

BEHAVIOR OF THE BARREN-GROUND CARIBOU

WILLIAM O. PRUITT, JR.



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... They poured over the hills, flowed up the valleys, running to a new patch of green vegetation, then stopping to feed while those behind ran to fresher vegetation ahead [leap-frogging]. They came to a little lake east of camp—some waded out and began to drink, others started around the edges, both sides. This caused them to bunch up and many began to wade and swim across. They came on toward me, stopping [when] downwind. These moved upwind around me, but there were always more coming on. They came to within 30 yards [27 meters] of me, all around, except downwind.

The clacking of their hoofs, the constant blatting of the fawns, the grunting of the females, the constant coughing and wheezing all made a roar that was deafening. Then some bolted from my scent; the movement spread to about 1,000 and the ground fairly shook with the pounding hoofs, the roar increased. Each stampede only affected a thousand or so, then sort of petered out after one half to one minute . . . I tried to segregate [by age and sex] but was almost overwhelmed by the constant movement. The herd kept moving northwest, it stretched fairly solid for about five hills [2 miles] but was only about half a mile wide.

Yearlings and two-year-olds (?) came closest, but males also came close, females with fawns were shyest. They are quite susceptible to social facilitation—not only by running or flushing but feeding, drinking, wading.

As they moved into the hollow north of the hill they split into two streams, moved across the flat, then up the hill where they spread out and flowed across several more ridges.

The vegetation is completely trampled and cut up—no wonder lichens are the dominant plants of the tundra—only such a plant, able to withstand being cut and chopped, could survive. (Author's field notes, 31 July 1958.)

BEHAVIOR OF THE BARREN- GROUND CARIBOU¹

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During the period August 1957 through August 1958, I was able to study the ecology and behavior of the Barren-Ground caribou in northern Manitoba, northern Saskatchewan and the Northwest Territories, Canada (Table 1; Fig. 1). Since the systematic relationships of the genus *Rangifer* are poorly known, it seems best to be conservative about the nomenclature of these animals. The population studied has been identified by Anderson (1946) and Banfield (1954, 1957) as *Rangifer arcticus* (Richardson).

I am deeply indebted to the Canadian Wildlife Service for the financial support without which this study could not have been made. The Canadian Wildlife Service also administered funds and services contributed to the Cooperative Caribou Investigation by the Government of the Northwest Territories, the Department of Natural Resources of the Province of Saskatchewan, the Game Branch of the Department of Mines and Natural Resources of the Province of Manitoba and the Indian Affairs Branch of the Department of Citizenship and Immigration.

To various members of the Cooperative Caribou Investigation I express thanks for aid in the field—Mr. Ernie Kuyt, Mr. Donald Thomas, Mr. F. W. Terry and Mr. Bert Wilk. I express appreciation to Mr. John P. Kelsall, Supervising Wildlife Biologist and to Mr. W. Winston Mair, Chief, Canadian Wildlife Service for aid and encouragement. Especial thanks should go to Dr. A. W. F. Banfield, formerly Chief Mammalogist of the Canadian Wildlife Service, for his great aid in instigating the research.

I am honored in having this paper illustrated by Mr. William D. Berry, whose intimate acquaintance with northern mammals qualifies him so well for the task.

¹ Received for publication December, 1959.

TABLE 1. LOCALITY, PERIOD OF THE YEAR, AND TYPE OF ACTIVITY OF CARIBOU OBSERVATIONS IN NORTH-CENTRAL CANADA IN 1957-1958.

(Numbers in parentheses refer to Figure 1.)

LOCALITY	TIME OF YEAR	TYPE OF ACTIVITY MOST COMMONLY OBSERVED
Manitoba:		
59°25'N. Lat., 97°45'W. Long. (Duck Lake, #1)	Sept., Oct., Nov.	Fall Migration
59°09'N. Lat., 95°58'W. Long. (#2)	Oct.	Rut
Saskatchewan:		
58°37'N. Lat., 105°50'W. Long. ("Camp 15," #3)	Dec., Jan.	General Winter
58°49'N. Lat., 105°52'W. Long. ("Camp 16," #4)	Jan., Feb.	General Winter
58°53'N. Lat., 109°08'W. Long. ("Camp 17," #5)	March	Late Winter, influenced by sun crusts and snow settling.
58°23'N. Lat., 105°51'W. Long. ("Camp 18," #6)	March	Late Winter, preceding migration.
59°15'N. Lat., 106°14'W. Long. (#7)	April	Spring Migration
59°15'N. Lat., 105°50'W. Long. (Stony Rapids, #8)	April	Spring Migration
Northwest Territories:		
63°14'N. Lat., 105°26'W. Long. (Tyrrell Lake, #9)	May	Spring Migration
64°23'N. Lat., 101°15'W. Long. (Spruce Grove Lake, #10)	Late May	Spring Migration, early fawning.
64°43'N. Lat., 100°15'W. Long. (Fawn Lake, #11)	June	Fawning
(Fawn Lake)	July	General Summer, Aggregations.
64°24'N. Lat., 101°48'W. Long. (Thelon River Camp, #12)	August	General Summer, Aggregations.
63°03'30"N. Lat., 107°53'W. Long. (Artillery Lake I, #13)	August	Fall Migration
63°02'N. Lat., 107°57'W. Long. (Artillery Lake II, #14)	August	Fall Migration

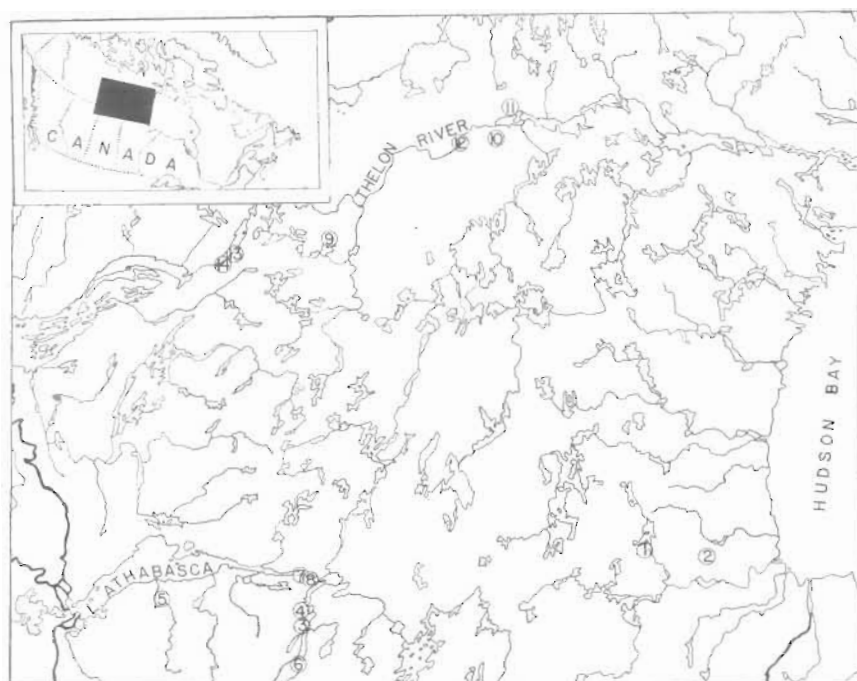


Figure 1. Outline map showing places mentioned in text. Numbers refer to Table 1.

BASIC CARIBOU BEHAVIOR

During certain periods of the annual cycle, caribou may occur in huge aggregations. Such herds are so impressive that their occurrence is generally believed to be more frequent than is actually the case. Although the herd is an important part of caribou life, these animals are usually found in small bands or as individuals. The normally low frequency of large herds is being further reduced by the severe decline in the total Canadian caribou population due to destruction of winter range by fire and, more recently, relatively excessive killing by humans.

I was fortunate in being able to observe large herds of caribou during 30, 31 July and 1 August 1958, when a herd of 15,000 to 20,000 animals streamed around me. The scene is described opposite the introductory page. Through ground observation I calculated that 50,000 caribou were in view from horizon to horizon at one time on 31 July. Thus almost one-quarter of the total Canadian caribou population (Banfield 1957; and recent unpublished reports by various authors in Canadian Wildlife Service files) was in this region.

One would expect that animals which occasionally congregate into such huge aggregations because of food supply, snow conditions or physiological rhythms should exhibit well-developed mechanisms tending to lessen strife or conflicts between individuals and to serve for species survival. This is indeed true for the Barren-Ground caribou. One of the most important mechanisms serving species survival is synchrony of behavior, movement and physiology among individuals. A caribou may travel some 1,900 to 2,400 kilometers during its annual cycle, from possible fawning grounds north of Beverly Lake, Northwest Territories (64°–65° N. Lat.) to possible wintering grounds in northern Saskatchewan (57°–58° N. Lat.) and return.

Because of the vast area involved, synchrony among individuals in regard to mating, for example, is imperative. This event, for the majority of breeding animals, is so phased that the following spring the gravid females reach the proper topographic and nival setting at the precise time when the fawns are ready to be born. Those which reach the fawning grounds prior to the completion of gestation (i.e., those that had come into heat later and had been served later than the majority) may pass on by and go farther, into a region less suited topographically, climatically and nivally for fawning. Those which were served earlier and reach fawning time when still away from the ideal region may give birth in a region of many rugged outcrops (as, for example, the vicinity of Tyrrell Lake) or extensive willow flats (as, for example, part of the shore of Beverly Lake) or where the snow cover has already melted enough

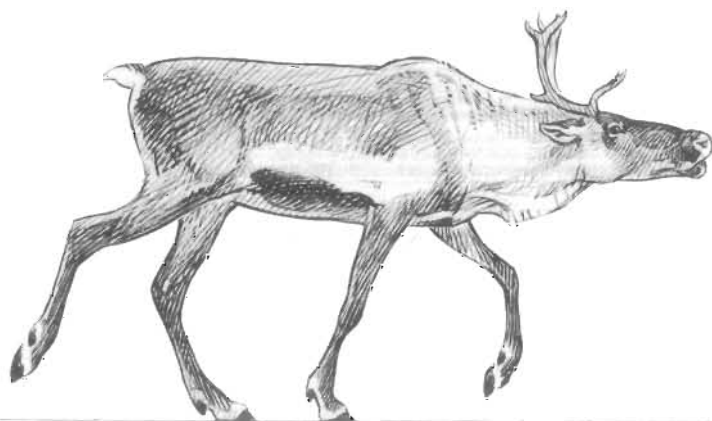
to lose its power of flotation for females and fawns, or even where the season may be advanced enough for flies and mosquitos to be a serious handicap for the new-born fawn. Since the caribou inhabit virtually all of northern North America, the advantages of regional synchrony would far outweigh the disadvantages caused by it, such as local elimination of fawns because of inclement weather. Consequently it is advantageous to species survival to have any non-synchronous individuals eliminated. Scientific accounts of caribou observers are virtually unanimous in agreeing that natural predation operates in precisely this fashion—a tendency toward elimination of non-synchronous individuals.

Among the synchronous individuals, at times in rather close contact with each other, there have evolved a number of signals or sign stimuli, which, in effect, deliver certain messages among individuals of the aggregation. Some of these stimuli appear to be mere silhouettes of other animals. Silhouettes of feeding caribou tend to elicit feeding in nearby animals and thereby reduce alarm or wariness. Thus a human observer can frequently approach a band of caribou quite closely by skillful use of the prevailing wind and by merely bending far forward at the waist, allowing one arm to project down toward the ground, and holding the other arm vertical, thus simulating the silhouette of a feeding caribou. O. J. Murie (1935) noted a similar response in caribou on the Alaska Peninsula. Although adequate data are lacking, I believe that the white mane of the bucks serves as a sign stimulus, as does the white undersurface of the tail when it is erected or flagged in certain situations (cf. O. J. Murie, *op. cit.*). Other sign stimuli which appear to act as social releasers occur as special postures or poses assumed by caribou whenever the particular motivation is of sufficient intensity. Some of these poses or postures are described below.

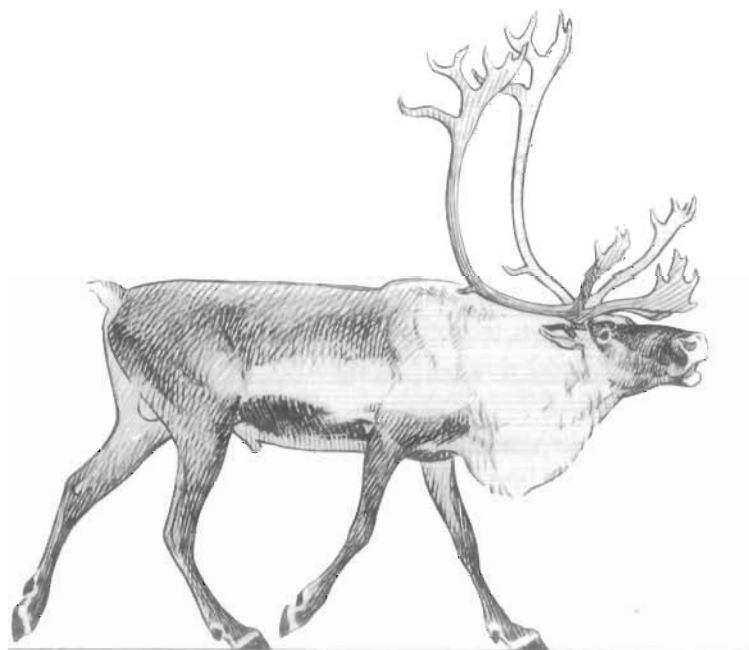
THREAT

Description: Muzzle extended, antlers laid back along the neck, ears back; animal usually advances rapidly (at a fast walk or a trot) toward antagonist (Fig. 2a). This posture is also well illustrated by photographs of bull wapiti (*Cervus canadensis*) in Seton (1913: 64; 1927: 20). Seton described this posture in bull wapiti in the following vivid manner "... His ears were laid back, his muzzle raised, his nose curled up, his lower teeth exposed, his mane was bristling and in his eyes there blazed a marvellous fire of changing opalescent green. On he marched, gritting his teeth and uttering a most unpleasantly wicked squeal." (1913: 70).

Occurrence: (a) Females warding off strange fawns, (b) Females warding off other adults from their fawns, (c) Females, even without fawns, showing antagonism toward bucks during fawning time, (d) Part of male



2a



2b

Figure 2a. Threat pose, exhibited by female caribou.

Figure 2b. Modification of threat pose by male caribou in courtship display. (Sketches by W. D. Berry)

courtship display (Fig. 2b). Figure 3a represents the outline and tone of "normal" and threat pose as presented to another caribou.

Discussion: Although the animal assuming the threat pose usually advances rapidly toward its antagonist, the head and neck only may be placed in a threat position when the animal is lying down. On 7 June 1958 at Fawn Lake I observed a new-born fawn totter to a strange doe which was lying down. The doe laid back her antlers and extended her muzzle toward the fawn. He immediately turned around and tottered away, getting no closer than one meter to her.

The head and antler portion of this pose also occurs as part of male courtship display. This aspect of the posture is illustrated in a photograph by Dugmore (1913: facing p. 48) of a buck Newfoundland caribou (*Rangifer caribou terraenovae*). On 3 October 1957 at 59°09' N. Lat., 95°58' W. Long. I observed an adult buck assume this posture and dash at a group of does and immature individuals. They scattered before him and he relaxed from the posture. His actions and posture were almost identical with those of a buck white-tailed deer (*Odocoileus virginianus*) which I once observed displaying on the E. S. George Reserve in southeastern Michigan (Pruitt, 1954). I do not interpret this action in caribou as it has been interpreted by most other observers. I look on it as part of the male courtship display. The attitude, posture and motions of the buck are expressions of the vigor of its sexual drive and of its readiness for copulation. The extended muzzle, grunts, and swift advance are sign stimuli giving this "message" to other caribou. These sign stimuli appear to act as sexual releasers (Tinbergen, 1951: 174-175). Daanje (1951) noted the close relationship between threat and sexual display in birds. If the buck's sign stimuli are seen by a doe, they elicit several responses which are in turn received by the buck. Figure 3b (left) represents the outline and tonal pattern of the threat pose as presented to a doe. If the doe is not physiologically receptive to mating, the buck's actions are "interpreted" as antagonistic and thus release flight. If the doe is sexually receptive, the display fails to release flight. Therefore the first response which a receptive female exhibits is not fleeing when a buck displays near her. Since my observations of the remainder of courtship are fragmentary, I cannot analyze this behavior sequence further at present. Possibly such courtship displays in bands of caribou during the rutting period may have a synchronizing effect on ovulation similar to that suggested by Darling (1938) for colonial birds. Presumably this posture sequence is what Altmann (1956) called "driving" in wapiti and moose (*Alces alces*).

Also on 3 October 1957 at the same locality, I observed a buck exhibit

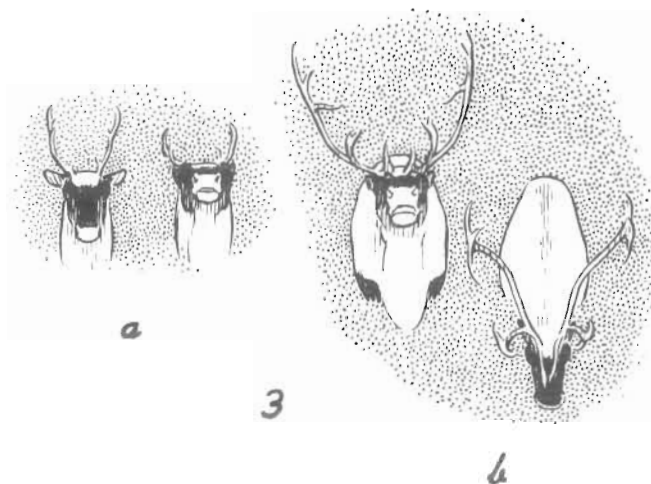


Figure 3. (a) Outline and tonal pattern of "normal" (left) and threat (right) poses as presented by a doe to another caribou.

(b) Outline and tonal pattern of threat (left) and attack (right) poses as presented by a buck to another caribou. (Sketches by W. D. Berry)

the male courtship display. I was kneeling behind a large rock on an open hillside, with the edge of a patch of bush about 45 meters away. The buck came trotting toward me through the trees. He joined another buck who was following a doe, and advanced to about 20 meters from me, trotting with a stiff-legged gait. At one time I apparently became the object of his display for he turned and moved back and forth in front of me, all the while swinging his tilted head from pointing forward to pointing at right angles toward me. During this display I received the distinct impression that he was "presenting" the tines or shovels of his antlers as an integral part of the display. Moynihan and Hall (1955) described postures characterized by "head-wagging" and "tilted head" in the courtship of spice finches (*Lonchura punctulata*). They explained these postures as conflicts between the drives for attack and for flight.

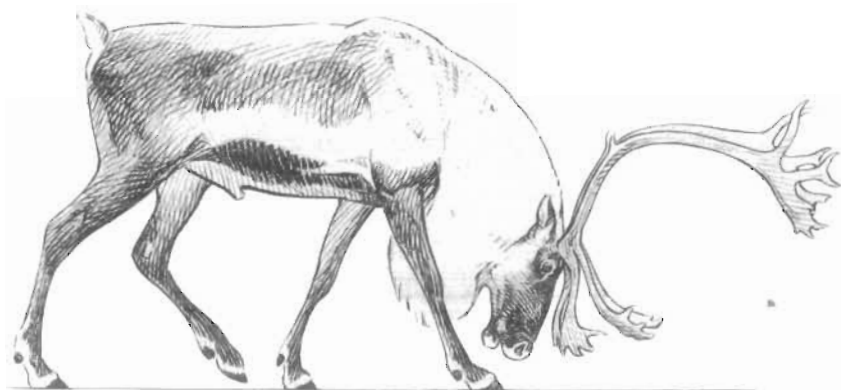
The stiff-legged gait was observed only in the fall. Possibly this is a courtship addition to the basic threat posture. Darling (1937) also noted a characteristic stiff-legged gait in buck red deer (*Cervus elaphus*) during the rut.

ATTACK

Description: Head lowered, muzzle nearly touching the ground and pointing somewhat backward to between the front hoofs. This attitude brings the main axis of the antlers vertical and points most of the tines forward (Fig. 4). Animal slowly advances.

Occurrence: (a) Any actual encounter between individuals when the threat pose fails to intimidate or when the motivation of one or both animals is of sufficient intensity, such as two females competing over a single fawn, (b) Yearlings, immature or subadult individuals testing their strength or playing, (c) Sparring between two or more mature bucks in late summer or fall. Figure 3b (right) represents the outline and tone of this pose as presented to another caribou.

Discussion: At 0730 on 27 September 1957 on the mainland northwest of Duck Lake, Manitoba, I observed a group of 11 bucks. They were in the open and were observed through 7x50 binoculars at a distance of 2 kilometers and under good light conditions. Two bucks sparred with their antlers, pushing one another back and forth. They broke free; one whirled around while the other rose on his hind legs and shook his head and rack. They sparred again. A third buck came up and intruded on the sparring pair, and they all had their antlers together for a few rattles. They then broke apart and resumed grazing. The group was seen about 15 minutes later on the lake shore, and two bucks were alternately pushing each other and feeding.



4

Figure 4. Attack pose, exhibited by a male caribou. (Sketch by W. D. Berry)

I again observed sparring between two adult bucks on a sandy lake beach at 59°09' N. Lat., 95°58' W. Long. on 3 October 1957. These two bucks alternated several bouts of sparring with walking along the beach for a total distance of about 270 meters.

I observed sparring between adult bucks as late in the winter as 23 March 1958 at Camp 18. On this date there were two continually sparring bucks (both antlered) in a band of 28 bucks on a snow-covered lake. Of these 28 bucks, nine had antlers. The two bucks sparred vigorously, whirling around and around, pushing each other back and forth, producing clashing sounds and sending up clouds of snow.

HEAD BOBBING

Description: Animal alert, ears forward, neck and head elevated (when expressing curiosity) or neck and head lowered to fawn level (when preparing to release following in a fawn); head is quickly lowered so that muzzle nearly touches the ground (Fig. 5a), then head is returned about one-half to two-thirds of the way to full recovery and stops (Fig. 5b). Head then slowly resumes original position (Fig. 5c). Movement seldom occurs more than three times in quick succession. Usually some other body movement, such as a major change of position, is interjected between bouts of head bobbing.

Occurrence: (a) When viewing an unknown object, curiosity without alarm (Preble in 1902 suggested that the white throat patch in caribou possibly functioned as a signaling device. Perhaps this pose serves to display the patch.); (b) Female trying to induce a young fawn either to get to its feet or to follow her (Since the doe is frequently heading away from the fawn, she sometimes turns only her head and neck to look back at it, and then she bobs.); (c) Frequently occurs, as a single bob, after being startled but before flushing.

Discussion: Head bobbing releases following in a fawn. It has been noted to occur when two females are each trying to get a single new-born fawn to follow them separately. The female that intrudes herself between the fawn and the other female and then bobs her head at the fawn usually induces it to follow her. The doe with the stronger motivation, presumably the actual mother, may exhibit the threat or attack pose when facing the competing female and then turn around and bob at the fawn which then may follow her. I observed this sequence of poses at Fawn Lake on 8 June 1958.

Since the motivations in situations (a), (b), and (c) appear to be different, I am doubtful that the elicited movements are basically the same. Possibly one or more of these are derived from still another movement or perhaps one from the others.

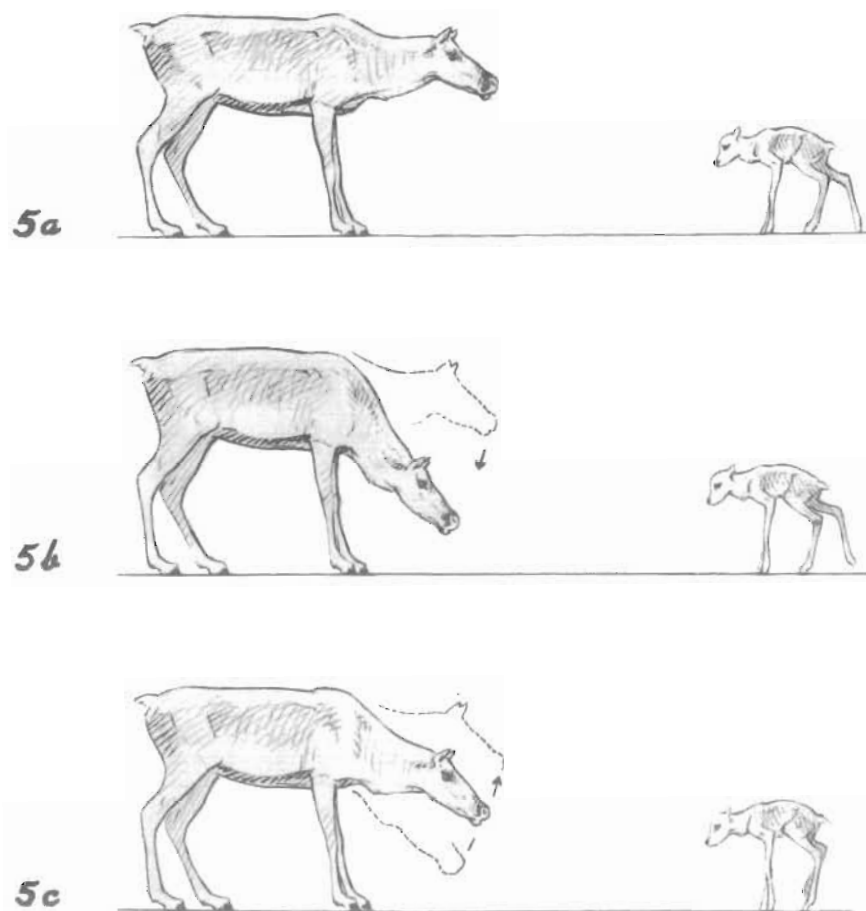


Figure 5. Head bobbing pose, exhibited by a doe to a new-born fawn caribou. (Sketches by W. D. Berry)

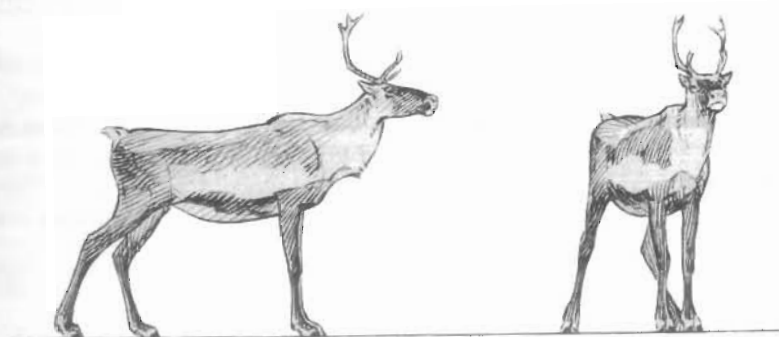
Bobbing is a technique which can be used to toll caribou to within close range of an observer. On the east shore of Artillery Lake on 24 August 1958, I saw a female standing quiet in a small sedge marsh surrounded by high rock walls. I walked slowly toward her. She spied me when I was about 90 meters away and trotted off at right angles to my approach. I stopped and bobbed (bowed from the waist down and up) and she wheeled and came toward me. She came forward about 18 meters, stopped and turned away. I bobbed again and she again approached. She did this twice more and got as close as 31 meters to me. I was in full sight, on bare rock, during all the above incident. Thus a crude imitation of the silhouette of bobbing acts to release following even in adult caribou.

ALARM

Description: The animal faces the alarming stimulus, head erect, one hind leg stiffly extended laterally, but with hoof remaining on ground (See Fig. 6). Well illustrated also by a sketch of reindeer (*Rangifer tarandus*) by Seton (1909: 204) and of caribou by Harper (1955: front cover).

Occurrence: This pose is assumed by caribou when they are alarmed by the sudden appearance of an unidentified object or movement near at hand or by a loud noise sometimes from as much as a kilometer away. Other caribou which see the pose stop and look in the same direction as the poser. The pose is maintained until the stimulus of supposed danger lessens to below some threshold or until the caribou flees.

Discussion: The alarm pose appears to be a ritualized derivation of the urination-defecation pose. Sometimes when alarmed by a shot or other strange loud noise or by the sudden appearance of an unidentified object nearby, instead of assuming this ritualized pose, caribou will assume the complete urination-defecation pose and actually urinate or defecate. The full urination-defecation pose has both hind legs separated, but usually not so far apart as in the ritualized one-legged alarm pose. Occasionally the alarm pose (Fig. 6b) will be changed into the urination-defecation pose (Fig. 6a) if the animal is not further alarmed. Since other animals frequently defecate when frightened and since ritualization of a displacement activity is frequently accompanied by an exaggeration of the activity or pose (Tinbergen, 1952; Tinbergen and Van Iersel, 1947) the alarm pose in caribou seems to fit into this general scheme of behavioral evolution. Tinbergen (1953) gave a lucid discussion of ritualization. Simmons (1952) noted that displacement activities are common predator-reactions.



6a

6b



Figure 6. (a) Urination-defecation pose, exhibited by a female caribou.
(b) Alarm pose, exhibited by a female caribou. (Sketches by W. D. Berry)

When caribou are moving in file and one becomes alarmed and assumes this pose, the ones following stop and look in the same direction, but the ones ahead do not stop or look. Therefore there does not appear to be vocal accompaniment.

EXCITATION JUMP

Description: The animal raises on its hind legs suddenly, turns while on its hind legs and usually flees, bounding once or twice before settling into a trot (Fig. 7). Inspection of the tracks resulting from excitation jumps reveals that the bounding turn causes the hind toes to separate and dig into the substrate.

Occurrence: When caribou have investigated a strange object by sight, the foremost caribou (or the one closest to the suspected danger) often performs the excitation jump before fleeing. I observed, as did O. J. Murie (*op. cit.*), that it usually was a buck that assumed this pose.

Discussion: I believe that the excitation jump has some relationship to the presence of interdigital glands on the hind feet, which were first noted by Caton (quoted in Seton, 1909), discussed by Dugmore (*op. cit.*), and described histologically by Quay (1955). While in the vicinity of Fawn Lake I carefully inspected the sites of several excitation jumps to examine the tracks. At this time I thought I could smell something characteristic at each site, but dismissed the idea as imagination. Near the camp on Artillery Lake, however, I repeated my careful scrutiny of the tracks where a mature buck had given a sudden frightened leap upon being shot with a drugged arrow. At this time I again smelled what I suspect is the scent produced by the interdigital glands. It has a characteristic odor strongly reminiscent of the smell of fresh *Populus* bark and sap or possibly similar to phenol, quite different from the usual odor commonly associated with caribou. The odor is readily discernible at a distance of several inches, even by a man's relatively insensitive nose.

While the alarm pose appears to be for strictly visual purposes, the excitation jump appears to leave behind this special scent, since other caribou that later come by will recoil or assume the alarm pose when they reach the same spot. Dugmore (*op. cit.*: 89-90) observed, "Often I have noted that when caribou . . . are startled they leave behind some signal on the ground which warns every animal that comes to the place. . . . but it is quite possible that the sudden jumping causes the hoof to separate and that in so doing the glands are brought into operation, so that a minute particle of the fluid is left on the ground." O. J. Murie (*op. cit.*) interpreted this posture as a "spy hop" and also noted that it followed a visual danger stimulus.



7

Figure 7. Excitation jump, exhibited by a male caribou. (Sketch by W. D. Berry)

As the following example shows, caribou do not always flee after giving the excitation jump. On 24 May 1958 about 8 kilometers north of Tyrrell Lake only the ridge tops were bare of snow. While driving a dog team along a zaboïs (a patch of snow, sometimes many feet thick, that endures far into the summer) situated on the protected slope of a rocky ridge, I was accompanied by an adult buck for nearly 2 kilometers. The caribou first appeared on the ridge above me about 70 meters away. He gave the alarm pose, then an excitation jump, but instead of running away from me he accompanied me along the ridge, trotting beside or slightly behind me about 70 meters distant. He repeated the alarm pose-excitation jump sequence several times in the course of traveling about 2 kilometers.

BEHAVIOR DURING SNOW SEASON

The Barren-Ground caribou walks upon or wades through snow for two-thirds of its annual cycle. Since the caribou is primarily a grazer and not a browser, for months at a time its food supply must be excavated through a snow cover. The act of pawing through the snow cover or digging a "feeding crater" is an integral part of the complex of behavior patterns that govern the caribou. The foreleg is extended, with the anti-brachium held almost parallel with the snow. The leg is bent at the carpal joint; and the lower leg and hoof are swung down, back and recovered several times at a speed almost too fast for the eye to follow. The leg returns to a normal supporting position and the head is lowered into the crater formed in the snow. In deep snow both forefeet are at ground level in the feeding crater, causing the animal's hind quarters to be quite elevated. The act of digging a feeding crater gives every indication of being a "consummatory act" (Tinbergen, 1951; Hinde, 1953). Consummatory acts are repetitive, circumscribed actions, that vary little, if at all, from a stereotyped pattern. They occur after and as a culmination of longer periods of less circumscribed "appetitive behavior" which is strongly influenced by environmental stimuli. In this sequence, appetitive behavior consists of (1) moving to snow which has hardness, density and thickness below critical thresholds (Pruitt, 1959) and (2) searching for the presence of suitable food under the snow by scenting the air rising through the snow cover from the substrate (Formozov, 1946; Nasimovich, 1956). Since consummatory acts are basic ones such as actual eating, nest construction, copulation, etc., it is clear that such adaptations to snow as digging a feeding crater have played a vital role in the evolution of caribou.

The usual feeding crater observed during the winter 1957-1958 had an exposed area of substrate approximately 1.5x3.5 decimeters, but the snow in a patch approximately 1x2 meters was trampled, dug out or otherwise disturbed. Regardless of the condition of the snow before being disturbed, its hardness and density increased markedly after cratering (Pruitt, 1959). Another factor, variable temperature, may become effective now, since at colder temperatures disturbed snow will "set" harder and more quickly than at warmer temperatures. Thus a prolonged spell of cold weather (-45° or $-50^{\circ}\text{C}.$) should cause caribou to shift their feeding grounds more frequently than they would in warmer weather (-15° or $-30^{\circ}\text{C}.$). I have observed (Elsner and Pruitt, 1959) that a period of approximately 4 hours at low temperatures is sufficient to "set" or consolidate disturbed taiga snow to a hardness sufficient to support the weight of a man (approximately 2,000 to 3,000 gm/cm² hard-

ness). Caribou whose tracks measured 105x85 mm, (without dew claw marks) have been observed to walk on the surface of a layer with a hardness of 1,500 gm/cm².

Caribou will feed over a previously cratered area only once, that is, a total of only two feedings before the snow becomes so hard that the caribou move on to softer snow. It is evident that this behavior alone is sufficient to account for a large share of their daily movements in winter.

Overwintering bands use snow-covered lakes as "escape cover" or "loafing cover" because lake snow is usually thinner than forest snow and especially because it is usually harder (frequently supporting caribou on its surface). The bands bed down usually no closer than 70 or 90 meters to the shore. It is noteworthy that this distance appears to be approximately the distance that the "wind shadow" effect of mature white spruce (*Picea glauca*) taiga extends onto a lake. Forestward within this shadow the snow gets progressively more like forest snow; lakeward beyond this shadow it is harder and denser. The bands stay on the lakes during the middle of the day, usually from about 0900 hours until 1500 hours. During this bedding period caribou shift about several times, each animal forming a series of smooth semi-circular beds in the snow. When they move to feed they go to the nearest shore and later return to their bedding ground, or loafing cover. The next feeding period they go to the same feeding area, or if the snow there is now too hard, they move on until they encounter soft snow. In this fashion the bands feed progressively farther and farther away from their loafing cover. Finally they are over the ridge in sight of the next lake which is then utilized as loafing cover. Thus the bands of caribou move back and forth through the snow cover of their winter range.

The caribou's threshold of nival tolerance appears to be snow with a hardness of about 50 gm/cm² for forest snow and 500 gm/cm² for lake snow and a density of about 0.19 or 0.20 for forest snow and about 0.25 or 0.30 for lake snow. The thickness threshold appears to be about 60 centimeters. The figures for lake snow serve as indicators of forest snow conditions since winds strong enough to produce 500 gm/cm² hardness on the lakes appear to raise the hardness of snow in adjacent forests above 50 gm/cm².

Because of forest fires most of the spruce taiga winter range has now been replaced by jack pine (*Pinus banksiana*). I have observed and calculated that mature, open jack pine forest will show 904 craters per hectare (366 craters per acre), meaning that about 1,800 craters can be dug per hectare before the snow becomes too hard. Apparently be-

cause of social interactions between individuals, one hectare rarely shows more than about 900 fresh craters at any one time. This number of excavations rather effectively covers all the snow surface with disturbed snow.

BEHAVIOR DURING MIGRATION

Since caribou appear to possess a threshold of tolerance to the hardness and density of the snow cover through which they wade for some two-thirds of their annual cycle, it follows that some aspects, at least, of their spectacular annual migrations might be correlated with nival factors.

As the solar radiation increases in the spring, the snow develops a "sun crust" and starts to settle. This settling is only the visible manifestation of morphological changes occurring within the snow cover. These changes are measured by the snow instruments as increases in hardness and density, although they are actually caused by enlargements in size of the snow particles with accompanying decreases in particle number. At the same time these changes take place there also occurs a change in the behavior patterns of the caribou. Individuals or small bands now frequently break away from a larger band and run or bound in a large circle, shortly rejoining the larger band. This behavior is easily deduced by aerial observation of the tracks. It is noteworthy that progression by bounding is characteristic of ungulates when they find themselves in snow above their critical depth. Darling (1937) observed a heightened sensitivity to external stimuli in red deer (*Cervus elaphus*) during periods of thaw. He, however, attributed the increased irritability to changes in atmospheric moisture.

When the forest snow attains surface hardnesses of 300 to 500 gm/cm² and densities on the order of 0.30, the caribou react the same as they do following a similar change produced by a winter storm—they move toward softer and lighter snow, which, in the overwintering region in northern Saskatchewan, is usually found to the north or northeast. In mountainous or hilly regions, such as some parts of Alaska, caribou accomplish this by comparatively short altitudinal migrations. Settling, crusting and melting sweep inexorably through the taiga toward tree line, herding the caribou along. Sometimes the progress of the thaw is interrupted by meteorological events which cause complete freezing of the granular snow cover. The snow at this time may become extremely hard. Surface hardnesses may rise to 3,000 gm/cm² or more in a few hours. Density does not change much, since it is governed by the water content of the individual layer whether frozen or not. At the time of a spring cold snap the caribou cease their movement down the hardness gradient simply because the gradient no longer exists. The migration stops. The brittle crusts which sometimes occur at this season can deter caribou movement because of sheer discomfort or pain accompanying constant breakthrough of the crust. After the cold snap is over or after the cold

night has passed and the sun again acts on the snow cover, the migration resumes its flow down the hardness gradient. As they move through the taiga, the main mass of migrating caribou are generally found northward (or tundra-ward) of the region where the thaw has progressed sufficiently so that the lakes are dark with slush and south (or southwest) of where the complete snow cover, including 0.1 qali (Pruitt, 1958), is present. The region frequented by migrating caribou bands is characterized by having only qamaniq (Pruitt, 1957) and steep south slopes of eskers bare of snow.

There is a definite tendency for females and young animals to pass through a given region on their way to the tundra in the spring before the bucks appear. Indeed, such sexual segregation is already evident in late winter. I believe that this segregation can be at least partially explained by the fact that the bucks appear to have a higher threshold of sensitivity to snow hardness, density and thickness than do the smaller, lighter females and young, and they therefore usually penetrate farther into the taiga. In other words, the snow cover acts as a sieve, holding back whole classes of small, light animals but allowing larger or heavier ones to filter through. Because of this hypothesized higher tolerance to hardness and density of the snow, the bucks, even though they are engulfed by the advancing thaw before the does are, may begin their northward migration at about the same time as the females and young; however, they start from several to many kilometers behind.

The bands of bucks which brought up the rear of the spring migration seemed to sweep up the stragglers of the entire migration. I noted limping individuals more frequently with these bands of bucks than with the main mass of caribou (cf. Crisler, 1956). The genes of many unfit individuals were undoubtedly eliminated from the species pool by wolves in former days, before man began to interfere with caribou evolution by reducing natural predation.

During the first half of July near Fawn Lake I gained the impression that caribou began to congregate into bands in late evening when the light intensity began to lessen and that the bands were more active at this time of day. Since in late July and early August at these latitudes there begins to be some darkness at night, I suggest, as pure speculation, that there may be a connection between the onset of nighttime darkness and the congregation of caribou into the large masses such as those I observed on 30, 31 July and 1 August in the vicinity of Fawn Lake.

While watching migrating bands of caribou moving along across the tundra, feeding as they went, I received the impression that the members of the band appeared to feed in a counterclockwise circle. Time and

again the animals would feed hurriedly or walk forward to the leading edge of the band, begin to feed and then drift to their left. Then, working around in a circle until they were the trailers of the band, they would hurry forward again. (The propensity for reindeer herds to be direction-specific in milling is well known.)

BEHAVIORAL REACTIONS TO INSECTS

During early August along the Thelon River, single caribou or doe-fawn pairs were frequently noted trotting swiftly across the tundra. This behavior undoubtedly was the result of insect activity. I suspect that attacks by the nose fly (*Cephenomyia nasalis*) or warble fly (*Oedamagena tarandi*) (Banfield, 1954) are responsible for these erratic excursions more than are attacks by mosquitoes (Crisler, *op. cit.*).

On 14 August 1958 about 16 kilometers south of Thelon River Camp, I observed a series of caribou reactions to insects. The Thelon River had at this point an extensive exposed gravel bar in its bed. A buck and several does were scattered over this bar, all standing motionless. The ones on the central, elevated part of the bar had their heads and necks elevated but the buck, who was on a small strip of sandy beach at the water's edge, had his head and neck depressed so that his muzzle nearly touched the water. These individuals stood motionless for nearly an hour while a band of about 500 caribou came into sight from the southwest, moved down the valley and finally out onto the opposite end of the gravel bar. The band was beset by insects, judging from the amount of stamping and head-tossing that was going on. The band started to cross the river (from south to north) but split up, part actually swimming across while approximately 350 individuals remained congregated at the water's edge. Here they remained in a compact mass, all facing downwind. Individuals were constantly stamping their feet. Since about one-third of the band was actually standing in the water at the river edge, the constant stamping lifted up a great curtain of spray nearly as high as the animals' backs. Standing in the spray or self-made shower undoubtedly reduced the intensity of insect attacks and is certainly an example of an animal temporarily modifying its environment for its own benefit. This aggregation closely resembled the "tandara" formation into which the herders of northern Eurasia concentrate their reindeer in order to reduce insect annoyance.

The buck, who had been standing motionless at the opposite end of the gravel bar all this time, suddenly exploded into action, showing all the typical reactions to an attack by a nose or warble fly. He threw up his head, stamped his feet, twitched his hide, and then began to gallop along the beach, bucking and tossing as he ran. He suddenly stopped and stood stock still. Then he wheeled, galloped back in his tracks, stopped again, shook his head, wheeled once more and galloped full speed toward the band at the water's edge. He literally burrowed his way into their midst where I lost him and presumably the nose fly did likewise.

During mid- and late August in the vicinity of the Artillery Lake camps, the caribou almost invariably spent the "heat of the day" standing alone on the tops of hills or in sedge marshes. Here they either fed or just stood motionless until about 1700 hours when they began to drift west toward the lake shore and then north along the shore and for about half a kilometer inland. This behavior is similar to that recorded earlier in the summer. Caribou became more tolerant of each other's presence and began to move in a definite direction in late afternoon and evening. A similar behavior pattern appears to hold also for early morning. When the animals stood motionless on a hilltop they usually faced down wind, but no such orientation was observed when they stood in a marsh. Hilltop caribou, however, stood with neck and head elevated while caribou in marshes stood with head and neck depressed, muzzle nearly touching the water-logged surface.

REPRODUCTIVE BEHAVIOR

RUT

During the first few days of October 1957 at 59°09' N. Lat., 95°58' W. Long., east of Duck Lake, the caribou which were moving northeast onto the tundra were congregated into bands which were composed as follows: First would come three to five large bucks, next at sometimes half a kilometer distance, was a group of does, fawns and immature individuals followed closely or interspersed with one to four adult but not very large bucks. Occasionally there were three to five large bucks following the bands. The vanguard and rearguard bucks were those with huge antlers and heavy, swinging manes. The bucks accompanying the females and young were adult but smaller than the vanguard and rearguard bucks and had lighter antlers; presumably they were younger. Apparently the smaller bucks accompanying the females and young were at this time feeling the beginning of the rutting urge. Since the only sparring observed was among the smaller bucks and since the only adult male with strips of velvet remaining on his antlers at this time was one of the vanguard bucks, the vanguard and rearguard bucks were apparently a little slower in their physiological rhythm. Dugmore (*op. cit.*) noted that young buck Newfoundland caribou began to rut in advance of the fully adult bucks. It would be interesting to know the relationships between age, behavioral status and reproductive synchrony in caribou.

FAWNING

My first observation of fawning took place on 5 June 1958 near Spruce Grove Lake. I saw a deer, far in the distance, acting peculiar. By a devious route I got to within 300 to 450 meters of her. She was in the center of a large flat grassy area about 0.8 kilometer across, surrounded by bare gravel and rocky ridges. She was on a slight rise, which was covered with tussocky grass (or sedge) and dwarf willow. I first saw her at about 1500 hours and got to my vantage point at 1520. She was lying down until about 1530. Then she stood up and appeared to feed until 1545, when she lay down again. She raised her tail several times while lying down. When she stood up again I could see she was bloody behind. Soon a fawn struggled to its feet and got a few sucks. It lay down again, or rather, collapsed, for five minutes and then stood for three minutes. It collapsed again and she lay down, too.

I gained the impression that females dropping their fawns either early or late tend to separate themselves from other caribou. Those dropping their fawns during the peak of fawning form "maternity bands" (see below for definition) which frequent optimum topographic and nival

sites. Kelsall (1957) noted that caribou frequent rolling or rugged uplands during fawning. They apparently avoid marshy, brushy or rocky regions during this time. Even when in a maternity band the female preparing to fawn usually moves a few meters away from the band to a spot bare of snow. She usually stays here only 15 to 30 minutes, and generally no more than one hour, apparently in labor. She sometimes stands up, hind legs spread and bent at the hocks, and apparently contracts, but the fawn is born while she is lying down. From my observations, birth takes less than 15 minutes to complete. As soon as the fetus is passed, the female gets up, sniffs it, and feeds for several minutes. She then turns to the fawn and begins licking and cleaning it. Usually she lies down again before the fawn gets up, but not always. Sometimes the fawn struggles to its feet before the doe lies down. Whatever the sequence, she soon lies down again, contracts (as evidenced by her tail raising and lowering) and passes the fetal membranes. She rests for a few minutes, gets up and then begins to eat the membranes. Frequently she stands or feeds with the fetal membranes partially passed. I saw one female pull the membranes from her vagina with her teeth and begin eating them. Eating the membranes is a comical process to watch, since the caribou's teeth are not adapted to such food. The doe shakes her head in an attempt to sever a bite and the bloody mass flies flapping through the air. About this time the fawn again struggles to its feet and attempts to suckle. Sometimes the female (possibly a primipara?) backs off as it nudges her, but the five fawns I watched being born all soon began to suckle. This first time lasts only 15 seconds to one minute. The pattern of events now varies according to circumstances, but usually the female and fawn lie down, the doe lying in the sternal position crosswind with her back to the wind, the little fellow snuggled up against her lee side. After 15 minutes to one hour the doe gets up and feeds or stands over the fawn. When it gets up she moves off about 8 to 10 meters and looks back, bobbing her head until it catches up; then she gives it a few licks about the face and moves off about 10 meters more and repeats the process. All the ones I saw born, plus two others where I saw only part of the full sequence, moved off with the mother from the maternity band to a smaller band, which I call a "false nursery band" (see definitions below). How long an individual doe and fawn stayed with this smaller band I do not know. At Fawn Lake there was a constant flow of does and fawns into the false nursery band and a constant flow of them out of it and up to a ridge top, along which they slowly moved northward, the fawns bumbling along after the females. Within a matter of hours the fawns can outrun a man, and by the age of

one day they can keep up with the female when she is trotting. Within a few days they can outrun the females.

I define the *maternity band* as a group composed almost entirely of gravid females which are in the process of dropping their fawns. This band usually stays near the top of a long down-wind slope. For example, at Fawn Lake, on 6 June 1958, there was a band of 55 does and seven fawns; at the same locality on 8 June 1958, there were 119 does and eight fawns in a band.

A *nursery band* is a group of caribou composed almost entirely of post-partum females with their new-born fawns. There are two main types of nursery bands: false nursery bands as mentioned above, and true nursery bands.

The *false nursery band* is formed by does with new-born fawns which have been led a short distance from the maternity band. The doe usually lies down with the fawn lying at her lee side. They stay here for an unknown length of time, I suspect several hours, until the fawn is able to travel better. I have counted 60 does in a false nursery band, probably all with fawns. Because the new-born fawns are so hard to see when lying down, I do not have accurate counts of their numbers in these aggregations. Does and fawns are constantly entering this band (or this area) and also constantly leaving it. Therefore I do not believe that it is a band in a social sense but is a moderately well-defined aggregation which occurs about the distance from a maternity band that a new-born fawn can totter before it is exhausted and has to rest for a while.

After the fawn has rested sufficiently so that it can travel at the female's side or shortly behind her, they move away from the false nursery band and join a *true nursery band* composed of does and mobile fawns. They gather together and move across the tundra more or less as a unit, at least keeping together because of the pressure of nival or topographic factors. As they move along they are joined by other females and their fawns and even yearlings and a stray buck or two. Two bands counted near Fawn Lake on 13 June 1958 were composed of 39 does and 24 fawns; and 93 does, 84 fawns, seven yearlings and one buck respectively. These nursery bands move very slowly at first, while the fawns are very young, but as the fawns become friskier the band moves faster and faster. When the fawns are a week old the band moves between a fast walk and a trot, the fawns galloping back and forth, the does hurrying here and there, head-bobbing their own fawns into following them, and intimidating strange fawns away from themselves, all the while snatching bites to eat as they move along. The nursery band is noisy, with females uttering their gurgling grunts, and the fawns blatting. During the time of these

discrete nursery bands the fawns have not as yet developed any social sense in the meaning of sociality between individuals. They gallop about and circle back and forth through the band, but each one runs by himself. I could detect no signs of play between individual fawns, no chasing or races. Such play apparently develops later.

Usually there is one doe and fawn preceding the nursery band at a distance of about 100 meters. This female is not a "leader" in the social sense, however. I have observed the leading doe and fawn catch my scent and flee back beside the band without alarming the remainder of the band or causing it to change its course. Any yearlings or bucks included in the band seem to bring up the rear.

Eventually the true nursery bands coalesce and lose their individual identity, become static, and are invaded by yearlings and bucks in greater numbers. This phase is unclear to me since at Fawn Lake it transpired rather quickly on the far northwestern horizon too far away from my camp to be observed critically.

Nursery bands may be of more significance than simply doe-fawn aggregations after fawning. Because of sexual segregation in caribou, the great majority of bucks (and those non-breeding does and immature individuals that accompany them) may not be anywhere near the actual fawning grounds. For example, the caribou studied in the fall of 1957 in northern Manitoba (during the rut when all are together) showed a sex ratio approximately equal ($N = 223$; 47 per cent males) while the sex ratio of the large aggregations observed at Fawn Lake in late July and the first day of August 1958 varied from 66 per cent males ($N = 450$) to 4.3 per cent males ($N = 457$) depending on which herd or portion of a herd was counted, but showed an over-all ratio of 28 per cent males ($N = 2,409$) for the animals segregated as to sex and age during the three days. Thus over half of the bucks were still missing from the herds at this time. Indeed, the herds in late July and early August strongly resembled those that made up the nursery bands earlier in the year.

A large nursery band of 185 animals segregated at Fawn Lake on 13 June contained less than 1 per cent bucks, 50 per cent does, 4 per cent immature individuals and 45 per cent fawns, with 90 per cent of the does followed by fawns. Compare this with the segment of the herd that passed Fawn Lake on 1 August near midday (837 animals): 2 per cent bucks, 52 per cent does, 7 per cent immature individuals, 38 per cent fawns, with 73 per cent of the does followed by fawns. Compare these percentages with the composition of the population observed in northern Manitoba during October 1957, when, according to Banfield

(1954), all sex and age classes are together for the rut: 35 per cent bucks, 32 per cent does, 12 per cent immature individuals, 15 per cent fawns and 2 per cent unidentified. I believe that one is justified in saying that the larger summer aggregations were actually regroupings of the nursery bands which had been in the region since June. Apparently the previously noted tendency for nursery bands to increase in size and to attract immature individuals and stray bucks continues throughout the summer. If this is the case, then a large segment of the caribou population may spend from one-eighth to one-quarter of the annual cycle aggregated into nursery bands or modifications thereof.

I believe it is significant that all the nursery bands I observed in the vicinity of Fawn Lake in June were travelling in a northerly or north-westerly direction. After they reached the extensive upland northwest of camp they became static and lost their identity. While travelling during the thaw they avoided areas of snow or zaboïs whenever possible. I noted that when a band did venture across a zaboïs many individuals frequently broke through the snow, went in up to their bellies and had trouble getting out. While the caribou were in the vicinity of Fawn Lake the snow had been very hard, surface hardnesses ranging from 1,000 to 3,000 gm/cm² or more.

Caribou have been observed to sink 10 to 12 cm. in snow having a hardness of 400 gm/cm², to break through a layer with a hardness of 600 gm/cm² and to be supported by a layer with a hardness of 1,500 gm/cm². I have observed that wolves were not supported by snow that had a hardness of 400 gm/cm², but cracked the surface when it had a hardness of 600 gm/cm² and only scratched the surface when it had a hardness of 900 gm/cm².

I believe it significant that the only wolf-caribou contact I observed on the fawning grounds occurred 2 kilometers north of Fawn Lake camp on 10 June 1958 when a wolf picked up what appeared to be a fawn that had become mired in a zaboïs and died.

On 11 June, when the nursery bands vacated the immediate vicinity of Fawn Lake for higher ground to the northwest, the snow, which still covered about 40 per cent of the ground, had suddenly become soft with surface hardnesses ranging from 100 to 1,000 gm/cm².

DOE—FAWN RELATIONSHIPS

The new-born fawns divide their time between sleeping, resting, following the female, suckling, and attempts at grazing. Sleeping and resting periods vary from 15 minutes to 1 hour. Suckling periods usually last only about 10 to 20 seconds, but one fawn, after a 40-minute nap, suckled continuously for 2 minutes, the longest period I observed. When the fawn terminates the suckling period, it frequently stands quiet alongside the doe and she licks its anal region or its face. When the doe terminates the period, she usually simply steps over the fawn and moves off, frequently to a new grazing spot a few meters away. If the fawn is on its feet and does not follow by the time she has gone about 10 meters, she usually turns her head and bobs at it. If it is lying down when she moves off she occasionally will get as far as 90 to 100 meters away, grazing slowly, before returning. I observed one doe that had slowly drifted some 100 meters away from her fawn who was left lying down. The fawn stood up and the doe, upon seeing the movement, immediately gave the alarm pose. She held the pose for several seconds, then slowly circled downwind of the fawn and came up to it.

The usual attitude assumed by suckling fawns is essentially similar to that which occurs in other ungulates. I have several times observed fawns suckling, apparently with success, from behind the doe, between her legs. Although the fawn usually initiates suckling, I have observed a doe, after lying near her resting fawn for 30 minutes, get up and nuzzle it until it stood up and suckled.

For a period of unknown length after birth a fawn will apparently follow any female who bobs her head at it. At Fawn Lake I observed a doe and new-born fawn approached by another doe while the first doe was feeding. The fawn tottered over to the second female and was received with a lick and a nuzzle. This second female moved away, the fawn followed; the presumed mother followed both. The second female would stop, look back at the fawn and bob her head until it caught up with her. They moved in this fashion for about 100 meters. Then the presumed mother moved between the fawn and the second female and assumed the attack pose when the second female attempted to move past her towards the fawn.

I have twice observed a doe and fawn being followed at about 25 meters distance by another female who was giving voice to the gurgling grunt used by does when searching for their fawns. In these cases the extra female followed the pair for at least 2 kilometers. The does with fawns gave every indication of attempting to avoid or outdistance the

extra female. Several times during the summer I observed two does and one fawn, three does and two fawns or four does and three fawns travelling or resting together as a unit. This situation has been observed too often to be coincidence. In several cases I could not tell which fawn belonged to which doe. In these groups the fawns appeared to follow first one doe and then another. To these extra females I have given the name "assistant mothers." Since postpartum caribou, as noted above, have such a well-developed instinctive behavior pattern for attracting new-born fawns, and since I have observed does and week-old fawns followed by a single female who was grunting in the manner characteristic of caribou when searching for a lost fawn, I strongly suspect that these "assistant mothers" are does who have been deprived of their fawns at an early date and who have attached themselves to a doe-fawn pair.

When female caribou are forcibly deprived of their new-born fawns by a human they exhibit a characteristic reaction. At the first sight of an approaching man they get up and move about 10 or 20 meters away from their fawn. If the man approaches closer they usually trot away when he gets within 100 or 200 meters of them. If he continues and reaches the fawn the doe frequently will approach as close as 70 meters and circle back and forth at a fast trot or a gallop. Frequently they will trot swiftly directly toward the intruder, veering off when about 25 to 30 meters away. If the human carries the fawn away the doe will follow, sometimes as close as 100 meters, but more often up to one-half kilometer away. The deprived female, highly sensitive to visual and scent stimuli, may remain in the vicinity for one or even two days.

The duration of this induced period of heightened sensitivity depends, I believe, upon the presence of other caribou in the area. When many other caribou are present the deprived doe does not linger as long as when only a few scattered caribou or none are in the vicinity. When there is a large maternity band present the deprived doe moves back and forth through the band from one edge to the other, constantly uttering low gurgling grunts. Such a doe, deprived of her own fawn by any agency, will attempt to kidnap any fawn that comes in her path. Consequently a maternity band or false nursery band presents a continuous spectacle of does bobbing their heads trying to get fawns to follow them, not only their own fawns but others as well. Therefore I believe that adoption of lost fawns by does deprived of their own fawns is quite common in caribou, at least during the peak of the fawning season. How long this situation obtains can only be ascertained by observing marked animals. (It is so easy to call recently deprived does to within 25 or 30 meters of an observer by imitating a fawn blat that this procedure might have possible value as a method of censusing the number of de-

prived does in a band, or in tolling them to within range of drugged arrows for immobilizing and subsequent marking.)

While the deprived does are receptive to strange fawns, does with fawns of their own are antagonistic toward strange fawns. I have observed a doe, lying down in a maternity band, give the threat pose (with head only) to a new-born fawn that tottered over toward her. It was about one meter distant when she assumed the pose. It immediately turned and tottered away from her. Thus it would seem that not only is the threat pose a true instinctive action, but my interpretation of it as a flight releaser in the threatened individual seems logical. I have also observed a doe with fawn strike viciously with her forefoot at a strange new-born fawn that wandered close to her. The action was quite similar to that of digging a feeding crater. I have observed adult buck domestic reindeer in Alaska, without antlers during the winter, rear on their hind legs and strike at each other with a similar action. I have also observed a caribou doe with fawn lower her head to the attack position and "hook" at a strange fawn that wandered too close. The distance at which a strange fawn is tolerated seems to vary with the degree of crowding of the maternity or nursery band, but appears to be no closer than about 3 or 4 meters. When the fawns are young a nursery band, even when moving, consists of doe-fawn pairs spaced equidistant from each other. Thus it seems that a doe with new-born fawn has a sort of moving, defended territory set up around her. It would be interesting to know if this territory is centered on her head, udder or entire body.

It is instructive to note the differences in post-natal behavior between caribou and red deer. Darling (1937) reported that red deer fawns in Scotland were left by themselves for the first few days of life and were visited by the doe only about twice a day to be suckled. He observed very little apparent maternal solicitude. Such striking differences in doe-fawn relationships between red deer and caribou suggest corresponding differences in levels and sequences of endocrine activity. These observed behavioral differences should also serve to warn against interpretation of caribou behavior within the same frame of reference as herds or aggregations of domestic cattle. Moreover, since Nasimovich (1956) recorded several thresholds of tolerance to nival factors in Eurasian wild reindeer markedly higher than I observed for Canadian caribou (Pruitt, 1959), and since domestic reindeer are more sedentary, phlegmatic and gregarious than wild caribou, I suspect that extreme care should be used in any attempt to interpret caribou behavior within the same frame of reference as wild or domestic reindeer.

MISCELLANEOUS BEHAVIOR OBSERVATIONS

Among female caribou possession of antlers carries substantial social dominance. I have watched antlered does intimidate unantlered yearlings and does. At Tyrrell Lake on 22 May 1958 I observed a band of seven does, six with antlers and one without. The doe without antlers was frequently intimidated by individuals possessing antlers. She rested apart from the remainder of the group for about half an hour in one instance and then rejoined it. She was immediately repulsed by two antlered does assuming the threat pose. Near Spruce Grove Lake on 3 June 1958 during gale winds and blowing snow, I observed a band of 18 caribou feeding, resting and chewing their cud on a partially sheltered slope of a hill. Four adult does of the band were without antlers. One antlered doe approached a non-antlered doe who was lying down and appeared to force her to get up and move. The antlered doe then lay down in the vacated snow-free spot.

During the fawning period, however, I could detect no advantage in the possession of antlers by females. The motivations associated with the new-born fawn are apparently strong enough to outweigh the advantage of antlers. For example, on 6 June 1958 at Fawn Lake I observed an antlerless doe with fawn assume the threat posture and charge an antlered doe without fawn that ventured too near. The antlered doe gave way.

During late May in the vicinity of Tyrrell Lake the bands of migrating bucks exhibited two distinct types or stages of antler growth. There was a short type, consisting of a burr, a short horizontal brow tine and a short main beam that was almost at right angles to the burr. On side view the heads of these animals resembled white sheep (*Ovis dalli*) ewes. The other type noted consisted of a burr, an upward sloping brow tine and a long (50 or 60 cm.) main beam which swept back, up and out. Size of the developing antlers seemed to bear no relationship to social dominance within the band; indeed, the individuals with less developed antlers (the first type) appeared to have a slight dominance over those with long growing main beams. Do the antlers become more sensitive as they elongate? And, therefore, are these individuals more fearful of contact than are the ones with only short, thick nubs?

Several investigators have remarked on the state of near-insensibility caribou sometimes acquire when asleep (cf. O. J. Murie, *op. cit.*: 30). On 11 February 1958 I observed this condition. Mr. Gus Burchenski of Saskatchewan Government Airways and I were flying in a light, ski-equipped aircraft east of Wapata Lake in northern Saskatchewan when

we noticed a band of eight caribou on a lake ($58^{\circ}52' \text{ N. Lat.}, 105^{\circ}27' \text{ W. Long.}$). As we passed over they jumped and ran, leaving one of their number curled up on the snow. We circled twice, then "buzzed" low with flaps down and confirmed that it was a caribou lying curled up. We landed and taxied up, stopping with one wingtip about three meters from the animal. We sat in the aircraft and debated whether we should take photographs or whether we should attempt to pick it up and carry it back to camp, for the animal appeared to be unconscious, although it was obviously breathing. Suddenly the caribou, a fawn, looked up and if ever a caribou had a surprised expression on its face, this one had. It had been asleep. It bounded up and was off like a flash.

Darling (1937) recounted a fascinating incident which illustrated how red deer relied almost entirely on scent as a sensory window. The animals fed undisturbed, moving to one meter of him. On 19 April 1958 near Stony Rapids during the spring migration I had a similar experience with caribou. I was observing migrating bands moving through scrubby jack pine and aspen on a burned-over rocky ridge. I was wearing a dark green parka with the hood up and was standing motionless close beside a ten-foot high pine. A band of six does and two fawns approached me, walking downwind. All passed to one side of me. One doe was so close that I slyly reached out and gently patted her rump as she walked by. She apparently thought it was a twig or a branch brushing against her for she gave no indication of perceiving the touch. After passing by me they all happened to angle slightly away and continued on without catching my scent even when past me.

On 12 July 1958 near Fawn Lake I observed the behavior of a band of seven adult bucks at a "lick." The lick was the bare earth of a frost boil or spot medallion (Sochava, 1944; Troll, 1944). This particular frost boil differed from the usual boils of the region in being composed of fine particles of parent material which tested on the fingers as silt and clay, no sand or pebbles. Other boils examined consisted of sand, silt and pebbles. The surface of the boil in question was smooth and hard packed; edges of all tracks were rounded and smoothed, probably from much licking. Most frost boils have a low ridge or dyke surrounding them, but this one was sunk slightly below the level of the bases of the surrounding tussocks. Most frost boils have a scattering of primary invading plants on them, but this one was bare. A sample of the earth has been submitted to the Canadian Wildlife Service for possible chemical analysis.

The seven bucks had been under observation for about two hours. They had rested together, fed, crossed a small stream and had shown a

remarkable lack of fear of man. My wife and I had maneuvered back and forth around them in a series of fruitless attempts to make them exhibit excitation jumps. On one of their dashes away from our scent trail they all suddenly stopped in their tracks and began to eat the earth of the frost boil described above. While they were engaged in this activity I was able to approach within 100 meters of them.

Although no signs of strife or attempts to enforce any social rank had been evident in the two hours the seven bucks had been under observation, within a few minutes after their arrival at the lick several threats and retreats had been made. This heightened sensitivity to the close approach of other individuals agrees with the observations by Altmann (1952) of wapiti although since all the caribou were adult bucks there was not such a marked social hierarchy as she observed when a lick was in use by individuals of different sexes and ages. Adolph Murie (1934) observed similar antagonism between individual moose at salt licks.

Altmann (1956) compared various aspects of social behavior in wapiti, moose, chamois (*Rupicapra rupicapra*) and wild pig (*Sus scrofa*) by means of a series of tables. In order to add the Barren-Ground caribou to this list I have summarized its behavior (Tables 2 through 6) under the same topical outline that she used.

TABLE 2. SOCIAL ORGANIZATION OF CARIBOU IN SUMMER.

Size of Group.....	Medium to large
Sexes.....	Almost completely segregated
Spacing:	
In group.....	Close
Between groups.....	Wide
Leadership:	
Male group.....	??
Female group.....	None evident
Communication:	
Long distance.....	Silhouettes, poses
Short distance.....	Poses
Reaction to Disturbance.....	Variable, delayed to immediate
Getaway type.....	Flight, in unison (cf. Crisler, 1956)
Schedule:	
Feeding.....	Early morning and late afternoon
Resting.....	Middle of day. Night?

TABLE 3. SEASONAL CHANGES IN CARIBOU GROUP STRUCTURE.

Winter.....	Small bands, in-group spacing wider than in summer.
Spring.....	Small to medium bands (10-100), occasionally large aggregations, sexes generally segregated.
Summer.....	Extension and aggregation of Nursery Bands. Males in separate bands.
Fall.....	Breeding males join small bands of females, fawns, immatures and subadults.

TABLE 4. ROLE OF MALE CARIBOU DURING RUT.

Prerut.....	Rub velvet, preliminary or excitation sparring, no great antagonism between males.
Rut.....	Males leave bands, become solitary, then antagonistic. Rejoin the bands of females, fawns and immatures. Display, and court females.

TABLE 5. SOCIAL TEST SITUATIONS FOR CARIBOU.

Narrow trail.....?	
River crossing.....	Social facilitation evident, female and fawn usually initiate crossing but only because female with fawn is more sensitive to stimuli than are males.
Saltlick.....	Males make sporadic attempts at dominance. Females—?
Severe storm.....	Because of habitat characteristics storms do not present tests of sociality. Caribou generally drift with a severe wind.
Miscellaneous.....	Males—see discussion of antler types in spring. Females — possession of antlers carries dominance, except when nonantlered doe has a fawn.

TABLE 6. ROLE OF YOUNG CARIBOU IN GROUP.

Birth.....	In a maternity band.
Activity.....	Female and fawn join a nursery band. Fawn is never left alone for more than a few minutes. Female remains within about 100 meters.
Sleep.....	? Resting: facing downwind, fawn rests on lee side of female.
Herd Integration.....	Nursery bands form nucleus of "Throngs" and summer migration.
Enforcement of signals.....	Female nudges newborn fawn. Head bobbing an especially strong releaser. Females grunt, fawns blat.
Reaction to intruder.....	Flight
Games and playing.....	Much running about, but no social play until about one month old.

SUMMARY

A one-year field study of the Barren-Ground caribou (*Rangifer arcticus*) in northern Manitoba, northern Saskatchewan and the Northwest Territories, Canada, included many aspects of behavior in relation to environment as well as to other individuals. Because their extensive yearly migrations encompass a wide variety of habitat types, regional synchrony of physiological and behavioral rhythms was judged to be of special importance to species survival.

Threat (muzzle extended, antlers back), attack (head lowered, antlers presented), head bobbing (releases following in fawn), alarm (one hind leg spread, head erect) postures and the excitation jump (rearing, pivoting, interdigital glands discharge) are described, illustrated and discussed in terms of the releaser concept.

Nival factors and food supply govern winter activity and migrations. The search for suitable snow and the location of forage under the snow is described in terms of an appetitive-consummatory behavior sequence.

The role of the threat posture as a part of male courtship display is discussed.

Fawning behavior is described. Gravid females congregate in maternity bands which frequent characteristic topographic and nival situations. Does with young fawns congregate in nursery bands. Nursery bands coalesce and become an important social aggregation in summer.

Miscellaneous observations are presented on: significance of antlers in social contact, profound sleep, reaction to insect attacks, dependence on scent, and behavior at a "lick."

Several aspects of caribou behavior are tabulated to complement Altmann's (1956) summary for wapiti (*Cervus canadensis*), moose (*Alces alces*), chamois (*Rupicapra rupicapra*) and wild pig (*Sus scrofa*).

РЕЗЮМЕ

В продолжение одного года полевых исследований по экологии тундряных карibu (*Rangifer arcticus*) в северной Манитобе, северном Саскачеване и Северозападных Территориях Канады изучались многие аспекты поведения животных как по отношению к среде, так и во взаимоотношениях между отдельными особями. Было установлено, что региональный синхронизм физиологического ритма и ритма поведения является особенно важным для выживания вида. Описаны следующие проявления, с обсуждением их общественно-отводных функций: угроза, атака, кивание головой, тревога, возбужденные прыжки.

В аппетитно-потребительной последовательности поведения описаны процесс разыскивания подходящего снега и его разрывание для добычи лишайникового корма. Хионические факторы, вместе с запасами корма, управляют зимней деятельностью и миграциями.

Обсуждается роль угрожающей позы при спаривании животных.

Описывается поведение животных при отеле. Беременные самки группируются в масеринские стада, которые держатся в местностях со специфичной топографией и снежностью. Самки с телятами группируются в воспитательные стада. Обсуждается значение воспитательных стад.

Обсуждается значение рогов в общественном контакте между особями.

Приводятся разнообразные наблюдения относительно глубокого сна карibu, реакции на атаки насекомых, зависимости животных от их нюха, как чувствительной отдушины, а также поведения на солонцах.

Некоторые аспекты поведения карibu приводятся в форме таблиц, представляющих собою дополнение к резюме АЛЬТ-МАНА /1956/ относительно вапити (*Cervus canadensis*), лося (*Alces alces*), серны (*Rupicapra rupicapra*) и кабана (*Sus scrofa*).

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