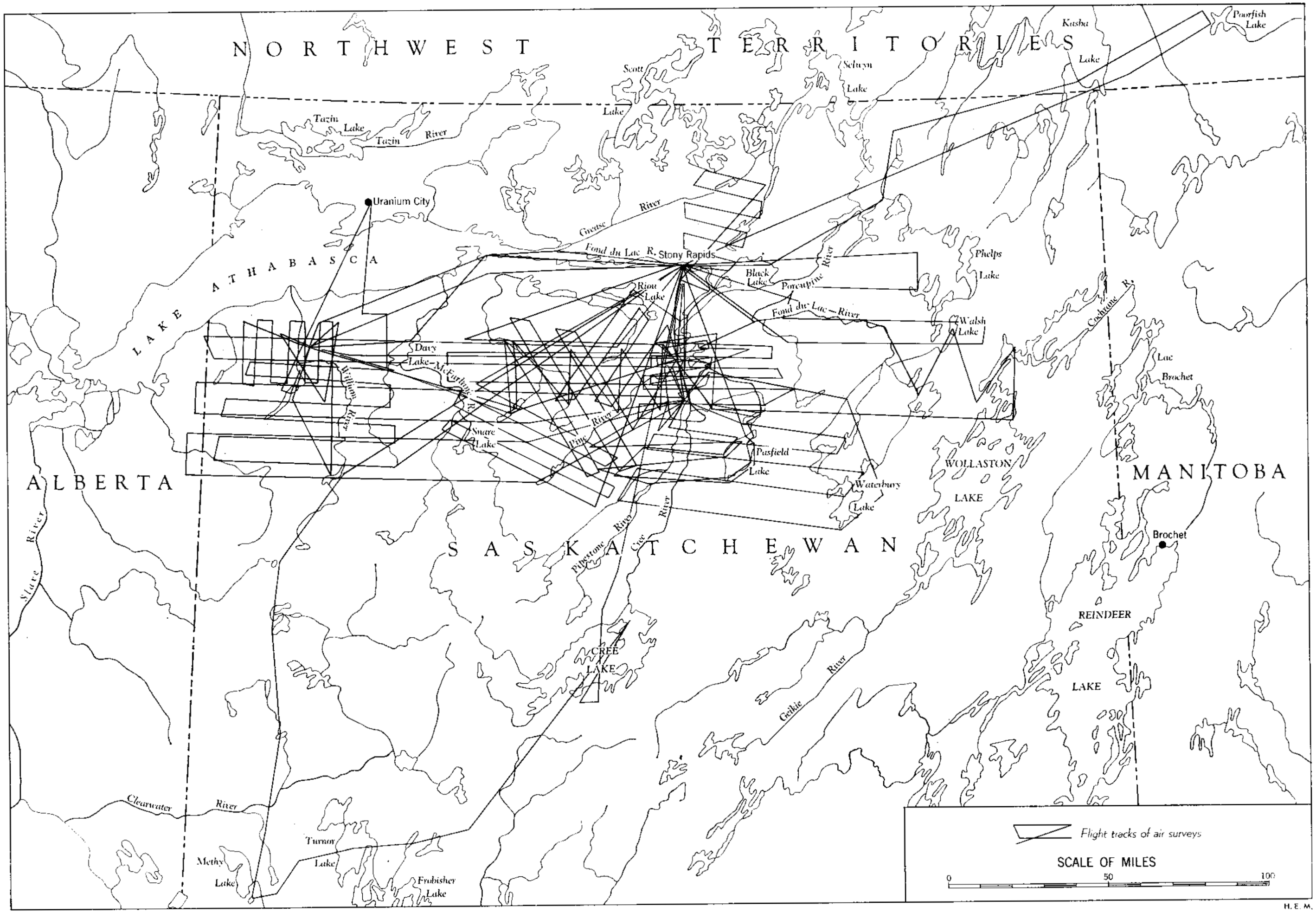

Fig. 1. Northern Saskatchewan and adjacent region, showing flight tracks of air surveys.

SNOW AS A FACTOR IN THE WINTER ECOLOGY OF THE BARREN GROUND CARIBOU

(*Rangifer arcticus*)

William O. Pruitt, Jr.*

ONE of the truisms of biology is that an animal cannot be considered apart from its environment. Yet in the brief history of northern biological research and especially in wildlife management this truism and its implications have frequently been forgotten in the haste to apply techniques used by biologists and wildlife managers in temperate zones. Too few biologists and wildlife managers have been cognizant of the fundamental ecological differences between the regions where the snow cover is permanent in winter and those where the snow cover is intermittent or lacking.

In the Subarctic many aspects of the animals' environment have an ecological effect quite different from that of the same aspects in the temperate zone. For example, it is widely known that deep snow or icing conditions seriously affect whitetail deer populations, but deer are subject to nival factors for only a short period of the year. In the Arctic and Subarctic the Barren Ground caribou encounters snow as an integral part of its environment for at least 8 months of the year. Yet subarctic snow is one of the least understood of natural phenomena and the ecological effects of a permanent winter snow cover have been virtually ignored in North America. Only a few northern biologists have fully understood the ecological importance of the arctic and subarctic snow cover. Possibly the first to bring this to the attention of biologists working only in the temperate zone were the naturalists Seton (1909) and Dugmore (1913). Others who have contributed substantially to our understanding of the ecological importance of snow have been Formozov (1946, 1948) and Nasimovich (1955) in the USSR, Vibe (1954, 1958) in Greenland, and Siivonen (1952, 1956) in Finland. A number of earlier Russian workers are cited by Formosov and Nasimovich. Murie (1935) noted the importance of snow in the migration and seasonal distribution of Alaska caribou, which are essentially mountain animals. Grinnell (1924) reproduced a letter dated November 17, 1846 from Thomas Lincoln of Dannysville, Maine to John James Audubon in which the nival environment of the woodland caribou (*Rangifer caribou*) was outlined in detail. Edwards and Ritcey (1956) discussed the effects of snow depth on the altitudinal migration of moose (*Alces alces*) in British Columbia and Edwards (1956) correlated snow depths and trends in ungulate populations.

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Description of the region

The study was made during the winter 1957-8. The region in which the snow cover was studied consisted of a large part of the northern quarter of the Province of Saskatchewan, a small part of the southeastern part of the District of Mackenzie, and a small part of the southwestern part of the District of Keewatin, N.W.T. (Fig. 1). The extensive survey included the region from near the mouth of William River on the south shore of Lake Athabaska east-northeastward to the vicinity of Poorfish Lake, N.W.T., thence south- and southwest-ward to the vicinity of Walsh, Cree, Frobisher, Turnor, and Methy (Lac la Loch) lakes, Saskatchewan. The extensive snow survey also included, for comparative purposes, a transect beyond the limit of trees into the tundra from the vicinity of Kasba Lake to Poorfish Lake, N.W.T. Intensive observations were made in the vicinity of camps situated at (a) 58°37′N., 105°50′W.; (b) 58°49′N., 105°52′W.; (c) 58°53′N., 109°08′W.; and (d) 58°23′N., 105°51′W. Observations on spring movements of caribou were made at 59°15′N., 106°14′W. and in the vicinity of the village of Stony Rapids, Sask. (59°15′N., 105°50′W).

An area of this size exhibits a wide variation in topography, vegetation, use by caribou, and history of use by man. On the basis of topography and geology two broad divisions can be recognized (Alcock 1936): (1) the region north and east of Lake Athabaska-Fond du Lac River-Black Lake, which has a great deal of exposed bedrock, is very rugged and has many elongated and deep lakes with steep, frequently precipitous banks. The country rock of this region is composed mainly of granites, gneisses, limestones, and volcanic lavas. The northeast-southwest orientation of the lakes has a great influence on the direction of caribou migrations through the region; (2) the region south of that outlined above has only scattered outcrops of bedrock (except along the south shore of Fond du Lac River where many high outcrops of Athabaska sandstone occur) and is mainly sandy and rolling. A prominent feature of the central part of the region is an extensive series of drumlins oriented north-south in the southern part of their range, changing to northeast-southwest and finally to east-west in the region just south of Stony Rapids. The region has several prominent eskers. A large part of the surface is covered by water in the form of marshes, rivers, and lakes in all stages of deposition, drainage, and maturity.

On the basis of vegetation two broad divisions also can be recognized. They agree quite well with the main topographic divisions and were identified by Halliday (1937) as the Northern Transition Section and the Northern Coniferous Section, respectively, of the Boreal Forest Region. The entire region, with the exception of the tundra stations to the northeast, is included in the Hudsonian Biotic Province of Dice (1943).

The use of the region by caribou varies widely and, until now, inexplicably. Generally, the caribou come into the region from the north and northeast in October and November and remain during the winter until leaving for the north and northeast in April or May. During some years the caribou winter in a small number of fairly dense, but discrete, concentrations, whereas during other winters they are thinly scattered over large areas. In some years they range south to Cree Lake, even going as far as Turnor or Frobisher lakes; in others they remain close to Lake Athabaska and Fond du Lac River. They may remain in one and the same general region a whole season; in other winters they may shift their wintering grounds several times.

On the basis of the use of the region by man one salient observation stands out — the amazing completeness of the destruction by fire of mature, stable vegetation associations. From Lake Athabaska-Fond du Lac River-Black Lake south to Cree Lake and Methy Lake, and from Black Lake-Pasfield Lake-Cree Lake west to the Alberta boundary there is scarcely a square mile that has not been burned at least once and often many times. The only remnants of unburned vegetation exist on islands, attenuated peninsulas and possibly in some muskegs. Repeated burning in conjunction with the sandy soil has caused quite xeric conditions to develop, resulting in jack pine *(Pinus banksiana)* becoming the most common tree species. The herbaceous layer is poorly developed. The forest floor is usually bare, needle-covered, or has a thin growth of lichens. The influence of this burned, xeric condition of the winter range on the size and density of the caribou population cannot be over-emphasized, particularly in the light of the results of the snow studies given below.

Methods

Two basic techniques were used for this study. First, the distribution of caribou was determined by extensive air surveys. Numerous flights, totalling some 8,850 miles, were made in order to plot accurately the distribution of wintering caribou (Fig. 2). During the middle of the day in winter caribou generally rest in small bands on frozen lakes. Flights were usually made during the hours from 0900 to 1500 in order to take advantage of this behaviour and were flown at 800 to 1,000 feet above the ground. Tracks and numbers of individuals seen were noted along the flight lines, which had been plotted on topographic maps. This information was collated after each flight so that any shifts of the areas of caribou concentration could be detected.

Second, a series of snow observations were made at stations installed at frequent intervals from December 10, 1957 to April 11, 1958. Snow observations have been made at 114 formal and many informal stations (Fig. 3). The majority of stations was installed between February 16 and 28, 1958. The stations were generally arranged in pairs, one at the north or northwest edge of a lake or occasionally off the south or southeast shore of a peninsula or island, so as to sample snow that had not been violently disturbed by wind. The other member of the pair was a forest station situated on the north or northwest shore far enough from the lake shore so that drifted snow was avoided. Each set of snow observations took

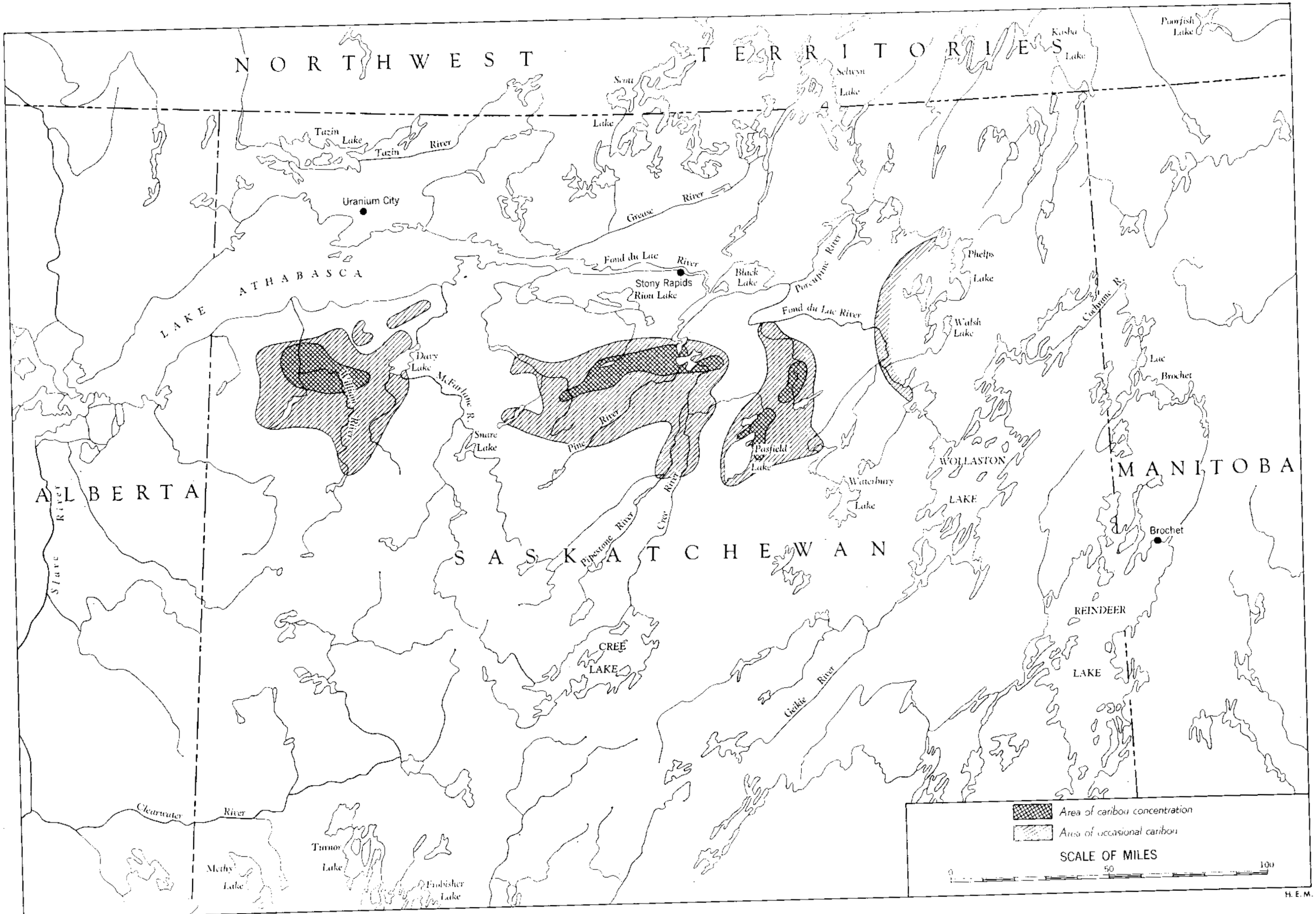

Fig. 2. Northern Saskatchewan and adjacent region, showing distribution of wintering caribou. Heavily shaded regions represent the areas of concentration and lightly shaded regions those of occasional caribou. The unshaded region represents the area of no caribou.

about 30 to 40 minutes to complete. Every effort was made to insure that forest stations were in situations that were similar as regards vegetation and topography and that lake stations were similar as regards exposure to wind.

The Committee on Snow and Soil Mechanics of the National Research Council of Canada kindly lent to the Canadian Wildlife Service a set of Standard Snow Instruments (Klein *et al.* 1950), which I used during this study. At each station the following data were taken: location of station, date, habitat, air temperature, pukak temperature (Pruitt 1959), vertical hardness of the snow surface, total depth, ground vegetation, and hardness of the snow to track depth. This last measurement was an improvisation that consisted of recording the resistance of the snow to pressure sufficient to make an artificial caribou track of a depth comparable to actual tracks that could be found in the vicinity. A vertical profile of the snow cover was exposed and the thickness, hardness, density, and grain size of each layer were measured and recorded. Since the Standard Snow Instruments were used, hardness was recorded as the pressure in gm. per sq. cm. necessary to collapse the structure of the snow of each layer, and density was calculated from the weight of a 500-cc. sample from each layer. In this system, therefore, hardness is a measure of the degree of cohesion between snow particles. It is an empirical expression of the condition dependent on crystal size, shape, contiguity, and strength of inter-crystal bonds. Calculations of density result in expressions of the ratio of the number of water (i.e. ice) molecules to air molecules in a given volume of snow. Grain size and type were recorded in reference to the classification put forward by the Committee. The number of layers in the profiles varied from one or two to as many as eight. A glossary of specialized snow terms is appended to this paper.

Results

A. Extensive survey

The survey flights revealed that the region could be divided into three categories on the basis of caribou distribution. First it must be understood that individual Barren Ground caribou may be found almost anywhere on the mainland of northern Canada at any season of the year. Some caribou winter far out on the tundra and others spend the summer well within the limit of trees. Therefore, even if a region is classified as having "no caribou", a very rare individual (the so-called "odd caribou" in Canadian parlance) may still be present. With this reservation in mind, most of the region studied was classified as having "no caribou." Next there was a series of caribou concentrations, or areas where every lake had caribou resting on it during the middle of the day, and where the snow cover was cut up by tracks and trails and pocked with feeding craters. Surrounding these areas of high concentration were fringe or marginal areas containing caribou in densities classified as "occasional." On survey flights over such

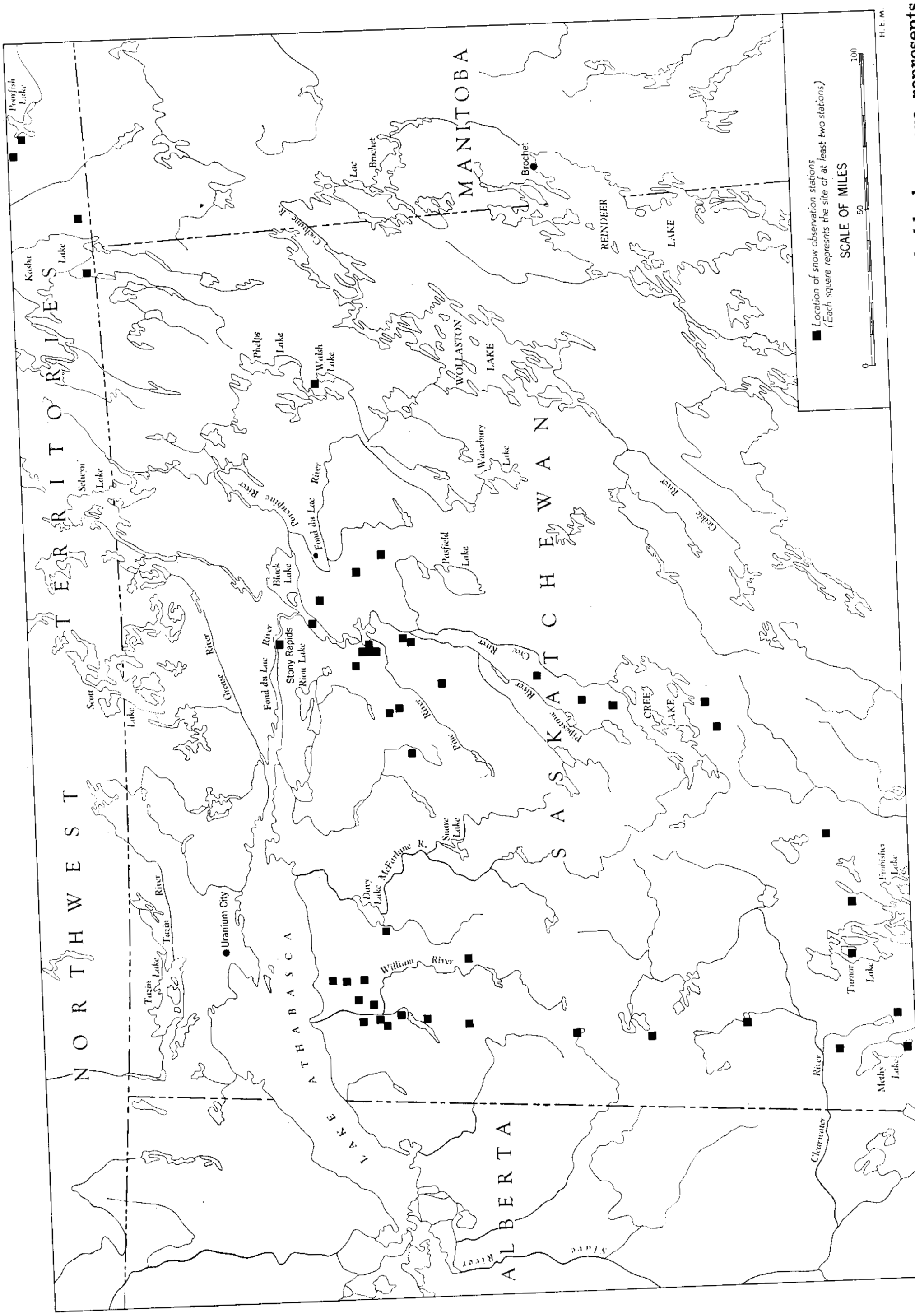

Fig. 3. Northern Saskatchewan and adjacent region, showing locations of snow observation stations. Each black square represents the site of at least two stations.

areas the observer sees only one or two tracks or trails every 2 or more miles. The boundary between the latter two divisions is usually quite sharp and is visible from the air as a marked difference in the appearance of the snow surface. These areas of concentration are outlined on Fig. 2 for February 1958. The heavily shaded regions represent the areas of concentration and lightly shaded regions those areas of occasional caribou.

Although an effort was made to establish snow stations in a systematic or grid pattern over the area, this scheme could not be adhered to. First there was the problem of poor maps, the Lake Athabaska sheet (National Topographic Series, Sheet 74 NW.) being particularly unreliable. Since the majority of proposed station sites could only be reached by light ski-equipped fixed-wing aircraft, there was a lower limit to the size of lakes on which it was possible to land and to take off. On account of the irregular outlines of the areas of varying caribou concentration many stations were shifted and established in, rather than outside of such areas. This applies particularly to those established by travelling on snowshoes or by dog team from the field camps, which were successively established in the areas of densest caribou concentration. Fig. 3 shows the positions of snow stations. Each square represents the site of at least two stations.

Forest or tree cover has a marked effect on reducing wind velocity (Geiger 1950). Wind is also one of the most effective factors in changing the characteristics of the snow cover. Therefore one would expect to find the snow cover on lakes consistently more modified than that in the adjacent forest. I found this to hold true. Therefore, data from lake, marsh, or non-forest stations have been kept separate from those from forest stations.

Table 1 gives mean values at the stations, segregated according to forest and lake and degree of caribou concentration for (a) the hardness of the hardest layers in the snow profiles, (b) the density of the densest layers, and (c) the thickness of the cover.

Inspection of the summary of a portion of the data in Table 1 reveals several important facts.

(1) The areas of heavy caribou concentrations were characterized by snow with the following features: (a) it was quite soft, the hardest layers ranged from 6.5 to 60 gm./sq. cm. for forest and from 50 to 700 gm./sq. cm. for lake stations; (b) it was light in weight, the densest layers ranged from 0.13 to 0.20 for forest and from 0.13 to 0.32 for lake stations; (c) it had a thickness below a critical 50 to 60 cm. at forest stations.

(2) The areas of occasional caribou were characterized by snow with these features: (a) it varied from soft to hard, the hardest layers ranged from 60 to 3,000 gm./sq. cm. for forest and from 50 to 6,000 gm./sq. cm. for lake stations; (b) it was denser than that under (1) and varied from 0.16 to 0.48 for forest and from 0.18 to 0.92 for lake stations; (c) thickness varied from 32 to 62 cm. for forest and from 20 to 38 cm. for lake stations.

(3) The area of no caribou was characterized by snow with these features: (a) it varied from occasionally soft to frequently very hard, the hardest layers ranged from 35 to 7,000 gm./sq.cm. for forest and from

150 to 9,000 gm./sq.cm. for lake stations; (b) it had occasionally extremely dense layers, the densest layers ranged from 0.16 to 0.92 for forest and from 0.17 to 0.92 for lake stations (0.92 is the density of freshwater ice); (c) thickness of the cover at forest stations was well above the critical value.

B. Intensive Observations

All snow covers undergo a process of maturation during which their morphology (thickness, hardness, density, grain size and structure) undergoes a series of well-known and fairly well-understood changes (Bader *et al.* 1954; Klein *et al.* 1950). These changes are believed to be the result of temperature and moisture gradients extending from the substrate, whether earth, rock, freshwater ice, or sea ice, through the snow cover to the air above. Striking as these changes are, their sequence can be completely upset and changed by wind strong enough to move the particles of the snow cover. Whenever wind is combined with high temperatures, or when liquid precipitation with its great supply of heat occurs, the changes produced in the snow cover are very conspicuous.

Such changes occurred in northern Saskatchewan during the winter of this study. From January 4 to 8, 1958 a sequence of weather disturbances passed over the region. In the neighborhood of Cree Lake rain fell for 5 hours at one time during this period, probably on January 4, according to Mr. Martin Engemann, resident of the region. This was followed by a cold snap, which caused an ice layer to form on the snow cover. The ice layer was found at the stations to the southwest, west and northwest of Cree Lake. On a flight on January 4, from Stony Rapids to the camp at 58°37′N., 105°50′W., the aircraft encountered rain at approximately 800 feet above the ground. This period of precipitation was followed by high winds (recorded as fresh to strong) and temperatures as high as +2°C., and later by the normal of —18°C. and lower. Before the storm the snow cover in the vicinity of the camp (in an area of heavy caribou concentration) had a hardness of the order of 6 to 15 gm./sq.cm. and a density of 0.05 to 0.15. After the storm the hardness at adjacent or comparable stations was of the order of 20 to 25 gm./sq.cm. and the density 0.12 to 0.18. The time of the storm and the period immediately following it were marked by a definite movement of caribou out of the area, probably northward. Counts of caribou on the lake where the camp was situated dropped from as many as several hundred individuals per day to five or ten per day. Survey flights on January 12 and 13 revealed that the southern boundary of the area of heavy concentration was some 15 to 20 miles north of the camp, whereas before the storm it had been an approximately equal distance south of the camp.

A similar sequence of events occurred on February 6 to 8, 1958 in the vicinity of the camp at 58°49′N., 105°52′W. Before the storm the hardness of the hardest layer of forest snow was of the order of 6 to 20 gm./sq.cm. and the density of the densest layer 0.03 to 0.17. After the storm the

Table 1. Hardness of hardest snow layers (gm./sq.cm.); specific density of densest snow layers; depth of snow (cm.).

Density of caribou	Concentration	Occasional	No
		Forest	
Snow hardness			
Mean	34	469	993
Range	6.5 — 60	60 — 3,000	35 — 7,000
Number of stations	19	12	23
Snow density			
Mean	0.17	0.25	0.31
Range	0.13 — 0.20	0.16 — 0.48	0.16 — 0.92
Number of stations	19	12	23
Snow depth			
Mean	45	45	56
Range	19 — 59	32 — 62	31 — 82
Number of stations	20	11	23
		Lake	
Snow hardness			
Mean	291	1,954	3,016
Range	50 — 700	50 — 6,000	150 — 9,000
Number of stations	16	12	25
Snow density			
Mean	0.19	0.35	0.49
Range	0.13 — 0.32	0.18 — 0.92	0.17 — 0.92
Number of stations	18	10	25
Snow depth			
Mean	33	30	41
Range	21 — 43	20 — 38	19 — 46
Number of stations	16	12	25

hardness ranged from 5 to 40 gm./sq.cm. and the density from 0.12 to 0.20. This particular storm is of interest since it developed barchans on the camp lake. Again, the caribou concentration decreased markedly.

Individual bands of caribou move from areas of greater hardness to areas of smaller hardness, and from areas of higher density to areas of lower density, but it might be well to point out here that the hindrance effect of snow appears to be relative. Whereas there appears to be a critical upper limit for each of these characteristics, the hardness range that causes one band of caribou or the caribou in one area to move away, may, in other distant areas, be the hardness range into which a band will move from an area with a still greater hardness. This relationship applies also to density. The caribou's threshold of sensitivity to the hindrance effect appears to rise as the winter progresses and the snow undergoes its maturation process, resulting in a progressive increase in hardness and density. That is, a hardness that in early winter would cause an exodus of caribou from a region appears to be tolerated by them in late winter as long as the critical limit is not exceeded. Thus sequential snow-caribou correlations are necessary; isolated observations are probably of little value and indeed may be misleading.

It might also be well to point out that hard or dense layers in the snow cover appear to have different hindrance effects depending on whether the layer in question occurs near the centre or top of the snow cover or at the base. A very thin but hard layer on the surface of the snow cover has a far larger hindrance effect than the same layer at the base. Both adults and fawns were observed to sink 10 to 12 cm. in snow having a hardness of 400 gm./sq.cm. (58°49'N., 105°52'W., February 8, 1958), they broke through a layer with a hardness of 600 gm./sq.cm. and walked on the surface of a layer with a hardness of 1500 gm./sq.cm. The tracks of the adults measured 105 x 85 mm., without dew claws. (58°47'N., 105°56'W., February 10, 1958). The dew claws of caribou are not effective in providing flotation until the snow cover reaches a thickness of 3.5 to 4 cm. A snow observation station was established at a spot where caribou were observed to have difficulty in walking. The snow at this spot was 33 cm. deep and showed a critical layer 2 cm. thick extending from 17 to 19 cm. above the substrate. This layer had a hardness of 900 gm./sq.cm. and a density of 0.31. The hardness above the critical layer ranged from 1 gm./sq.cm. to 80 gm./sq.cm., and the hardness below the layer was 200 gm./sq.cm. Density above the critical layer ranged from 0.02 to 0.21 and below it was 0.14. (58°49'N., 105°52'W., January 28, 1958).

One must not assume that snow acts solely as a hindrance to caribou progression. Since the caribou is primarily a grazer, not a browser, its food supply must be excavated from beneath the snow cover. The act of pawing through the snow cover (digging a "feeding crater") is an integral part of the complex of behavioural patterns that govern the caribou. It gives every indication of being a "consummatory act" (Tinbergen 1951). Consummatory acts are repetitive, stereotyped actions that deviate little, if at all, from a set pattern. They occur after, and as a culmination of, longer periods of less circumscribed "appetitive behaviour", which is strongly influenced by environmental stimuli. This shows what a vital role such adaptations to snow must have played in the evolution of caribou, since consummatory acts are such primary ones as actual eating, nest construction, copulation, etc.

The usual feeding crater observed during the winter 1957-8 exposed an area of substrate approximately 15 by 35 cm. While pawing through the snow the caribou trampled, dug out or otherwise disturbed the snow in a patch approximately 1 by 2 metres. Regardless of the condition of the snow before being disturbed, after cratering its hardness and density increased markedly. A period of approximately 4 hours at very low temperatures is sufficient to "set" disturbed taiga snow to a hardness that will support the weight of a man (approximately 2,000 to 3,000 gm./sq.cm.

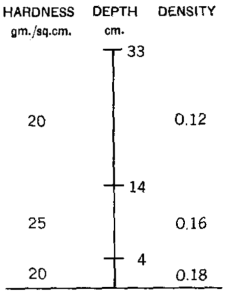

Fig. 4.

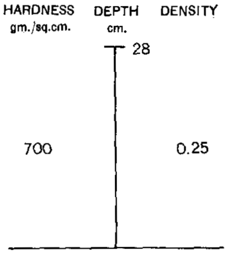

Fig. 5.

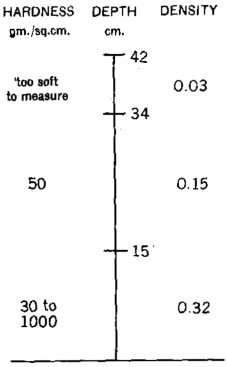

Fig. 6.

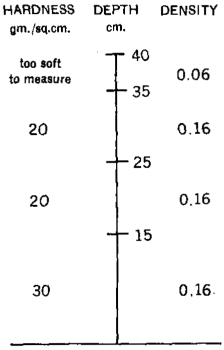

Fig. 7.

Fig. 4. Undisturbed snow, Jan. 5, 1858, at 58°37′N., 105°50′W.

Fig. 5. Snow excavated from a feeding crater, Jan. 6, 1958, approximately 300 yards from station of Fig. 4.

Fig. 6. Snow disturbed by crater excavation but not trampled, Jan. 28, 1958, on a heavily cratered and trampled jackpine slope at 58°49′N., 105°52′W.

Fig. 7. Undisturbed snow, Jan. 29, 1958, approximately 500 yards from station of Fig. 6.

hardness, Elsner and Pruitt 1959). In January 1958 I measured the snow at four stations with the results shown in Figs. 4 to 7.

I have observed that caribou will feed in a previously cratered area only once more, after which the snow becomes so hard that they move on to softer snow. I have observed and calculated that mature, open jack pine forest will show 366 craters per acre (904 craters per hectare), which means that a total of 732 craters can be dug per acre before the snow becomes too hard. Apparently on account of social interactions one acre rarely shows more than about 366 feeding craters at any one time. This number of excavations rather effectively covers the whole surface with disturbed snow. Another factor, that of variable temperature, enters the picture here, since at lower temperatures disturbed snow will set quicker and harder than at higher temperatures.

Since caribou use a given spot for feeding only twice, it is evident that this behaviour alone is sufficient to account for a large share of their daily movements in winter. Because on lakes the snow usually is not as deep as in the forest and especially since it is usually harder (its surface is frequently supporting caribou), wintering bands use snow-covered lakes as "escape cover" or "loafing cover." Undoubtedly, ideal conditions for escape or loafing cover would be provided by very hard lake snow. In order that such snow conditions develop the winds would have to be so strong that they would reach the feeding grounds through the trees and modify the snow there beyond the critical thresholds. The bands usually bed down more than 75 to 100 yards from shore. It is noteworthy that this is the distance to which the wind-shadow effect of mature spruce forest extends on a lake. Forestward within this shadow the snow becomes progressively more like forest snow; lakeward beyond the shadow it is harder and denser. The bands stay on the lakes during the middle of the day, usually from about 0900 until 1500 hours. During the bedding period caribou move around several times, each animal making a series of smooth semi-circular beds in the snow. When they move to feed they go to the nearest shore, and then return to their bedding ground or loafing cover. For the next feeding period they go to the same feeding area, or if the snow there is too hard they move beyond it until they encounter soft snow. In this fashion the bands feed at progressively greater distances from their loafing cover. Finally they pass the ridge and are in sight of the next lake and it is then used as escape or loafing cover. In this manner the bands of caribou move back and forth through the snow on their winter range.

C. Spring Movements

Since caribou appear to be responsive to variations in the hardness and density of the snow through which they wade during about two-thirds of their annual cycle, it logically follows that at least some aspects of their spectacular annual migrations are correlated with nival factors. This appears to be true.

The threshold of sensitivity appears to be reached by snow with a hardness of about 50 gm./sq.cm. for forest snow and 500 gm./sq.cm. for lake snow. The density threshold appears to be about 0.19 or 0.20 for forest snow and about 0.25 or 0.30 for lake snow. The depth threshold appears to be about 60 cm.

As the insolation increases in the spring the snow develops a sun crust ("na-hó-t(ch)ran" in the local Chipewyan dialect) and starts to settle. This settling is only the visible manifestation of morphological changes occurring in the snow cover. These changes are measured by the snow instruments as increases in hardness and density, although they are actually caused by growth of the snow particles with an accompanying decrease in particle number. At the time when these changes take place there also occurs a change in the behavioural pattern of the caribou. Individuals or small groups now frequently break away from a larger band and run or bound in a large circle. This behaviour is quite noticeable during air observation of tracks. It is noteworthy that bounding is characteristic of ungulates when they find themselves in snow above their critical depth. There may be a resemblance between this behaviour and the increased sensitivity to external stimuli during periods of thaw noted by Darling (1937) in red deer (*Cervus elaphus*).

In the spring when the forest snow attains a surface hardness of from 300 to 500 gm./sq.cm. and a density of the order of 0.30, the caribou react in the same way as that following a similar change produced by a winter storm: they move toward softer and lighter snow. Settling, crusting, and melting advance gradually through the taiga toward the limit of trees, herding the caribou along. Sometimes the progress of thaw is interrupted by meteorological events that cause intense freezing of the melting snow cover. At such times the snow becomes extremely hard. Surface hardness may rise to 3,000 gm./sq.cm. 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 along the hardness gradient, simply because the gradient no longer exists. The migration stops. The brittle crusts common at this time of the year under such conditions may be a factor deterring movement because of sheer discomfort or pain accompanying constant breaking through 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 is resumed along the hardness gradient.

On April 24, 1958, after the caribou migration had already passed through the Stony Rapids region, I flew a survey in northern Saskatchewan and southern District of Mackenzie (National Topographic Series, Sheet 74 NE., Black Lake and Sheet 75 SE., Wholdaia Lake). The ground in the vicinity of Stony Rapids was 90 per cent bare of snow, but approximately 30 to 35 miles to the northwest only the south slopes were bare. In the vicinity of Dunvegan Lake only qamaniq (Pruitt 1957, 1959) and steep south slopes were bare, lake surfaces were still white, and showed no signs of slush. This state of thaw occurred along a line running from approximately 60°N., 107°W. through the northern part of Wignes Lake and thence north of Ingalls Lake. In the region near Jardine, Rutledge, Brûlé, Atkinson, and Mountain lakes there was even 0.1 or 0.2 qali (Pruitt, 1958) remaining. From Hostile Lake on northward the snow cover was complete, even the south-facing slopes of eskers were covered and snow cornices were intact. From the vicinity of Gozdz Lake northward the snow surface was crystalline and showed light and dark wind streaks. These wind streaks are caused by parallel alignment of the frost crystals on the snow surface. The migrating caribou were north of the region where the lakes were dark with slush and south of the region where the snow cover was complete (including 0.1 qali). This region was characterized by having only qamaniq and the steep south slopes of eskers bare of snow.

Possibly the presence of 0.1 or 0.2 qali or the presence of bare qamaniq, both identifiable from the air, may be used as indicators of the progression toward the tundra of the spring thaw and of the critical limits of the nival factors that govern the spring migration of the caribou from taiga to tundra.

Undoubtedly, similar correlations between snow conditions and caribou movement could be obtained during the fall migration from the tundra to the taiga.

Discussion

From the foregoing exposition it is evident that the snow cover through which the caribou wade and from beneath which they gather most of their food exerts a profound influence on their behaviour, migration and species survival. Formozov (1946), in his classic work on the biological effects of snow, classified mammals as chionophobes (avoiding snow), chioneuphores (adapted to snow) and chionophiles (highly adapted to snow or even restricted to snow). Examples of chionophobes, according to Formozov, are the smaller cats and the steppe antelopes. Examples of chioneuphores are mice, wolverine, fox, voles, etc., whereas the varying or "hoofed" lemming and the snowshoe hare are examples of chionophiles. Formozov classified the Old World reindeer as a chioneuphore. Since the New World caribou, because of its migrations, is subjected to snow factors for two-thirds of its annual cycle and because it exhibits behavioural and morphological adaptations to snow we are justified in classifying the Barren Ground caribou as a chionophile or an animal that is highly adapted to life on snow. Indeed, the name "snow caribou" would be more suitable for this species than is the term "Barren Ground caribou."

As my snow studies progressed it became evident that the wintering caribou in northern Saskatchewan were surrounded by a fence of snow having different characteristics from that in which they aggregated and that they were herded about over the countryside by this fence. To both the north and the south there was snow of greater depth than in the areas of concentration. To the south and southwest there was a sharp nival ecotone between soft, light taiga snow and hard, dense or iced snow almost temperate in its characteristics. The areas of caribou concentration had a snow cover that was softer, lighter, and thinner than that in the surrounding areas. Whereas the snow in the areas of occasional caribou was at times as soft and as light as that in the concentration areas it was at other times much harder and denser. The areas of no caribou had snow that consistently exhibited greater hardness, density or depth (occasionally all three qualities) than that of the areas of concentration. Variations in hardness appeared to influence caribou distribution more than variations in density. Obviously the presence of suitable food under the snow cover is also a factor of major importance as far as wintering localities are concerned. Under conditions of little modification of the winter range by man, probably the effect of nival factors was more prominent. Under such primeval conditions, before the extensive destruction of the winter range took place, nival factors probably were responsible for the location and density of wintering bands. Under present conditions the lack of food over extensive areas must be reckoned with.

Since snow conditions may prevent the wintering caribou from using extensive regions that are potential wintering grounds as far as food supply is concerned, it is obvious that winter range for any given number of animals must be substantially larger than the amount calculated from food intake per caribou per day and range recovery. In other words, a given amount of winter range can only support safely a much smaller number of caribou than that calculated on the basis of food intake and range recovery, because snow conditions in different years may herd the caribou about so that they cannot use all the range that is vegetationally suitable. Calculations of the carrying capacity of caribou winter range must be related to the caribou's ability to dig feeding craters, the number of craters that can be dug per unit area in a given habitat type and the amount of food secured per crater.

Ideal snow conditions for caribou winter range appear to be (1) hardness not over 60 gm./sq.cm. for forest snow and not over 700 gm./sq.cm. for lake snow; (2) density not over 0.20 for forest snow and not over 0.32 for lake snow; (3) depth not over 50 or 60 cm.; (4) continuous low temperatures during the snow season (no invasions of moist tropical air masses) and low wind speeds during this period. Undoubtedly, if sufficient meteorological and climatological data were available, areas where such conditions are the rule could be mapped out. Of all the vegetationally suitable winter range those parts that are nivally suitable are the most valuable as far as species survival is concerned and should receive the maximum possible protection from artificial modification.

Nasimovich (1955) described similar reactions of Eurasian wild reindeer to nival conditions. The thresholds of sensitivity he recorded were in some instances significantly higher than those reported here. Thus it would appear that the behavioural responses of New World caribou to nival conditions are sufficiently different from those of Old World reindeer so that direct comparisons are not valid.

It is not by accident that all references to caribou in this paper are in terms of individuals or bands. Since the areas of wintering concentrations and the timing, direction and speed of migration are intimately related to the characteristics of the snow cover, I suspect that the actual geographic location of the migration routes themselves are governed by snow (and topography). Thus the "herds" of caribou (Banfield 1954) are actually the summation of individuals and bands aggregated because of the fencing or restricting action of snow. The discreteness of the several "herds" is but a biological reaction to areas or channels of softer, lighter, and thinner snow cover between and among areas of harder, denser, and thicker snow cover. If sufficient meteorological and climatological data were available this hypothesis undoubtedly could be tested.

Thus it appears that a profitable approach to the problem of caribou migration would be to develop further the idea of nivally suitable pathways and wintering areas or "deer passes." This approach has been singularly successful in dealing with the problems of migratory birds, resulting in the "flyway" concept.

On many survey flights during early winter and midwinter I observed that the presence of barchans on lakes was a quite reliable indicator of the lack of caribou in the surrounding area. Obviously barchans themselves had little to do with the caribou, but as indicators of nival environment they seem to be of value. As the winter progressed and as the several storms mentioned above passed over the region barchans began to appear on lakes in the areas of occasional caribou and rarely in areas of concentration. When barchans appear on fall or early winter snow it means that the entire snow cover down to the substrate has been moved by the wind and is therefore hard. Barchans in late winter may be formed on top of the snow cover, particularly if there is a harder layer midway through the cover. I observed this condition on February 8, 1958 on a lake where the camp at 58°49′N., 105°52′W. was situated. The snow cover was 21 cm. thick and had a hardness ranging from 15 gm./sq.cm. to 50 gm./sq.cm. and densities ranging from 0.14 to 0.20. On top of this cover were barchans made by the storm of February 6 to 7, 1958. The barchans had a hardness of 400 gm./sq.cm. and a density of 0.29.

Conversely, the presence of qali (Pruitt 1958) indicates a lack of wind and usually soft and light snow. Since this phenomenon, as well as barchans, can be readily seen from the air, these two snow formations give promise of being valuable indicators of the nival environment. Further observations of barchans and qali in relation to caribou distribution might disclose principles which could be of value in plotting wintering grounds and fall migration routes.

Suggestions for future work

The National Research Council Standard Snow Instruments should be used, if for no other reason than standardization of data. Certainly some modifications could be made in the instruments themselves and in their packaging. The hardness gauge is sometimes difficult to use because of the large size of the pressure disc necessary for measuring thin layers of very soft snow (1 to 10 gm./sq.cm.). Possibly an additional gauge with a weaker spring could be devised, thus permitting a smaller pressure disc to be used.

I would suggest that for biological purposes instead of the present technique of cutting two or four 250-cc. samples of snow for density measurement that a more suitable cutter be devised. This cutter could contain 500-cc. and be so shaped that it could be used to weigh the snow directly. It would be a simple matter to adjust the scales to the tare of the cutter. This procedure would eliminate the need for the present pan and hanging chains.

I would also suggest that some sort of wind shield be devised for the snowkit when the scale is assembled, possibly along the pattern of the wind shield on a Coleman stove. It is virtually impossible to obtain an accurate weight whenever there is a wind blowing. This is not too important when working in the forest, but on lakes and on the tundra it is a constant worry.

I found that because mittens or even gloves were too clumsy to wear when taking snow measurements, that tape or heavy cotton twine wound around the hardness gauges made these chunks of brass more comfortable to handle at extreme low temperatures.

Although the Cessna 180 aircraft on skis served us well, a more rugged type of aircraft would be better. If any sort of systematic grid series of stations is contemplated then I urge that a rotor-winged aircraft be used for those stations which cannot be reached by conventional fixed-wing aircraft. The present study suffered from my inability to reach stations which fell on or near lakes too small for the Cessna 180 and from my inability to sample sufficiently the uplands, and the interiors of extensive burns.

I believe that the "track depth" measurement is promising and should be perfected. One of the first questions to be answered is: what are the foot loadings for caribou of various ages and weights *in the winter?* This qualification is important since caribou hoofs differ markedly in size from summer to winter. The Chipewyans have different names for short summer hoofs (eh-keh-gúna-ne-dúa), for long winter hoofs (eh-keh-gúna-ne-néth), and for winter hoofs when they become abraded and broken at the tips in spring (eh-keh-gúna-nah-tRé). Seton (1909) stated that reindeer feet are loaded at 2 pounds per square inch (357.2 gm./sq.cm.), contrasted with moose *(Alces americana)* which are loaded at 8 pounds per square inch. Nasimovich, however, (1955) listed wild Altai reindeer as having foot loadings of only 140-180 gm./sq.cm. Once a satisfactory artificial hoof is devised the procedure should be to measure the depth it penetrates at loadings approximating those of caribou of various ages and weights. A wealth of information could be gained from isolated tracks by an observer familiar with this measurement and its use.

It is evident from the data presented in this paper that the snow cover on the caribou winter range may vary greatly in its characteristics over a comparatively short distance and time. Therefore it is clear that conventional snow data as reported by the existing net of meteorological observatories are not only insufficient but may actually be misleading. The data for biological purposes apparently will have to be collected by the biologists themselves, at least until many more meteorological observatories have been established in far greater concentration than that existing at present and until the observers have been trained in an ecological approach which is, to temperate-zone people, somewhat esoteric. Because of the variability of the snow cover over short distances a large number of snow stations are necessary in order to gather data that are reliable. I consider my 114 stations as the absolute minimum number.

Since snow cover varies from winter to winter as well as from place to place, it would be well to sample it in years of little snow as well as in years of much snow. Various parts of the winter range should be sampled. There should be a comparison between snow and its relation to caribou on unburned and on burned winter range. It would be extremely interesting to investigate the nival environment of those bands of caribou that spend the winter on the tundra. Such an investigation might well reveal facets of caribou-snow relationships that would go far toward formulating general principles. Are these caribou in pockets of suitable snow? Are they channelled into cul-de-sacs of suitable snow in the fall and then have their routes of egress cut off by unsuitable snow conditions? What sort of physical condition do these caribou show in relation to those that winter in the taiga? This sort of information probably would be of great value in interpreting Pleistocene climates and the present composition and distribution of the mammalian fauna.

Undoubtedly there is a relationship between the areas where caribou habitually winter, their migration routes (and possibly the "pockets" of caribou that winter on the tundra) and the routes usually taken by cyclonic disturbances as they move across the continent. The tracks and the frequency of these storms are fairly well known. Do these air masses regularly deposit their load of snow along certain lines? Are there certain regions where polar air is more liable to encounter moist tropical air masses and how are these regions situated in relation to the known usual or specific wintering grounds? Finally, has the recent warming trend in the climate produced any northward shift of the zone in which winter thaw or rain may occur? This may be of extreme importance for the overall picture of caribou populations and movements. These questions could be answered, I believe, by a trained climatologist who is familiar with the ecological aspects of the problem. If these questions were answered and the various phenomena plotted on maps I suspect that many of our questions regarding caribou distribution and movements could be at least partially answered.

I believe that investigation of the behavioural aspects of the caribou-snow relationship would be a fruitful line of endeavour. When the varying "hindrance factors" of the snow cover reach critical thresholds they appear to act as releasers of migratory behaviour. The peculiar bounding circles that caribou describe when the spring snow conditions approach their limits of hardness and density tolerance should be investigated further. Is this behavior initiated on the edges of the region that is nivally suitable? Darling (1937) attributed the increased irritability in red deer to changes in atmospheric moisture. Further work should be done also on investigating the level of integration of such acts as pawing a feeding crater. The behaviour exhibited by a caribou in preparing to lie down on a snow-covered lake is interesting and deserves interpretation. A great deal of behavioural work can be done from movie films, especially if they are taken by an observer who is also familiar with the characteristics of the particular type of snow cover concerned.

Summary

1. During the winter 1957-1958 114 snow observation stations were established in parts of northern Saskatchewan and the southern Northwest Territories. Approximately 8,850 miles were flown at low altitudes over the region. During these flights the positions of bands and wintering individuals of Barren Ground caribou *(Rangifer arcticus)* were plotted on topographic maps.

2. Numerous ground observations were made of caribou behaviour in relation to snow conditions.

3. The areas of heavy caribou concentration were characterized by snow cover that was quite soft, light, and thin (hardness range of 6.5 to 60 gm./sq.cm. for forest stations and 50 to 700 gm./sq.cm. for lake stations; density range of 0.13 to 0.20 for forest stations and 0.13 to 0.32 for lake stations; thickness range of 19 to 59 cm.).

4. The areas of no caribou were characterized by snow cover that was sometimes soft but also could be very hard, dense, and thick (hardness range of 35 to 7,000 gm./sq.cm. for forest stations and 150 to 9,000 gm./sq.cm. for lake stations; density range of 0.16 to 0.92 for forest stations and 0.17 to 0.92 for lake stations; thickness range of 19 to 82 cm.).

5. Caribou appear to have a threshold of sensitivity to the hardness, density and thickness of the snow cover. The threshold of hardness sensitivity appears to be approximately 50 gm./sq.cm. for forest snow and 500 gm./sq.cm. for lake snow. The density threshold appears to be approximately 0.19 or 0.20 for forest snow and 0.25 or 0.30 for lake snow. The thickness threshold appears to be approximately 60 cm. When these thresholds are exceeded caribou react by moving until they encounter snow of smaller hardness, density or thickness.

6. Caribou will dig feeding craters only twice in a given unit of snow after which it becomes so hard that they seek undisturbed snow for feeding.

7. Some of the relationships of snow to the evolution, behaviour, species survival and management of caribou are discussed.

8. Various aspects of necessary future research and improvements in techniques are enumerated and discussed.

Acknowledgements

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

I am grateful to the other members of the winter field party, Mr. Ernie Kuyt, Mr. F. W. Terry and Mr. Donald Thomas, for their unstinting aid. 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 grateful to Mr. Gus Burchenski, pilot for Saskatchewan Government Airways, for his skillful handling of the Cessna 180 aircraft and for acting as field secretary during parts of the snow survey. I am indebted to Dr. Frederick C. Dean of the University of Alaska for critically reading the manuscript.

Glossary of specialized snow terms

Barchan — crescent-shaped drift of snow (or sand), convex upwind, with gentle windward and steep leeward slopes.

Chionophobe — an animal that on account of morphological or behavioural specializations is unable to adapt itself to snowy conditions.

Chioneuphore — an animal that is able to exist in snowy regions, but does not have special morphological or behavioural adaptations to snow.

Chionophile — an animal that possesses definite morphological or behavioural adaptations enabling it to live in snowy regions, and that is limited in its distribution to snowy regions.

Nival — adjective referring to snow.

Pukak — Kobuk Valley (Alaska) Eskimo term for the fragile lattice-like structure of snow grains formed at the base of a snow cover by redistribution of water molecules by sublimation. Also called "depth hoar".

Qali — Kobuk Valley Eskimo term for the snow that collects on trees, as distinguished from api, the snow that collects on the ground.

Qamaniq — Kobuk Valley Eskimo term for the bowl-shaped depression in the snow cover under coniferous trees.

Sun crust — the crust that forms on the surface of a snow cover in the spring when the sun is high enough to cause slight melting of the topmost layer during the day, which refreezes at night.

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