 - 158

#### Introduction

The annual use of specific areas for calving by barren-ground caribou (Rangifer tarandus groenlandicus and R. t. granti) was known to local hunters for many years, but not by biologists until the 1940s (Lent, 1964; Skoog, 1968; Thomas, 1969). Consequently, quantitative data on the use of calving areas only spans some 45 years, at most. However, qualitative documentation of calving over longer periods is possible for some areas from historic and prehistoric records. Evidence for the use of specific areas for calving by barren-ground caribou cows of one herd is convincing. For example, the calving grounds of the Beverly, Kaminuriak and Bathurst herds in the Northwest Territories (NWT), Canada, have been surveyed 54 times between 1957 and 1985 and calving cows were annually observed, (although densities varied between years). The return of individual cows to the same calving grounds has been documented mostly in Alaska from the radio-collaring of caribou (e.g., Cameron *et al.*, 1986).

Bergerud (1974) suggested that annual fluctations in the numbers of caribou on a calving area would contravene the idea of a discrete homing population. Wide differences between annual counts supposedly, however, resulted from sampling errors and difficulties rather than movements between populations (Bergerud, 1971). Annual differences in numbers of caribou counted on barren-ground caribou calving grounds are also attributable to changes in the numbers of barren cows, juveniles and yearlings accompanying the parturient cows, or environmental conditions such as deep late-lying snow

delaying the return of the caribou, and or survey bias.

Investigating the annual return of individual parturient cows to the same calving ground has only been feasible since the use of radio-telemetry. In the Central Arctic herd (Alaska), about 90% of the radio-collared cows were annually relocated on the summer ranges (Cameron et al... 1986). However, the fate of the other 10% was inexplicable, because mortality of the missing radio-collared cows or failure of the radio transmitters could not be ruled out (Cameron et al., 1986). Timing of the surveys did not always verify exact use of the traditional calving grounds. However, no known instance of a radio-collared cow being located on other herds calving grounds was determined dispite overlap of other herds on the Central Arctic herd's wintering ranges.

Lent (1964) and Skoog (1968) were among the first to emphasize that annual use of calving grounds was one of the most consistent behavioural characteristics of caribou and called the use «traditional». The use of the term «traditional» has continued but the concept and implications of traditional behaviour have been little discussed. Questions about the fidelity of caribou cows to their calving grounds and the nature of traditional calving grounds have been raised in regard to human activities on those areas (e.g., Cameron, 1983; Bergerud et al., 1984; Gunn, 1985). Likewise, the recent large increases in the numbers of caribou estimated in the Kaminuriak herd (Gates, 1985; Heard and Calef. 1986) and the Bathurst herd (D. C. Heard, pers. comm.) have raised questions about the fidelity of caribou cows of each herd to traditional calving grounds. Our paper reviews the reported changes in the use of traditional calving grounds by various herds and relates those changes to traditional behaviour. We advance definitions of an annual calving ground and traditional calving grounds and discuss the implications of those definitions for caribou management.

# Definitions of an annual calving ground and traditional calving grounds

Annual calving ground

The «annual calving ground» of a herd is restricted in time to 1-year and is the land area occupied by the majority of parturient caribou

from that herd. The «annual calving ground» should not be referred to directly as a traditional annual calving ground because of its restriction to a single year. That is, it is not traditional in itself as it occurred only in 1-year but it is an annual calving ground within the area of the traditional calving grounds.

## Traditional calving grounds

The «traditional calving grounds» of a herd is the overall (known) land area where at least the majority of the parturient caribou of that herd come annually to calve. It includes all of those known locations where caribou of that herd have calved, including areas occupied during years when environmental stress (poor travelling conditions) apparently prevented parturient cows from reaching more central sections of their traditional calving grounds, (because we reason that it was their traditional behaviour that enforced their movements to that point in time and space).

## Majority

Technically the majority only requires 51% but to be practical as a basis for defining a specific caribou herd it would require between 80% and 90% of the parturient caribou in a herd maintain their affinity for their specific *traditional calving grounds*.

Wilson (1975:168) called tradition the «...ultimate refinement in environmental tracking» and he described tradition as a specific form of behaviour passed between generations by learning. Wilson (1975) characterized traditional behaviour as that which can be altered or initiated by one successful individual; can quickly spread through a population in less than a generation; is cumulative and is precise in application often to specific localities. The key feature is, however, that it is a learned behaviour which then allows a relatively rapid and flexible response to environmental changes. Bergerud (1974) described several lines of evidence to support the role of learning in the annual return of caribou cows to calving grounds. Wilson's (1975) definition of traditional is similar to the everyday usage of the term: e.g., Webster (1980) defines tradition as «...The handing down of information, beliefs and customs by word of mouth or by example from one generation to another without written

instruction». The synonym for traditionalist (meaning strongly favouring retention of existing order) is «conservative» and «conventional» is the synonym for traditional (Roget's Thesaurus, 1980).

The connotation of conservative may have sometimes lulled us into thinking that caribou calving grounds are permanent fixtures in the annual use of time and space. The evidence is, however, that, while cows of each herd exhibit long-term fidelity for a specific calving area, locational changes have occurred in the areas traditionally used by calving caribou cows.

# Variations in the use of caribou calving grounds

Overlapping shifts in calving ground location

The boundaries of calving grounds of many barren-ground caribon herds are delineated during aerial surveys to count caribou. Annual variations in the areas delineated (e.g., Davis et al., 1978b; Fleck and Gunn, 1982) may result from shifts in the distribution of calving cows or may result from different criteria used (which are rarely reported) between years to determine the boundary. Timing of the survey relative to the peak of calving can significantly change the area delineated as the calving area.

There is sometimes a directional trend among years in the location of the calving grounds even though there is general overlap in the boundaries of calving grounds. For example, that of the Beverly herd has shifted to the northeast between 1957 and 1982 (Fleck and Gunn, 1982) onto areas used for early postcalving. There are no obvious environmental factors that account for that directional shift. Changes in the distribution or density of denning wolves (*Canis lupus*) during and after wolf control in the 1950s and 1960s may, however, have been the environmental change to which the Beverly calving cows responded.

## Temporary abrupt changes in calving ground location

Environmental changes on travel routes to the calving grounds, or on the calving ground itself, can cause some or all cows to calve on an area with little or no overlap of the area used in the preceding year. For example, deep or wet snow occasionally slows the migration of cows, and calving may occur before reaching the usual calving area. Deep snow delayed the Beverly herd in 1979, and cows calved up to 200 km south of the usual calving grounds (Fleck and Gum, 1982)

The Delta herd (Alaska) has used the same mostly *Eriophorum* spp. tussock covered calving area since late 1950s. In 1981, however, about half the cows calved in areas up to 40 km west of the traditional area. Davis et al. (1982) speculated that the shift may have occurred because part of the herd foraged on the traditional calving area during April and Mav when it was snow free and may have diminished the quantity or quality of forage, though now they believe that explanation to be improbable (J. L. Davis, per. comm.). In 1982, the Delta calving ground was still snow-covered in late May; and 90 — 95% of the cows calved on a snow free area 16 km northwest of the traditional area (Davis and Valkenburg, 1983).

Distinction between temporary or permanent abandonment of traditional calving grounds is partially dependent upon the time period implied or stated. The Fortymile herd between 1977 and 1983, annually calved in areas not contiguous to the area used in the 1960s and early 1970s. However, in 1984 calving occurred contiguous to the calving area that was «abandoned» in the early 1970s (Valkenburg and Davis, 1986).

## Permanent abandonment of traditional calving grounds

In the NWT, a small proportion of cows of the Bluenose herd calved on the Cape Bathurst area in 1974, 1975 and 1976 (Hawley et al., 1978). Counts of calving cows dropped from 4500 in 1974 to almost zero in 1978 and 1979 (Brackett et al., 1979), and cows have apparently not calved there since. Other examples of permanent abandonment of calving grounds include only situations where the habitat has become unusable. The George River herd used two major and one minor calving grounds in the 1970s (I. Juniper, pers. comm.). Between 1975 and 1979, the Lac Champdone calving ground was progressively abandoned after severe natural flooding in 1975, and the numbers of caribou using the other main calving ground (Ford River) increased during that period.

## Formation of new calving grounds and emigration to or interchange between calving grounds

Creation of a new calving ground (i. e., a discontinuous distribution of calving cows from all previously used areas) has been rarely documented, but if the initial colonization of a new calving ground involved only a few individuals, it likely would go unnoticed during aerial surveys. The Mulchatna and Big River herds in Alaska are examples of caribou herds apparently using new areas for calving (Patten, 1985; Pegau, 1985).

Skoog (1968) hypothesized that a caribou herd increased in number to a «threshold» density which caused erratic movements and ultimately lead to emigration. Davs et al. (1978a) pointed out that Skoog's hypothesis requires a triggering mechanism such as a correlation between densities of caribou on the calving ground and population size. Their data from the Western Arctic herd suggest, however, that there is no relationship between population size and use of the calving grounds, nor was there evidence for the formation of new calving areas or abandonment of the traditional calving grounds as the herd changes in size. Similarly, the traditional calving grounds used by the Bathurst and Kaminuriak herds have not apparently shifted despite large changes in population size. Davis et al. (1978b), noted, however, that «drawing lines around the calving area is a subjective and somewhat arbitrary process». Thus, the apparent absence of any correlation between population size and density on the calving grounds is not conclusive.

The Big River (375 caribou in 1984) and Mulchatna (33 000 in 1984) herds are both increasing in size and occupying new ranges (Patten, 1985; Pegau, 1985). In 1983, both herds used new summer ranges and some cows returned to calve there the following year (Patten, 1985; Pegau, 1985) although other cows in the herd continued to use their traditional calving grounds.

Emigrations, possibly from herds in the Northeast Keewatin to the Kaminuriak herd's calving ground has been suggested on the basis of the increase in numbers of caribou estimated on Kaminuriak calving grounds, which exceeded the intrinsic rate of increase (Gates, 1985; Heard and Calef, 1986). Likewise emigration of caribou

to the Bathurst herd has been advanced to explain the apparent doubling in the number of caribou estimated to be in the Bathurst herd from 1982 to 1984 (D. C. Heard, pers. comm.). However, change in survey techniques, inadequate definition of annual calving grounds and annual variations of the dispersal of calving cows are also plausible explanations, especially, in the absence of supporting evidence for immigration. Large numbers of breeding cows moving from one traditional calving grounds to another traditional calving grounds have not been previously documented which is not to say that it is not possible. However, such an unusual event should not be accepted without supporting evidence.

Possible emigration of calving caribou from the calving grounds of one herd to the known calving grounds of another herd may have occurred between the Delta and Yanert herds. The Yanert herd was only recognized as a discrete herd in 1980 (from radio-collaring of caribou) on what used to be considered as part of the annual range of the Delta herd (Davis and Valkenburg, 1985a). In 1984, 10 of 25 radio-collared Delta cows calved on the Yanert herd's calving area, but in 1985 those cows returned to the traditional Delta calving grounds (Davis et al., 1986). The area of overlap for calving was used by yearlings and subadult females of the Delta herd in previous years which may be partly the explanation for the limited calving and movement of other cows into this area (the upper Wood River area) during or shortly after calving in 1984. There is, then, no compelling evidence to distinguish between the temporary expansion of a new calving ground by the Delta herd or temporary emigration to the Yanert herd's calving ground. There is also the question of whether the two herds are in fact separate herds, as overlap in distribution occurs during the rut (J. L. Davis, pers. comm.).

# Human activities and abandonment of traditional calving areas

Strength of the caribou's affinity to, and potential abandonment of, traditional calving grounds in the face of human activities has been central to debates about those activities on calving grounds (e.g., Cameron, 1983; Bergerud et al., 1984; Gunn, 1985). The concerns over human activities potentially causing abandon-

ment of calving grounds are twofold. Besides the possible direct effects (Cameron, 1983; Gunn, 1985), there is also the untested assumption that if the activities were sufficiently severe to cause the cows to abandon the calving grounds, the enforced use of a new calving grounds could be deleterious. The key factor would be the availability of suitable calving habitat. Strong affinity to an area could mean that caribou will tolerate more human activities, through local redistribution of cows and calves, before abandoning the area. The density of cows and calves is low in the vicinity of pipelines and roads on the Central Arctic herd's calving grounds (Whitten and Cameron, 1985), but the area has not been abandoned.

The initial responses of the caribou to human activities on their calving grounds were not documented in the 1950s for the Delta herd whose calving grounds are on a military training area (Davis and Valkenburg, 1985b), nor early 1970s for the Central Arctic herd. But evidently, some cows habituated to the aircraft (Delta herd) or adopted avoidance behaviour (Central Arctic herd) and those adaptions would have spread quickly in a small population (Bergerud, 1974) and both herds then had only or less than a few thousand caribou.

# Management implications of traditional behaviour and traditional calving areas

Traditional calving areas are not discrete physical entities and are not readily recognized by physiographic or vegetation characteristics (Bergerud, 1974; Fleck and Gunn, 1982). It is the caribou cow's traditional behaviour that characterizes use of those areas (e.g., Fleck and Gunn, 1982). Recognition of the role of traditional behaviour emphasizes that the use of a specific area is not permanent. New traditions can be learned even through the new experience of only a few dominant members of the population.

Bergerud (1974) has stressed the optimal and dynamic use of space by caribou and the emphasized that the use could change with time. Bergerud (1974) suggested that social facilitation was a contributing factor to that dynamic use of space. We believe that traditional behaviour is also a likely mechanism in imparting both stability and the potential for change if the caribou's environment changes. The source of a change could result as individuals in a population

do not necessarily all follow identical foraging or reproductive strategies (e.g., Smith, 1983). Not only do some individuals follow different strategies, but there is individual variation in the consistency and demonstration of behaviours within a strategy. This individual variation as a factor in population ecology often seems overlooked — possibly because of our reliance on statistical procedures that smooth over individual variation or merge it with sampling error. The presence of a few individuals in a population that, for example, do not gregariously calve, may rapidly increase that behaviour in the population if, for example, the level or type of predation changes. Bergerud (1971) reported that calving in the Avalon herd became dispersed and less synchronized in time as lynx (Felis lynx) predation increased. However, direct evidence is lacking that the experience of individual caribou on the calving grounds can modify their subsequent use of the area. Likewise, there are virtually no published data on the variation of affinity among individuals to their calving grounds.

The current concept of herd identities is based on the fidelity to calving grounds (Skoog, 1968). Some workers have recently questioned the fidelity to the calving grounds and thus herd identity (e.g., D. R. Carruthers, 1983. The Central Arctic herd myth, unpublished paper read at 1st North American Caribou Workshop, Whitehorse, Yukon Territory. 36 p.). Two points have to be considered in evaluating the concept for basing a herd's identity on fidelity to its calving grounds. Firstly, that the original designation of the calving grounds included all the previously used areas. Core (principal), secondary and satellite calving grounds are terms used but require definition as well as inclusion in the boundaries of the traditional calving area. Cows can rapidly move considerable distances even when with calves only a few days old. Thus, care must be taken in categorizing areas as calving grounds based on sightings of cow — calf pairs in mid to late June (i.e., calving grounds must be delineated during the peak of calving). Secondly, that although patterns of caribou migration change and calving may be in «unexpected places» (Davis et al., 1978b), the presence of some calving cows in an area for 1 or 2 years is not necessarily evidence for the existence of a separate herd. Additional supporting evidence would be needed as the cows may return to their original calving grounds (e.g., Delta and Fortymile herds).

Predation is part of the environment of a caribou calving ground. Predation is, however, especially prone to variation because predator numbers vary in response to many factors including harvest or control by humans. If the level of predation changes over a period of years the caribou may also respond by a change in behaviour, including gradually shifting their distribution. Bergerud (1974) emphasized the influence of predators on the density and distribution of where caribou cows calved. The gradual change (partial overlap between years) in calving distribution of the Fortymile herd may reflect changes in the numbers of wolves on those calving grounds or in the type of wolf hunting such as wolves supporting cubs or non-breeding wolves (P. Valkenburg, pers. comm.). Bergerud (1971, 1974) reported a change in the behaviour of breeding cows in the Avalon herd as the introduced lynx increased predation of newborn calves.

The examples of abrupt (discontinuous) changes in calving distribution in the absence of drastic habitat changes such as flooding are from herds increasing in size and expanding their range distribution. The occupation of new calving grounds has occurred on previously used summer ranges (i.e., familiar area sensu Baker, 1978). What or how environmental change leads to the behavioural change is unknown but. speculatively, in an expanding population (which had a high proportion of younger animals) there may be a higher proportion of caribou with a tendency toward pioneering or explorative behaviour. Explorative behaviour and or a threshold density response may explain a change in traditional behaviour. Possibly, the higher proportion of younger animals in an expanding population could mean that the affinity to an area is not so strongly developed as in older animals who have strengthened the affinity through repetition. The expansion in areas of winter and summer range use by herds increasing in number of individuals may indicate that explorative behaviour increases with population size.

The status of caribou herds in 1984 was determined from aerial surveys for 16 of the 23 herds in Alaska: 10 herds were increasing and 6 were stable in number (Seward, 1985). Similarly, in the NWT, most herds that are surveyed are increasing in number and those and other herds

are expanding their distribution (Williams and Heard, 1986). Caribou learning to use new ranges can overlap with other herds or occupy unused ranges, though so far the overlap of ranges has not lead to documented examples of herd interchange on calving grounds.

Previously, when caribou numbers were increasing or decreasing, the inability to positively recognize and track movements of individual caribou meant that assertions of immigration and emigration were largely based on circumstantial evidence. Hence, discussions as to whether some shifts in caribou distribution are density-dependent were inconclusive. Increasing use of radio-telemetry with its capability to repeatedly locate individually identifiable caribou will increase the probability of correlating changes in population size with distributional changes. Current radio-telemetry data have reinforced the validity of the concept of traditional behaviour in maintaining the fidelity of caribou cows to specific calving grounds (e.g., Cameron et al., 1986). Radio-telemetry data have, however, identified an apparent exception to that fidelity (Davis et al., 1986). Time has been too short to interpretate whether the movement of some Delta cows to the Yanert herd's calving grounds in 1984 was temporary and reflected individual variation, or was a change in traditional behaviour. The example of the Delta herd does indicate that before individual shifts are designated as emigration or herd interchange, some criteria (hypothesis testing) will be required. For example, how many radio-collared caribou (what proportion of the population of breeding cows) will constitute a change or individual variation and for how many years — a generation?

The dependence of caribou management on the herd concept which is currently based on the practical convenience of ascribing herd identity by use of a traditional calving grounds may require refinement. The dependence of the herd concept on a behavioural pattern whose definition includes the potential of change implies identification of herds may also be subject to change. The use of morphometrics, genetics and radio-telemetry (to identify isolation of breeding populations — distribution during the rut) would likely result in more biological and stringent definitions of herds.

The implications for managers of traditional behaviour resulting in fidelity to caiving ground:

is that (1) the use of calving grounds although relatively stable, is flexible in space and time, (2) the experience of individuals on the calving grounds can modify their subsequent use of the area, and (3) individual variation in the use of a calving ground may be expected. The most recent radio-telemetry data (e.g., Cameron et al., 1986; Davis et al., 1986) emphasize that some individual variation in the degree of fidelity may occur by insignificant numbers of females. Management decisions will be required to identify when the level of individual variation becomes a population-level change and over what time period. The evidence to date still suggests that, in the absence of major habitat changes such as flooding, long-term abandonment of calving grounds is rare, and fidelity to calving grounds is still the rule rather than the exception. The general increase in caribou numbers in Alaska and in Canada will lead to situations to test the relationshop between use of traditional calving grounds and herd size. As our knowledge of caribou increases, our concepts and definitions, which are only working models, may require flexibility and modification.

To date, however, only insignificant levels of change have been measured, none that would demand or justify a change in the criteria used for defining a caribou herd.

### Acknowledgements

We thank J. L. Davis and P. Valkenburg, Alaska Department Fish and Game, who helped us by providing data and reviewing an earlier draft. We also thank G. D. Hobson, Director, Polar Continental Shelf Project, Energy, Mines and Resources Canada, for his continued support of our caribou research.

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