

FEEDING ECOLOGY OF WOLVES ON BARREN-GROUND CARIBOU RANGE
IN THE NORTHWEST TERRITORIES

A THESIS

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by

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ABSTRACT

The interrelationship of wolves and barren-ground caribou was studied mainly between 1960 and 1965, although some facets of the study continued until 1968. The work was conducted in spring and summer in the Thelon Game Sanctuary about 450 miles northeast of Fort Smith, N.W.T., with supplementary winter work on caribou winter range north of Yellowknife, N.W.T. and east of Fort Smith. This dissertation reports the results of the study of feeding ecology of tundra wolves.

Tagging studies showed that tundra wolves travel great distances and that their movements are associated with those of the barren-ground caribou, their major prey species. Study of the food habits of tundra wolves confirms that, during the winter, they are completely dependent on caribou for food. During the spring and summer the diet of wolves is much more varied than in winter and small rodents, passerine birds, eggs and fish are then resorted to, particularly in areas temporarily devoid of caribou. Caribou calves are subject to heavier predation than other age classes. Caribou of 8 to 9 years and 10 years and older are also heavily preyed on. Wolves kill at least four times as many female caribou as males.

Strategy of wolves' attacks on caribou was deduced from tracks and from marks on the body of the prey. Neck and shoulder region of the prey were the favourite locus of attack by wolves. Caribou killed in winter are completely utilized by wolves; in summer, parts of carcasses are often left to scavengers.

A short term, high wolf density of one wolf per 6.9 square miles of caribou winter range is described. Studies of food requirements of a colony of captive wolves showed that these wolves could be maintained on an average daily ration per wolf of 3.23 pounds of bison meat and fat and 0.26 pounds of commercial dog food. Weights of three litters of cubs, born in captivity, were recorded weekly. Per cent relative growth rates were calculated and showed no apparent differences in character between the sexes. Mean growth curves for the three litters of cubs were plotted and illustrated rapid early growth of young wolves followed by a reduction in rate of growth.

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INTRODUCTION

Purpose of study

Wolf control in the Northwest Territories to conserve the dwindling stocks of barren-ground caribou was recommended to federal and provincial agencies on the basis of caribou studies by Banfield (1954). After considerable experimentation, wolf control was undertaken by the federal government in 1951, with the knowledge that the full effects of wolves and lesser predators upon barren-ground caribou were not adequately known. By 1961 the numbers of wolves taken annually in the Northwest Territories had shown a considerable decline with a corresponding increase in costs per wolf killed and the Northwest Territories' Administration reduced its attempt to control the number of predatory animals on the range of the barren-ground caribou.

In 1957 the Canadian Wildlife Service initiated a study of wolves on the range of barren-ground caribou in the Northwest Territories. The objective of the study was to know more about this wolf which is an important predator of a resource still of great value in the economy of the northern native population. Specific objectives were investigation of factors affecting wolf populations on the range of the barren-ground caribou, the significance of those factors in influencing wolf numbers and to learn the relationships of wolves to barren-ground

caribou populations. The study of the food habits of wolves on barren-ground caribou range, that of the gross food requirements of wolves and of movements of wolves on the range of the barren-ground caribou are reported here.

Intensive studies in the Thelon Game Sanctuary began in 1960 when the author was assigned to the project. Summer field work in the area was concluded in August 1965. Winter field studies were carried out in 1960 and 1961 in the Beniah Lake area and in 1964 near Bishop Lake. Some aspects of the study, such as the examination of wolf-killed caribou on winter range, were continued until 1968. It was unfortunate, as has been pointed out by Kelsall (1968), that the work began after wolf populations had been greatly reduced and when possibilities for observing wolves in the field were limited.

Study of the feeding ecology of wolves on barren-ground caribou range is an important aspect of wolf-caribou studies. There have only been few of such investigations and Pimlott (1967) has recently pointed out the need for intensive studies of the summer food habits of wolves in tundra regions inhabited by barren-ground caribou. It is hoped that the present research will contribute significantly to our knowledge of the feeding ecology of wolves on the range of barren-ground caribou.

Caribou migration

When wolves and ungulates inhabit the same range, the ungulates are usually the main prey of wolves. For the present study of food habits of wolves it was essential to be familiar with the migration routes of barren-ground caribou. Although some sections of the caribou range are occupied almost every year by migrating caribou, the unpredictability of caribou movements is known and has been commented on by many biologists, notably by Kelsall (1957, 1968). Banfield (1954) describes 19 main caribou herds but indicates that exchange of peripheral bands of adjoining herds may occur. Kelsall (1957) also refers to the frequently observed overlapping of herds.

A large herd usually winters in the southern part of Mackenzie District and northern Saskatchewan including the Fond-du-Lac River system. In late April the herd migrates northeastward from the winter range and funnels into the land mass bordered on the west by the upper Thelon River and on the east by the Dubawnt River drainage (Figure 1). Frequently, part of the herd remains on the west side of the upper Thelon River and crosses the Hanbury River near Dickson Canyon (Banfield's "Hanbury" herd). The main portion of the herd moves through the apex of the funnel formed by Beverly Lake and the mouth of the Dubawnt River. Major caribou crossings occur here each spring. Calving generally occurs near Beverly Lake,

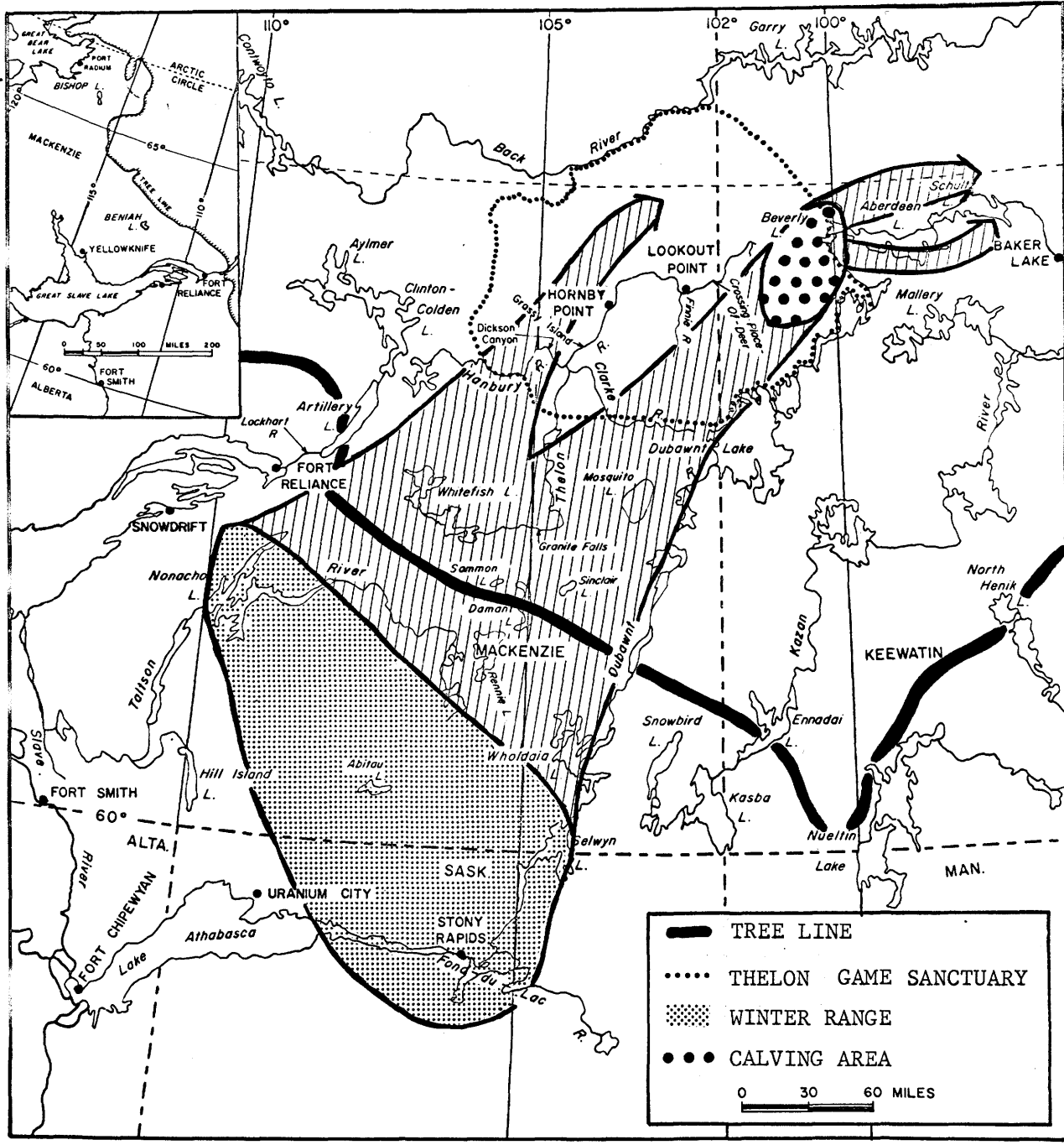


Figure 1 — GENERAL PATTERN OF SPRING AND SUMMER CARIBOU MIGRATION

beginning in the last week in May, with most calves being born during the second week in June. Post-calving movements in some years may carry the herd, or part thereof, as far east as Baker Lake.

During July, the herd travels westward along Schultz and Aberdeen Lakes and by the end of July, caribou in large numbers have started to cross the Thelon system on their way south in the vicinity of Beverly Lake (Figure 2). Dispersal of the herd (Kelsall, 1960) takes place around the middle of August and caribou are soon widely scattered. By then the herd has reached the southern part of the tundra region.

A late summer caribou migration southwestward along the Back River system in the northern part of the Thelon Game Sanctuary, was observed several times during summer field work. From July 24-29, 1963, over 6,000 caribou crossed the middle Thelon River between Lookout Point and Hornby Point. Those southward moving caribou are believed to be part of the "Hanbury" herd (Banfield, 1954). Other parts of the herd sometimes continue southwestward to Clinton-Colden and Aylmer Lakes. Parts of that herd may then turn south and cross the Lockhart River to re-enter the winter range near Nonacho Lake. Here the herd segment will join the major herd which migrates south into northern Saskatchewan on a wide front sometimes extending from Nonacho Lake to the Dubawnt River system.

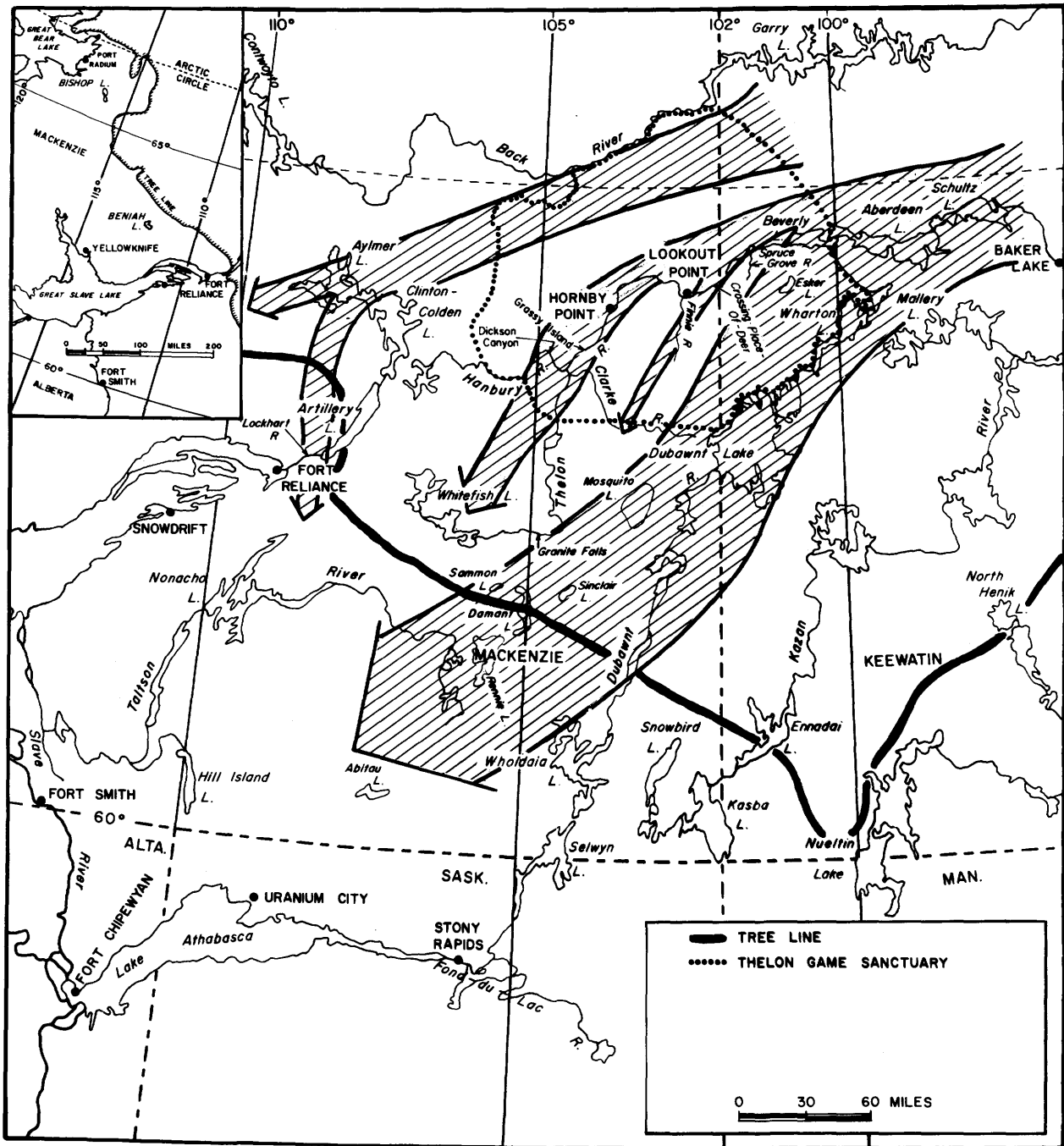


Figure 2 – GENERAL PATTERN OF AUTUMN CARIBOU MIGRATION

Wolf movements

Tundra wolves apparently travel long distances accompanying caribou herds. Hunters and trappers living on barren-ground caribou range often observe wolves following caribou on their seasonal migrations. Certainly wolves are almost invariably associated with caribou. Aerial surveys frequently reveal wolves and wolf trails trending in the same direction as caribou or their trails and also show that wolves winter with caribou in forested areas. Conversely, areas unoccupied by wintering caribou are also devoid of wolves. During the caribou spring migration, wolves move back to the tundra with the caribou or sometimes, as has been pointed out by Critchell-Bullock (1930) and Kelsall (1960) may even move out ahead of them.

The areas near the tree line south of the Thelon Game Sanctuary appear to be favoured by breeding wolves. When wolves have reached their denning sites in these areas, the caribou will continue their migration to the calving grounds near Beverly Lake. Although some wolves are found at Beverly Lake, most of the adults are confined to the immediate vicinity of their dens further south near the tree line. Consequently there exists a temporary separation of at least 100 miles between the calving caribou and the denning wolves. The autumn caribou

movement towards forested areas in the south carries the herds through these wolf denning areas when the young wolves are able to travel well. The wolf families then re-associate themselves with caribou and return with them to their winter range in forested regions.

LITERATURE REVIEW

General

Clarke (1940) has discussed the history of the Thelon River area, the general biology of the more important mammals, the relationship between wolves and caribou and other aspects of the biology of the area.

Food habits

Adolph Murie's classical study "The Wolves of Mount McKinley" (1944) was one of the first and most comprehensive studies of the interrelations of wolves and their prey. He found a 69 per cent occurrence of ungulate prey in the annual diet of Mount McKinley wolves. Cowan (1947) working in the Canadian National Parks in the Rocky Mountains found that the wolves' annual diet consisted of 80 per cent big game and 18 per cent rodents. Thompson (1952) found that white-tailed deer remains occurred in 97 per cent of 425 wolf scats collected throughout the year in northern Wisconsin. Mice and snowshoe hare remains were found in 9 per cent of the scats. In northern Minnesota Stenlund (1955) showed that in winter, white-tailed deer comprised 95.5 per cent of the total volume of wolf stomach contents. Smaller animals were found to be of greater importance in summer than in winter. White-tailed deer were the

main prey of wolves in Algonquin Park (Pimlott, et al. 1969) with moose and beaver of secondary importance. Four wolves introduced in Coronation Island in southeastern Alaska and their offspring fed mainly on black-tailed deer with the incidence of deer remains in scats increasing from 78 per cent in 1961 to 95 per cent in 1964 (Merriam, 1964). Pulliainen (1965) in a study of wolves in Finland, classified domestic animals (chiefly reindeer) and moose as the most important food of wolves in forested areas. Moose is the only ungulate species occurring on Isle Royale, and Mech (1966) determined that wolves and moose were in dynamic equilibrium, with the wolves culling out undesirable individuals and stimulating moose reproduction.

Of greatest interest to the present study are those investigations dealing with wolf-caribou relationships. Murie (1944) found that in interior Alaska, caribou furnished the main food of the wolf and that when calves were available, they constituted the main food supply. Kelly (1954), Banfield (1954) and Kelsall (1960) studied the food habits of wolves on barren-ground caribou range and found them to be preying almost exclusively on caribou. Mowat's (1948) analysis of 61 wolf scats from denning sites in Keewatin District, although based on a small sample, provides the only available information comparable with the present study. Mowat indicated that his information has no quantitative value and that no valid conclusion may be drawn from it. Limited information on summer and winter food habits of arctic wolves in the U.S.S.R. has been provided by Makridin (1960). Unfortunately, his food studies are largely undocumented quantitatively. Pulliainen (1965) has discussed food habits

of young wolves in captivity.

Movements of Caribou and Wolves

The migratory movements of barren-ground caribou through the study area have been described in detail by Banfield (1954), Kelsall (1957, 1960, 1968) and Thomas et al. (1968). Although there is strong circumstantial evidence that wolves raised on the tundra are associated with barren-ground caribou practically throughout the year, no definite records are available. Kuyt (1962) reported on the movement of a litter of three wolves raised on the tundra. The young wolves taken from a den near the Back River were ear tagged and released. Almost seven months later the three young wolves and two adult wolves were killed by a predator control officer near Aylmer Lake, a distance of about 185 air miles west-southwest from the den site.

The few records available for forest dwelling wolves show that they, too, are capable of long travels. Young and Goldman (1944) describe movements of leg-trapped wolves and give the record of an ear tagged red wolf (Canis niger) which had travelled a distance of 125 miles. Banfield (1952) records the movements of two ear tagged wolves in Banff National Park one of which travelled a minimum distance of 162 miles.

Hunting by Wolves

Observations made by biologists of wolves hunting caribou are numerous,

yet few instances of a successful hunt are recorded. Crisler (1956) witnessed several kills and Wilk (in Kelsall, 1960) described such an incident while he was engaged in the 1957-58 co-operative studies of barren-ground caribou. The latter event was the only wolf-kill witnessed during that 18-month study, although up to eight men were in the field simultaneously and caribou were under observation almost daily. Burkholder (1959) has provided details of wolves hunting caribou and moose in Alaska. A large number of well-documented accounts of wolves hunting moose on Isle Royale are described by Mech (1966).

DESCRIPTION OF STUDY AREAS

Since the two study areas, the Thelon Game Sanctuary and the Bishop Lake-Beniah Lake area, are similar in many respects, the descriptions of the two areas have been combined.

1. Location

The Thelon Game Sanctuary and the adjacent area south to the tree line, totalling about 25,000 square miles, are located in the east central mainland portion of the Northwest Territories. The 102 degree of longitude, which constitutes the boundary between Mackenzie and Keewatin districts, divides the Sanctuary in two unequal parts. The Clarke River is part of the southern boundary of the Thelon Game Sanctuary (Figure 1).

Collections in the Bishop Lake-Beniah Lake study area were made in various locations in an area approximately 50 miles by 200 miles approximately parallel to the tree line and extending from Beniah Lake, about 100 miles northeast of Yellowknife to the Bishop Lake area, about 225 miles north-northwest of Yellowknife.

2. History

The Thelon Game Sanctuary was established in order to give protection to the muskox. In 1925, John Hornby and

J. C. Critchell-Bullock travelled down the Thelon and discovered that muskoxen still occurred there (Hornby, 1934). As a result of Hornby's report to the Dominion Government, an area of some 15,000 square miles was set aside as the Thelon Game Sanctuary by Order-in-Council of July 15, 1927. In 1956 the Sanctuary was reduced to 11,200 square miles and its boundaries shifted eastward to the positions shown on Figure 1.

With the exception of Canadian Wildlife Service field parties, geologists and occasional tourists, there are no residents in the Thelon Game Sanctuary. Indian hunters and trappers no longer visit the area from the south and only scattered signs of old campsites indicate their former presence. Similarly, Eskimos no longer visit the area from the north and east although several families still hunt and trap near Aberdeen Lake, immediately to the east of the Sanctuary. Signs, such as old tent-rings and cuttings in isolated clumps of spruce along the river indicate that Eskimos formerly travelled up the Thelon River at least as far as Lookout Point. Clarke (1940) has provided an excellent account of the historic use of the Thelon Game Sanctuary by man.

The Bishop Lake-Beniah Lake study area contains winter ranges favoured by barren-ground caribou. Indian hunters and trappers from the settled areas to the south and west frequently visit the area, and probably have done so for many years. In recent years, mineral exploration has intensified and several winter roads, air strips, exploration and mining camps have been constructed in the area.

3. Climate

There do not appear to be great climatic differences between the Thelon River area and the Bishop Lake-Beniah Lake area. The regions are characterized by cold, long winters and short summers with a few hot days. The mean monthly temperature is below 32°F from October to May and is about -25°F in January, the coldest month. The mean daily maximum is below 32°F from October to May. The minimum temperature recorded by me in the Lookout Point cabin on the Thelon River reached -45°F in the 1961-62 winter and -50°F in 1964-65. Temperatures below -60°F may occur in the region.

The mean monthly temperature rises to about 50°F in the warmest month (July), and is above 40°F only in July and August. The mean daily maximum exceeds 50°F in July and

August (Kendrew and Currie, 1955). From 1960 to 1965, temperatures of over 80°F were recorded by me near Lookout Point in 1960 (six days), 1961 (two days) and 1964 (two days).

Spring breakup usually occurs in the first week in June, although in 1963 the ice on the Thelon River at Lookout Point did not disappear until June 14. Air temperatures generally rise above 32°F during the third week in May in the Bishop Lake-Beniah Lake area and about a week later in the Thelon River area. The first frosts occur before the end of September.

The total mean annual precipitation ranges between 10 and 16 inches and about half of this is in the form of snow. Rain may occur any time in summer, while in the spring or fall rain is often accompanied by sleet. Wind occurs at all seasons, often accompanying rainy weather, but providing welcome relief from insect harassment during warm weather. Fog is common, thunder storms are rare. For further information on the climate of this region the reader is referred to Kendrew and Currie (1955) and Bird (1967).

4. Geology and topography

Although the age and distribution of rocks in much of the Canadian arctic are insufficiently known, it appears that the two study areas are underlain by Precambrian rocks (Bird, 1967). Much of the Thelon River study area including practically all the area west of the Dubawnt River from north of the Thelon River south to the tree line, is covered by the Dubawnt sandstone formation (Bird, 1967). Rocks of a granitic nature, normally in the form of rock barrens of low relief, are predominant near Dubawnt Lake in the south-east corner and western portion of the study area where the contact zone between granite and sandstone runs from the upper Thelon River at Granite Falls, roughly just west of that river to Dickson Canyon on the Hanbury River and thence almost straight north (Wright, 1957).

Most of the Thelon River study area underlain by sandstone is a vast expanse of treeless land, mainly gently rolling to monotonously flat. A few features, indicative of the influence of glaciation, break the uniformity of the landscape. Of these, eskers are most prominent, particularly from the air. They are prevalent in the area south of Beverly Lake, near the Clarke River and in the southern parts of the Thelon River study area from Mosquito Lake

to the tree line. Sand dunes, irregular in form, are found in various locations, along the Thelon River, east of Dickson Canyon, near Mosquito Lake, north of Beverly Lake and frequently associated with esker systems. Hills of sandstone rising to 500 feet above Thelon River are found south of Grassy Island in the western part of the Thelon study area. Just south of Beverly Lake the strikingly terraced sandy hills on the north end of a long esker were formed in glacial times as a massive esker-delta (Bird, 1967).

Drumlinoids are encountered in many parts of the Thelon River study area, particularly near Lookout Point on the Thelon River, where the till lowlands are marshy. From the air, the dry bouldery tops of the drumlinoid ridges are clearly distinct from the marshy depressions between them. Near Lookout Point, the sides of the ridges are covered with small spruce and birch and seen from the air, this ridged terrain complete with numerous elongated lakes has a most impressive fluted grain.

Other features noticeable in the Thelon River study area are two long ridges composed of a red weathering rock found trending in a northwest to southeast direction in the Lookout Point area. The southern ridge, visible

from Lookout Point at a distance of less than four miles, is about 30 miles long. The more northern ridge, some 40 miles long is found about 25 miles north of Lookout Point. The prominent ridges vary in width and height but in places rise abruptly to 40 or 50 feet above the surrounding country. For further information about these dykes, the reader is referred to Wright (1957).

Another interesting feature is the only pingo in the area, a well known landmark about 60 feet high and located 13 miles north-northwest from Lookout Point.

The Bishop Lake-Beniah Lake area consists entirely of the hard, smoothed rocks of the Precambrian Shield. The land is rugged and the relief much bolder than in the Thelon River area. The great eskers and sandhills so common in the other study area are almost lacking in this area and where they occur, are much reduced in length and prominence. As only a brief period was spent here in February and March 1964, a more detailed description of the Bishop Lake-Beniah Lake area is not necessary. The reader is referred to Bird (1967) for further information.

5. Fauna

The mammals and birds in the two study areas will be briefly mentioned where they are considered to be significant to wolves, potentially as prey or as competitor. As the Bishop-Beniah Lake area was visited briefly and only in the winter, little information can be given on the animal life in that region and most of the comments refer to the Thelon River area. Muskoxen (scientific names of animals mentioned in the text are in Appendix B) are not found in the Bishop-Beniah Lake area but they are frequently seen in the Thelon River area. Caribou are common in both areas, depending on season. Moose have only recently been seen in the Thelon area (Kuyt 1965b) and they are also considered to be rare in the second study area. Barren-ground grizzlies are often seen along the Thelon River and near Beverly Lake but also occur in the Bishop Lake-Beniah Lake area near the tree line. Porcupine and beaver are extremely rare in the Thelon River area (Kuyt 1965a, 1965b). Arctic hares are sometimes seen on rocky terrain and on eskers, particularly in the Thelon River study area. Ermine and wolverine are encountered rarely, the latter more frequently in the Bishop Lake-Beniah Lake area than in the Thelon Game Sanctuary. In the summer, arctic foxes are seen only in the northern and eastern portions of

both study areas but during winter migrations they may occur anywhere and migrate far into timbered areas to the south. Red foxes have been found denning along the Thelon River. Ground squirrels are frequently seen, particularly in sandy areas and on the high banks of the Thelon River. Both collared and brown lemmings are common and subject to periodic fluctuations in numbers. Red-backed voles and masked shrews have also been observed.

Waterfowl of many species may be seen on all of the larger water bodies (Clarke, 1940). During the flightless period these birds can be considered potential prey for wolves. Golden eagle, bald eagle, gyrfalcon and peregrine falcon as well as rough-legged hawk, raven and herring gull have been observed scavenging. Rock ptarmigan and willow ptarmigan and the flightless young of many Passerine birds constitute further potential prey.

Vegetation

The Thelon River study area and the region south to the tree line fall within the Arctic life zone (Dice, 1952, Hall and Kelson, 1959). The Thelon River valley and the valleys of some of its tributaries near their confluence

with the Thelon River, as well as the southern portion of the study area near tree line, are Hudsonian in nature (Dice, 1952, Hall and Kelson, 1959). Indeed, to the aerial traveller in the winter time, the dark ribbon of the Thelon forests contrasts vividly with the snow and it resembles a green finger-like oasis projecting into the monotonous expanse of the tundra landscape. White spruce (for scientific names of plants, see Appendix B) is the predominant tree with black spruce of lesser importance. Balsam poplar and tamarack are encountered only in discontinuous clumps along the Thelon and some of its tributaries, especially the Finnie River. Willows are abundant, particularly along the rivers. Vast expanses of dwarf birch thickets can be found near rivers and ponds. On drier sites, birch and willow form low shrubs.

The plant associations are discontinuous with bare soil or rock between. In addition to the birch and willows mentioned above, there are many other dwarfed or matted woody plants, notably the ericaceous plants. Many of the herbacious plants display a tufted growth form. Sedges form an important part of the flora. Lichens are common everywhere.

The vegetation of the Bishop Lake-Beniah Lake area is that of the coniferous forest and falls within the

Hudsonian life zone. It is similar to the southern portions of the area already described for the Thelon River study area.

MATERIALS AND METHODS

1. Ear tagging of wolves

Wolves were marked to determine their migration route and to relate this information to the movements of barren-ground caribou. During summer field work efforts were made to locate occupied wolf dens and to capture and ear tag young wolves. Eleven occupied wolf dens were found and 31 cubs were measured, weighed and ear tagged, using numbered aluminum or brightly-coloured plastic tags. Cubs were estimated to be 5-7 weeks old when tagged. One plastic tag was attached to the ear of a captive wolf in Fort Smith to determine whether or not there would be tag loss from freezing and subsequent cracking or from removal by littermates or by the tagged wolf itself. The plastic tag remained intact for two winters. Predator control officer C. F. Riddle, who recovered five ear tagged wolves, observed a loose tag in the ear of one wolf suggesting that some tag loss may occur.

2. Food habit studies

When the author was engaged in barren-ground caribou studies from 1957-58, it became apparent that there would be few opportunities for observing direct predation by

wolves. Subsequent surveys of the literature show that predation by wolves is rarely witnessed. The indirect method of studying food habits by collecting and analysing wolf scats has therefore been used extensively in this project.

a. Collection and examination of scats

A total of 595 wolf scats was collected in the Thelon River study area in the spring and summer from 1960-1965. Practically all were collected in the vicinity of active or vacant dens. The droppings were placed in small paper or plastic bags and labelled with date and location. In the laboratory, each dropping was broken up and the components, such as bone, claws, teeth and hair of prey animals were identified and recorded. Reference material of skeletons and hair of potential prey animals in the study area, was used in the analysis. The remains of lemmings and voles were lumped as "Microtines". Similarly, remains of birds were not segregated except for ptarmigan and geese.

It was not possible to age the scats as to the year in which they were deposited except for a small number found fresh near occupied wolf dens.

In 1965 at least 17 wolves were seen between the Clarke River and the tree line to the south, although no caribou were observed in that area during our aerial surveys. All wolves south of the Clarke River were associated with dens containing cubs. Clearly, food resources other than live caribou were being utilized by the wolves during that time. Summer caribou distributions patterns in past years have been similar to those prevailing in 1965.

In order to compare the summer diet of wolves in areas temporarily devoid of caribou with that of wolves associated with caribou, I selected the Clarke River as an arbitrary line dividing the two different areas in which wolf scats were collected.

One hundred and sixty-eight of the 595 wolf scats collected during the study were those of cubs. Scats of wild wolf cubs could be distinguished from those of adult wolves by their small size. They are always found near wolf dens occupied by cubs and presumably date from when cubs begin to eat solid food. A further division of the scat collection into scats of cubs and wolves other than cubs was therefore warranted.

b. Determination of stomach contents

One of the difficulties in the study, particularly in the

first few summers, was finding enough wolves. Even under undisturbed conditions, wolves may never be found in dense concentrations except on caribou winter range. It has been suggested that low wolf numbers in 1960 and 1961 can be attributed to the wolf control program in 1957-1958.

For several reasons I have been reluctant to kill wolves in the summer for study specimens. Five wolves were shot by me in late July and early August of 1963, 1964 and 1965 in the area within 60 miles of Beverly Lake. In June 1965 a sixth wolf was found dead in the same area. Each year, at the time of collection, scattered caribou were seen in the area. These six wolves are the only summer specimens.

The stomachs of 298 of 300 wolves killed in winter were obtained for analysis. These include the stomachs of 12 wolves killed by strychnine baits during the winters of 1960 and 1961 on barren-ground caribou winter range about 125 miles north of Yellowknife, N.W.T. The caribou meat used for the baits was skinned to facilitate analysis of the stomach contents of the dead wolves. From its appearance and location in the cardiac portion of the stomach, the bait meat could be distinguished from the other stomach contents. In the laboratory, total stomach contents were weighed to the nearest 5 grams. Bait meat and other stomach contents were separated and weighed on a triple-beam balance.

In February and March, 1964, 57 wolves were taken on strychnine baits on caribou winter range in the Bishop Lake area, 65 miles southeast of Port Radium, Great Bear Lake. Two damaged stomachs were discarded.

Most of the several thousand wolves killed by predator control officers in the Northwest Territories from the beginning of the program to the present have been taken by C.F. Riddle who operates in the winter range of the "Saskatchewan" barren-ground caribou herd. That herd calves in the Beverly Lake-Aberdeen Lake region and is the herd upon which the wolves in the study area chiefly prey. A total of 226 stomachs of wolves killed by Riddle from 1957-1967 was examined superficially by him and the information recorded on autopsy cards. Riddle does not skin caribou used for baits.

Five wolves were killed on strychnine baits during the winter of 1960 in the vicinity of Yellowknife on range not used by caribou. Bait meat and other stomach contents were separated, identified and weighed.

c. Examination of caribou remains

i. Summer

All remains of caribou found in the field were examined. They included mostly caribou skeletons, a few caribou freshly killed by

wolves and caribou in various stages of decomposition which had died of unknown causes. Usually only a few bleached bones were found, as predators and scavengers drag away the remains. Cause of death of only a few caribou could be determined with certainty. Since caribou rarely remain on the barrens in the winter, the collection of caribou remains reflects summer mortality.

Usually at least one mandible could be recovered from each carcass and only those carcasses with a mandible were recorded. The mandibles, when their condition permitted, were aged using the method developed by R. P. Skoog (1956). Sex of the specimens was determined on the basis of a difference in length between the jaws of both sexes. Examination of the jaws of 102 adult known sex caribou (42 females and 60 males) showed that only two of the 42 female jaws attained or surpassed 272 mm. and that only three of the 60 male jaws measured as little as 272 mm. or less (J. McGillis, pers. comm.).

Concentrations of remains were frequently found in areas of present (and presumably past) wolf activity such as wolf denning areas and wolf routes. Similar observations have been made by Young and Goldman (1944) and Kelsall (1968). About a third of the 151 jaws were of calves, although no special efforts were made to find remains of calves nor were exhaustive searches made on major calving grounds.

ii. Winter

During aerial surveys in March 1968 over a concentration of caribou wintering near Abitau Lake, N.W.T., I examined 17 carcasses believed to have been killed by wolves. Flights were made over the area at intervals of several days. It was noted that when caribou moved into new areas wolves were not found with them for at least a day and no carcasses were observed in these newly-occupied areas. After several days, wolves would again be seen with the caribou and carcasses were seen frequently, usually on lakes and close to shore. There was no human hunting of caribou in the areas surveyed and

even though no kills were witnessed, I feel confident that the carcasses examined were killed by wolves.

d. Examination of wolf-killed caribou

During the present study, 14 caribou found dead in summer were certainly killed by wolves and were sufficiently fresh and intact so that a good deal could be learned from them. Six of the 14 kills (No. 1, 7, 8, 9, 11 and the 1958 kill, Appendix A) were remarkably similar in body parts attacked and in initial parts eaten. In five cases, wolves were in the vicinity and fresh tracks and tufts of caribou hair indicated that a struggle had taken place before the caribou was killed. The other eight carcasses all displayed the same signs of wolf activity found on the six kills, although wolves were seen nearby only once.

e. Observations on wolf predation

Although freshly-killed caribou were found during this study, the act of predation was not witnessed. Patterns of the actual kill, as far as I was able to determine them from tracks, are described in Appendix A.

3. Food studies of captive wolves

a. Source of captive wolves and history of colony

A colony of from three to eleven captive wolves kept at Fort Smith enabled me to make observations on the feeding behaviour of wolves. Originally, the colony consisted of two wild-caught cubs, brother and sister, probably of the subspecies Canis lupus arctos, received in 1961 from Axel Heiberg Island in the District of Franklin. They were joined the same year by a male cub, probably Canis lupus hudsonicus, from a den along the Thelon River. In 1963, a live female cub and a still-born cub were born to the female and the Thelon River male. This female cub and the same Thelon male (her father) produced a single cub in 1965 which was killed by the mother on the day following birth. The mother was sacrificed in 1965.

In 1964, the original two littermates from Axel Heiberg Island produced five cubs, one of which was killed by the Thelon male, one escaped from the compound and was shot and one was sacrificed for study material. The original Axel Heiberg male died after a fight with the Thelon male. One of the two remaining wolves and the Thelon male

produced three cubs in 1966. One of the three cubs died of pneumonia, one was donated to a private zoo and one was used for study material. In the same year, the Axel Heiberg female and the Thelon male produced four cubs, all of which were eventually sacrificed. The Thelon male was sacrificed in 1967. The Axel Heiberg female and her three-year-old arctos son mated in 1967 and six cubs were born. One of the cubs died and two were killed for study purposes. The same two parents produced seven cubs in 1968, three of which were destroyed by me on the day of birth and one escaped while on display in Yellowknife. The other three cubs died of a hookworm infection. The remaining six wolves, all C. l. arctos were donated to a zoo late in 1968.

One wolf has been in captivity since 1961 and seven litters totalling 28 cubs were born in our pens. The colony of wolves, therefore, included wolves of various ages ranging from new-born cubs to a wolf seven years of age.

The wolves were kept in an outdoor pen, measuring 100 by 65 feet, surrounded by a 10-foot-high, chain-link fence. Wire is buried near the edges of the

pen at ground level to discourage the wolves from digging their way out. The compound can be subdivided into three smaller pens by closing two gates. During the breeding season one member of the colony sometimes has to be separated to eliminate fighting.

b. Type and quantity of food fed

Most of the food fed to our captive wolves was meat, fat and bones from bison slaughtering operations in Wood Buffalo National Park and from traffic-killed bison in the park area. Commercial dry dog food was used occasionally.

To determine the weight of meat and fat eaten by the wolves, the weight of bone left uneaten in the pens was subtracted from the total amount of meat, fat and bone offered in a number of trials. Estimates of the weight of rejected bone were made prior to feeding and compared with the known weight of rejected bone. Although it was possible after some practice to estimate closely the amount of bone in the meat and fat fed to the wolves, the rejected bones were weighed at weekly intervals and their weight subtracted from the total food.

Because our captive wolves usually occupied one compound and consisted of several age groups, it was decided to classify them into three age groups to determine the

approximate daily meat consumption per wolf. Wolf cubs up to 1½ months of age depend largely on their mother's milk. Cubs older than 1½ months live almost entirely on meat but because of their small size do not eat as much as an adult wolf. The following arbitrary figures were assigned to the captive wolves in terms of their meat consumption: cubs up to 1½ months (up to July 15) were counted as 0 wolf units, cubs from 1½ months to four months (up to September 30) were ½ wolf unit, and wolves older than four months were 1 wolf unit.

The number of wolf "units" per day was based on the age of the individual captive wolves. For example, on July 8, 1967 our captive wolf colony consisted of four wolves older than one year and five one-month-old cubs. The total wolf units for that day was $(4 \times 1) + (5 \times 0) = 4$ wolf units. The same group on July 16 consisted of $(4 \times 1) + (5 \times \frac{1}{2}) = 6\frac{1}{2}$ wolf units and on October 1 the group would consist of $(9 \times 1) = 9$ wolf units.

Approximate food intake, in terms of meat and commercial dog food eaten, was recorded for a three-year period from November 25, 1964 to November 30, 1967. Average daily food consumption per wolf unit was calculated.

c. Weighing of captive wolves

Young cubs were weighed to the nearest ounce several times each week during their first month of life. From the end of their first month to the end of August, the cubs were weighed once per week. After that the wolves became difficult to handle and weighings became less frequent. Weights were recorded whenever captive wolves were killed. On a few occasions, a muscle relaxant (succinylcholine chloride) had to be used in order to obtain weights.

RESULTS

1. Den location, litter size and recovery data

Nine (29 per cent) of 31 ear-tagged wolf cubs have been recovered; an indication that man's activities are an important mortality factor for wolves. Three cubs of one litter were killed by a predator control officer (Kuyt, 1962), five ear-tagged wolves were taken by another predator control officer and one tagged wolf was shot by an Eskimo hunter. Seven of these wolves were killed during their first year of life. One was shot as a 14-month-old and one wolf carried both aluminum ear tags for 5½ years.

The results of tagging work are summarized as follows (numbers refer to movements indicated on Figure 3):

1. A litter of three wolves, tagged on July 24, 1960 near the Back River was killed on or about February 10, 1961 near Aylmer Lake, a distance of 184 air miles from the den site. (Kuyt, 1962).
2. A wolf, tagged on July 15, 1962 as a cub from a litter of five, was shot when 14 months old by an Eskimo hunter north of Schultz Lake in August 1963. That wolf was 188 air miles east-northeast of the den site.

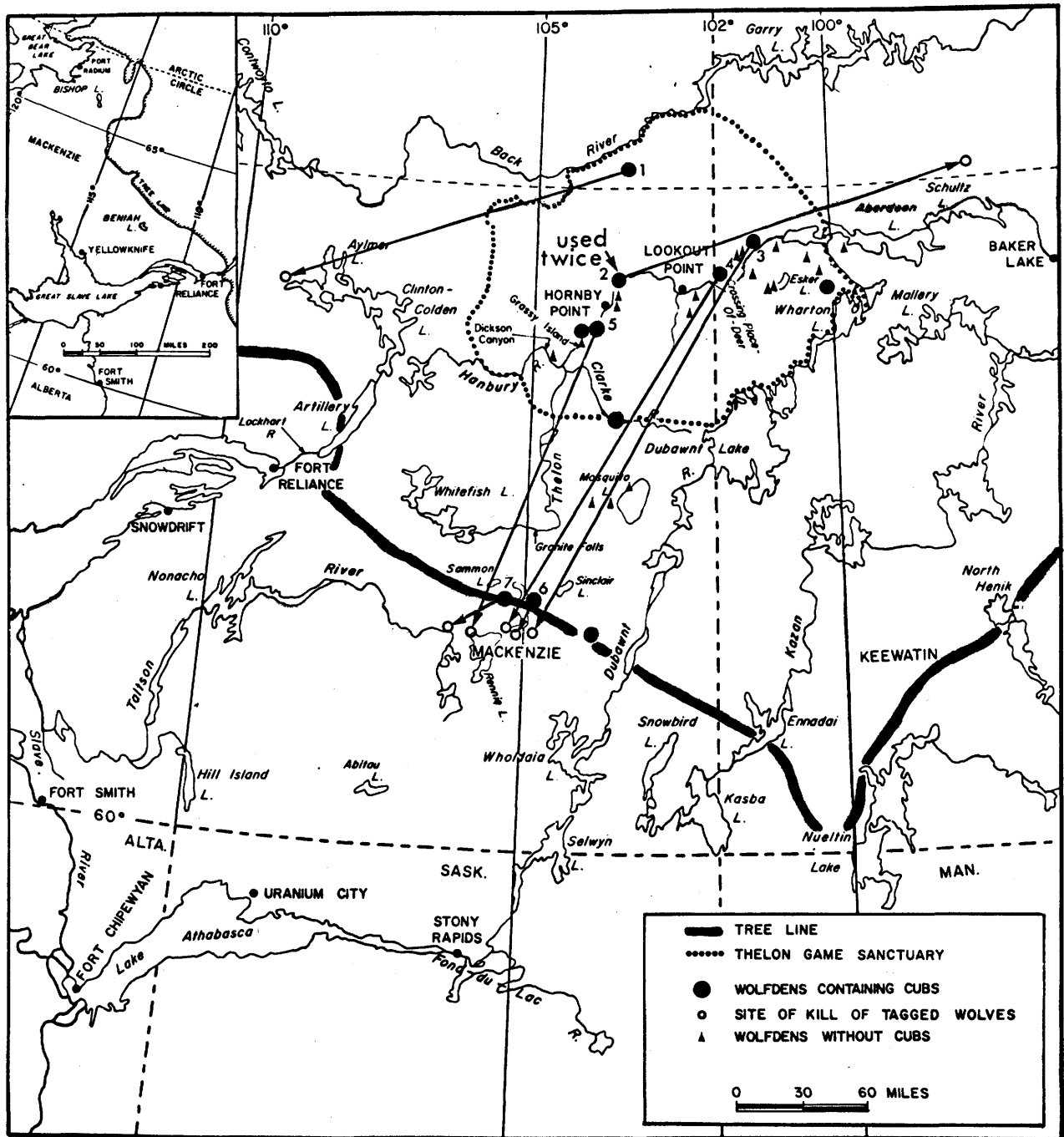


Figure 3 — MOVEMENTS OF EAR TAGGED TUNDRA WOLVES

3. A cub from a litter of six wolves, tagged on July 1, 1960 near the Thelon River was killed on December 7, 1965 (age 5½ years) near Damant Lake or 225 miles southwest of the den site.
4. A cub from a litter of four tagged on June 29, 1965 near the Thelon River, was killed on December 15, 1965 near Damant Lake, a distance of 208 air miles southwest of the den site.
5. A cub from a litter of five tagged on July 4, 1965 near Hornby Point on the Thelon River was killed on April 29, 1965 near Rennie Lake, or 184 air miles southwest of the den.
6. A cub (the only one in the litter) tagged on July 21, 1965 near Sinclair Lake was killed on November 1, 1965 near Damant Lake, 16 air miles south of the den site.
7. A cub from a litter of three tagged on July 22, 1965 near Sammon Lake was killed on April 27, 1965 on the Taltson River, 38 air miles southwest of the den.

Eight litters of wolves were observed in caribou-occupied areas north of the Clarke River. The litters consisted

of six (1960), five (1962, 1965), four (1960, 1964, 1965) and three cubs (1960, 1961). A litter of a single cub was found in 1965 on the north bank of the Clarke River and two litters of three cubs and a litter of one cub were observed south of the Clarke River in areas devoid of caribou. As the Clarke River was the arbitrary boundary between caribou-occupied areas and areas devoid of caribou and as no caribou were seen within 10 miles of the river, the wolf den on the river's north bank was included in the area without caribou. Average litter size of wolves denning in caribou-occupied areas was 4.3 and 2.0 cubs in areas devoid of caribou. A statistical analysis of the data (Student's t test) has shown that the means differ significantly ($t = 3.50$; d.f. = 10; $P < .01$). Kelsall (1960) reported a litter of three wolf cubs north of the Clarke River and a litter of four south of that river. Active wolf dens found during the present study are indicated on Figure 3.

2. Food habit studies

a. Examination of scats

The results of the examination of 595 wolf scats are in Table 1. One hundred and sixty-eight scats were of cubs. These data reflect the spring and summer food habits of tundra wolves.

Table 1. Analysis of 1039 food items in 595 wolf scats from spring and summer range of wolves, Thelon River study area, 1960 - 1965.

FOOD ITEMS	CUBS			NON CUBS [#]			NORTH*	SOUTH**	TOTAL FOOD ITEMS
	NORTH	SOUTH	TOTAL	NORTH	SOUTH	TOTAL	TOTAL	TOTAL	
	## + No. %	No. %	No. %	No. %	No. %	No. %	No. %	No. %	
Caribou, adult	25 30.5	66 31.4	91 31.2	203 46.3	101 32.7	304 40.7	228 43.8	167 32.2	395 38.0
Caribou, calf	21 25.6	16 7.6	37 12.7	46 10.5	10 3.2	56 7.5	67 12.9	26 5.0	93 9.0
Muskox	-- --	-- --	-- --	19 4.3	-- --	19 2.5	19 3.7	-- --	19 1.8
Wolverine	-- --	-- --	-- --	2 0.5	-- --	2 0.3	2 0.4	-- --	2 0.2
Ermine	-- --	-- --	-- --	1 0.2	-- --	1 0.1	1 0.2	-- --	1 0.1
Wolf	1 1.2	-- --	1 0.3	6 1.4	1 0.3	7 0.9	7 1.3	1 0.2	8 0.8
Arctic Fox	-- --	-- --	-- --	4 0.9	3 1.0	7 0.9	4 0.8	3 0.6	7 0.7
Red Fox	-- --	-- --	-- --	-- --	1 0.3	1 0.1	-- --	1 0.2	1 0.1
Unidentified Carnivore	-- --	-- --	-- --	6 1.4	2 0.6	8 1.1	6 1.2	2 0.4	8 0.8
Arctic Hare	3 3.7	-- --	3 1.0	4 0.9	2 0.6	6 0.8	7 1.3	2 0.4	9 0.9
Arctic Ground Squirrel	1 1.2	-- --	1 0.3	10 2.3	-- --	10 1.3	11 2.1	-- --	11 1.1
Microtines	13 15.9	22 10.5	35 12.0	60 13.7	38 12.3	98 13.1	73 14.0	60 11.6	133 12.8
Unidentified Mammal	7 8.5	7 3.3	14 4.8	17 3.9	3 1.0	20 2.7	24 4.6	10 1.9	34 3.3
Goose	1 1.2	-- --	1 0.3	2 0.5	-- --	2 0.3	3 0.6	-- --	3 0.3
Ptarmigan	-- --	1 0.5	1 0.3	5 1.1	10 3.2	15 2.0	5 1.0	11 2.1	16 1.5
Unidentified Bird	9 11.0	52 24.8	61 20.9	21 4.8	54 17.5	75 10.0	30 5.8	106 20.4	136 13.1
Egg	-- --	9 4.3	9 3.1	10 2.3	26 8.4	36 4.8	10 1.9	35 6.7	45 4.3
Fish	-- --	17 8.1	17 5.8	8 1.8	31 10.0	39 5.2	8 1.5	48 9.2	56 5.4
Carrion	-- --	-- --	-- --	6 1.4	1 0.3	7 0.9	6 1.2	1 0.2	7 0.7
Beetle	1 1.2	17 8.1	18 6.2	8 1.8	19 6.1	27 3.6	9 1.7	36 6.9	45 4.3
Hymenoptera	-- --	3 1.4	3 1.0	-- --	7 2.3	7 0.9	-- --	10 1.9	10 1.0
Total No. of food items	82 100	210 100	292 99.9	438 100	309 99.8	747 99.7	520 100	519 99.9	1039 100.2
Total No. of scats	58	110	168	297	130	427	355	240	595
No. of food items/scat	1.41	1.91	1.74	1.47	2.38	1.75	1.47	2.16	1.75
<u>Non-food items</u>	No.	No.	No.	No.	No.	No.	No.	No.	No.
Diptera	--	1	1	4	5	9	4	6	10
Grass, sedge	2	5	7	17	5	22	19	10	29
Other plant material	3	12	15	20	2	22	23	14	37
Sand, clay, ash	7	14	21	55	10	65	62	24	86
Other	--	--	--	2	--	2	2	--	2

* Area north of Clarke River, where caribou are present during most of wolf denning season.

** Area south of Clarke River, temporarily devoid of caribou.

Wolves other than cubs at dens.

Number of scats in which each of listed food items occurred.

+ Percentage occurrence in total number of food items.

The number of food items per scat may be considered as an indication of the variety of the wolves' diet (Table 1). There is practically no difference between the two broad age groups, that of cubs and of wolves other than cubs (1.74 and 1.75 food items per scat). Statistical analysis (Student's t test) has shown that a highly significant difference occurs between the means of the number of food items per scat found in the areas north and south of the Clarke River ($t = 8.256$; d.f. = 593; $P < 0.001$). This difference can be considered as an indication of the greater variety in the diet of wolves temporarily separated from the main prey species.

The interiors of occupied wolf dens which I examined in the study area were devoid of droppings without exception. Young captive cubs in our wolf compound, prior to walking, are kept meticulously clean by their mother. Urination by the cub is initiated at first by the bitch licking the cub's urogenital area. Droppings deposited by the cubs in the dens are eaten by the parents and study of our captive wolves showed that the mother would also eat the cubs' droppings (milk scats) outside the den at least until weaning. The bitch reacted quickly to the characteristic pose of the defecating cub.

Caribou

Scats of cubs and other wolves, in caribou-occupied areas as well as in areas south of the Clarke River temporarily devoid

of caribou, show the predominance of caribou in the wolves' diet. Since the droppings cannot be accurately dated and may, therefore, have been deposited early in the spring when caribou are migrating northward through the wolf denning areas south of the Clarke River, interpretation of the data is difficult. It is apparent, however, that caribou constitute the main food.

Thirty-eight per cent of the food items found in wolf scats were remains of adult caribou (Table 1). Figures from cub scats, both north and south of the Clarke River, as well as the figures from scats of wolves other than cubs south of that river, show that about 30 per cent of the food items were caribou remains. The sample of scats of wolves other than cubs, collected in areas north of the Clarke River, where caribou were available for a longer part of the summer, shows that 46.3 per cent of food items were remains of adult caribou. Cub scats from this area were lower in adult caribou remains (30.5 per cent) but that figure was complemented by 25.6 per cent of caribou calf remains, a much higher percentage of calf remains than for any of the other three samples. Young wolves in the area north of the Clarke River therefore appear to depend heavily on calves. Presumably these were killed by adults or found dead and carried to the dens. Many young calves die in some years due to inclement weather. Wolves would then have no difficulty in obtaining food. Since few wolf dens were found near Beverly Lake (main caribou calving

grounds) and consequently few droppings were collected, the data indicate selection of calves (dead or alive) by wolves. My data indicate that in those areas adult wolves, associated with dens containing cubs, ate mostly adult caribou, whereas the cubs ate a higher proportion of calves than did their parents.

Muskoxen

It is evident that muskoxen are not heavily preyed on by wolves in the area studied.

Nineteen droppings of 595 examined contained remains of muskoxen. Scats containing muskox remains were collected only in 1960 (two scats), 1964 (four scats), and 1965 (13 scats). Two of the four scats collected in 1964 were found at the remains of a 15-18 year-old bull muskox. The carcass was found in late July in willow thickets along the Thelon River. Broken branches and dead leaves on the willows, tufts of muskox and wolf hair indicated that the bull had been killed perhaps a month earlier, apparently not without a struggle. Nine of the thirteen scats which contained muskox remains were found in 1965 near an occupied wolf den at the Crossing-Place-Of-Deer on the Thelon River. The remaining four scats were collected near an unoccupied wolf den in the Dickson Canyon area. One of these

droppings contained teeth and fragments of the lower jaw of a week-old muskox calf.

Muskoxen are commonly seen along the Thelon River and several of its tributaries in summertime. I have not seen them south of the Clarke River in that time of the year and neither have they been observed there on a recent winter survey, when 568 muskoxen were counted within the Thelon Game Sanctuary (Tener and Kuyt, 1966). No wolves were observed on that survey.

Wolverine

Wolverine are rare in the study area. During five summers in the Thelon Game Sanctuary, I have seen wolverine on only six occasions, all along the Thelon River. Wolverine remains (claws) were found in two wolf scats, both collected near an occupied den located on an island in the Thelon River.

Ermine

Ermine are only rarely encountered in the Thelon River area. Because of their low density they are not important in the wolf's diet. Only one wolf scat (collected in 1963) contained several bones and hair of an ermine.

Wolf

Murie (1944) found wolf remains in one of 1,174 wolf scats and Kelly (1954) found wolf remains in six of 156 wolf stomachs examined. Kelsall (pers. comm.) reported that a Yellowknife wolf pack ate one of its members on a road one night about 1953. Here, and elsewhere, it is not clear whether the wolves killed their victim or whether their prey was killed by man or had died of injury or disease and consequently could more accurately be described as carrion. Wolf hair was found in six wolf droppings in the present study and one scat contained the lower first pre-molar of a wolf. Moulting in wolves begins around the end of May and frequent scratching and licking by the wolves during the moult could account for occasional hairs being ingested. The one scat with the pre-molar indicated that the possibility of wolves eating their kind does exist.

Several small teeth recovered from wolf droppings appeared to be deciduous teeth of young wolves. The teeth, upon being replaced by permanent teeth, may have been swallowed with the food. These small teeth were collected near Sammon and Sinclair Lakes where skeletal remains of wolf cubs were found near wolf dens, a further indication that cannibalism may

have taken place. These teeth were classified under "Unidentified carnivores".

Examination of 61 diaphragms of wolves collected in the Bishop Lake-Beniah Lake area and elsewhere indicated approximately 50 per cent of wolves examined to be infected with Trichina spiralis (Choquette, L.P.E. and E. Kuyt, unpublished data). That would be indicative of wolves' feeding on prey species having trichinosis, including possibly other wolves, wolverine, ermine, foxes and rodents.

Arctic fox

Remains of arctic fox were found in seven wolf scats. Four were collected in 1963 near a wolf den along the Kazan River. That den, an enlarged arctic fox den, was vacant when examined by me but had contained wolf pups earlier in the same year (A.H. Macpherson, pers. comm.). It is possible that the occupant was killed by the wolves and the den taken over by them. When I examined the den the following year, tracks of a single arctic fox indicated that that species was again using the den. The other three wolf scats containing remains of arctic fox were gathered on an occupied wolf den near Sammon Lake close to the tree line. That area is well south of the breeding range of the arctic fox suggesting that the fox was on migration at the time of its death.

Red fox

The only occurrence of red fox was several claws recovered from a wolf dropping near Sammon Lake. Red foxes are seen several times each summer along the Thelon River where I have found three dens with young.

Unidentified carnivores

The items classified in this group were entire or fragmented claws or teeth. There were no remains of carnivores in cub scats, whereas eight scats of older wolves contained remains of carnivores. Adult wolves apparently do not carry dead carnivores to their dens or, less likely, cubs at dens do not eat them.

Arctic hare

Nine wolf droppings contained remains of arctic hares; seven were found north of the Clarke River, along the Thelon, Finnie and Hanbury Rivers.

Ground observations and low altitude aerial reconnaissance in winter, early spring and summer, show that arctic hare distribution in the Thelon Game Sanctuary

varies with the season and topography. In late winter and early spring, tracks of hares are common on the willow-clad banks of the rivers whereas hares are rarely seen there in the summer. A few hares were seen in the summer on eskers, on boulder fields and on other rocky terrain, chiefly in areas north of the Clarke River.

Arctic ground squirrel

Ground squirrels are abundant along the Thelon River and its tributaries and on eskers. They were particularly common in 1964 and 1965. Eleven wolf droppings contained remains of that species. No scats containing ground squirrel remains were found south of the Clarke River although those squirrels occur there. My Labrador dog was able to catch several of them by simply rushing upwind and - if the quarry was out in the open - running it down. It is somewhat surprising that ground squirrels are not found in the wolf's diet with greater frequency; apparently wolves make no special efforts to catch these mammals. Murie (1944) found ground squirrel remains in 28 of 101 and 64 of 156 wolf scats collected during two periods of caribou scarcity.

Microtines

Occurrence of microtines in number of food items of cub wolves was 10.5 and 15.9 per cent for areas devoid of caribou and caribou-occupied areas respectively. Similar figures for wolves, other than cubs were 12.3 and 13.7 (Table 1). The figures for the four different samples are of the same magnitude, suggesting that microtine rodents were eaten by pups and adults to the same extent, whether caribou were present or not. Murie (1944) describes in detail mouse hunting by cub and adult wolves, not only when caribou were available as stragglers but also when caribou were plentiful.

Brown and collared lemmings as well as red-backed mice are known to occur in the area. Lemmings (especially Discrostonyx) were common in the study area in the summer of 1960. In 1962, the lemming population was low in many locations and appeared to have "crashed" during the summer of 1961. At least until 1965, the lemming population had not reached its former high density. Density of these small mammals varies from year to year but also with location (Macpherson, 1966) and it is somewhat difficult to assess their relative importance in the wolf's diet from year to year.

Remains of microtines were surpassed in frequency of occurrence only by caribou remains and those of unidentified birds. They occurred with almost equal frequency in the droppings of cubs and in the droppings of other wolves (12 per cent versus 13.1 per cent).

Unidentified mammals

Most of those remains were bone chips and their frequency of occurrence in caribou-occupied areas is somewhat higher than south of the Clarke River. It is possible that most of the bone chips were of caribou.

Geese

It appears that wolves are not important as predators of geese in the Thelon River study area.

Three droppings containing goose remains (feathers) were found. Parts of legs of Canada geese were found on wolf dens on two occasions. A wolf stalking Canada geese was observed near Grassy Island in 1962. A group of five tourists canoeing down the Thelon River in 1966 reported to me that they had seen a wolf catching a goose, also near Grassy Island

(R. E. Matteson, pers. comm.). The goose was one of a flock of moulters accidentally driven on shore by the travellers. Kelsall (pers. comm.) reported a pilot's observation of a wolf's swimming after flightless Canada geese on a tundra pond in 1958 in an apparent effort to herd the birds ashore.

White-fronted geese and Canada geese are common along the Thelon River system where they breed (white-fronts) and moult (both species). Canada geese are not known to breed along the Thelon River but are found in large moulting flocks. My Labrador retriever caught many of these flightless, moulting birds during banding operations (Kuyt, 1966).

Ptarmigan

The low number of wolf droppings containing remains of ptarmigan (16) indicates the relative unimportance of ptarmigan in the wolf's summer diet, although willow ptarmigan are common throughout the study area. Only one cub scat contained that species (Table 1). Adults are better able to hunt ptarmigan judging from the number of scats (15) containing ptarmigan remains. The tabulated scat analysis shows that ptarmigan, in the area south of the Clarke River are somewhat more important in the wolf's diet than in the area north of the Clarke River.

A wolf chasing two ptarmigan was observed near Mosquito Lake in late July, 1965. The two birds would allow the wolf to approach closely and then they would flush and land a short distance away. Young ptarmigan were on the wing at the time and the behaviour of the adult birds indicated that a brood was nearby. No captures were made by the wolf. My Labrador retriever was able to catch young ptarmigan on a few occasions and undoubtedly wolves are equally capable.

Unidentified birds

Bird remains other than geese or ptarmigan were lumped under this classification and 136 wolf scats contained remains of these birds (Table 1). Although feather shafts of a few large birds, possibly ducks, were found, most unidentified bird remains were feet and skulls of fledgling passerine birds. At fledging time the feeding calls of these ubiquitous birds are heard everywhere. I have no records to show whether passerine birds fluctuated in numbers throughout the study. Wolves in areas south of the Clarke River temporarily devoid of caribou, depended more heavily on small birds (20.4 per cent) than do wolves north of the Clarke River (5.8 per cent). Especially in the cub's diet, small birds were important with a

much greater dependency on these birds in areas devoid of caribou (Table 1).

Eggs

Remains of egg shells and egg membranes were more common in the scat of older wolves than of cubs; in 36 and 9 droppings respectively. Egg remains were more frequent in areas temporarily devoid of caribou, as these remains were found in 35 droppings south of the Clarke River but only in 10 droppings north of that river. On several occasions ptarmigan feathers were found intermingled with egg shells. All egg remains were of a thickness to suggest eggs of ptarmigan or duck-sized birds.

Fish

Fish are an important part in the diet of wolves in areas where caribou are absent during most of the denning season. Seventeen cub scats and 31 of older wolves contained fish bones and scales whereas in caribou-occupied areas north of the Clarke River only eight droppings (all of them of wolves other than cubs) contained fish remains. Only once or twice were teeth of fish found in wolf droppings, indicating that a trout or pike had been eaten. Part of the jaw

of a trout or pike and a piece of an unidentified fish skin have also been found at wolf dens during the study. No attempt was made to identify to species fish bones and scales found in wolf scats.

I have not been able to determine how wolves obtain fish, and whether fish are caught alive or found dead. Most whitefish are fall spawners and may then gather in schools in shallow waters. On several occasions in late summer I have seen whitefish trapped in small creeks where they could easily have been caught by a wolf.

Kelsall (pers. comm.) in the spring of 1950 observed a red fox catching lake trout in the Bathurst Inlet area. The fox was using small sedge tussocks in the shallow part of a lake as stepping stones. When a fish approached, the fox would pounce on it from its vantage point on the tussocks. The skins of several freshly-killed trout lying at a den nearby were indications of the success of the fox.

Young and Goldman (1944) record instances of wolves catching spawning salmon in British Columbia and Alaska. Francis (1960) reports six wolves feeding on a concentration of minnows and water bugs in a hole in the frozen Torch River, Saskatchewan.

Grayling, pike and suckers (for scientific names, see Appendix B) are early spring spawners and may then be found in small streams or shallow lakes where they would be vulnerable to predation.

Carrion

Several pupal cases of the black blow fly (Phormia regina) were found in wolf droppings. It is likely that the wolves had fed on fly-blown meat. Seven scats contained remains of carrion. All scats were from wolves other than cubs and with the exception of one scat, were found in caribou-occupied areas north of the Clarke River.

Dead caribou are often encountered in the wake of their migrations. Some of those undoubtedly have been killed by wolves, others not showing external wounds may have died as a result of injuries received in crushes or from other unknown factors. One wolf is not able to eat an entire adult caribou in a day, or even several days, and if the wolf moved away, much of the carcass would remain to be eaten by scavengers or left to spoil. In most areas wolves have no difficulty finding live prey in the summer. Carrion is not often resorted to then, as suggested by the food data (Table 1).

Beetles

The chitinous cuticle of beetles (Coleoptera) is highly resistant to digestive juices of the wolf. Mouth parts, legs and elytra of beetles pass through the wolf's digestive tract almost intact and can be readily identified.

Vast quantities of beetles would be required to nourish a large animal such as the wolf and it seems unlikely that wolves would bother with such small food. Yet wolves in the area temporarily devoid of caribou appear to eat beetles when they can. In that area, 17 (8.1 per cent) cub scats and 19 (6.1 per cent) of older wolves contained remains of beetles. In caribou-occupied areas only an occasional dropping contained beetle remains. As in the case of fish and small birds in the wolf's diet, beetles are probably resorted to when larger prey is temporarily unavailable.

Hymenoptera

Remains of hymenopteran insects were found in 10 droppings. These droppings contained parts of bees or wasps which were classified as food items. Their contribution to the wolf's diet is insignificant.

Non-food items

The cuticle of larvae of the caribou warble fly (Oedemagena tarandi) was found on occasion. Since these larvae were most likely ingested with the flesh of caribou, their remains were not classified as food items. Similarly, the pupal cases of blow flies were not tabulated as they are believed to have been part of carrion which was classified as such. They, together with the warble fly larvae, occurred in 10 scats (Table 1).

Grasses and sedges were recorded but not classified as food items. They occurred in 29 scats of 595 examined (Table 1). Murie (1944) believes grass may act as a scour to assist the wolf in ridding itself of internal parasites as he found grass in several droppings which also contained roundworms. One fresh scat collected by me on a wolf den near Helen Falls on the Hanbury River was a solid mass of grass containing several tapeworms (Taenia sp.).

Wolves kept captive in Fort Smith frequently eat grass although these animals are not heavily infested with intestinal parasites. Other vegetation, such as spruce needles, leaves of ericaceous plants (Ledum, Vaccinium, Arctostaphylos) and Bogmoss (Spaghnum sp.)

was infrequently found in the droppings. These items and occasional berries are believed to be ingested with prey and are not classified as food.

Of the 595 scats examined, 86 contained various amounts of unidentified material, resembling dried clay. Several scats were made up entirely of that material. The material is probably undigested remains of meals consisting mainly or entirely of meat, as droppings of captive wolves, after having been fed on meat only, were identical in appearance and consistency.

The two non-food items recorded under "Other" (Table 1) were an unidentified piece of metal found in one scat and a No. 4 shot pellet found in another dropping. The pellet may have been ingested by the wolf with the flesh of a migratory bird.

b. Determination of stomach contents

i. Wolves collected in summer

One of six stomachs was accidentally discarded. Two stomachs contained only a small amount of fluid and a few stalks of sedge, and some caribou hair respectively. Two stomachs

contained three pounds (1360 g) and 5.75 pounds (2610 g) of fresh caribou meat. The first of these stomachs contained one kidney, the tongue, larynx, liver and trachea of a caribou which appeared to be fresh. The latter stomach contained the trachea, tongue and esophagus as well as the heart, liver, lung and a kidney, of an adult caribou and a few pieces of discoloured meat and connective tissue (perhaps from an earlier meal). Kelly (1954) reports finding reindeer and caribou tongues in two wolf stomachs. Another stomach examined by him contained an estimated 15-18 pounds (6810 - 8170 g) of caribou including ear, tongue, lip, two kidneys, liver, windpipe, hair and large chunks of meat. The wolf stomach containing 5.75 pounds of caribou meat also contained a few fragments of bone with a piece of a rifle bullet imbedded in it. Larval tapeworms (Cysticercus tenuicollis and C. tarandi) found in the caribou meat were indicative of the freshness of the wolf's meal.

The sixth wolf, which was lactating, was found dead on June 30, 1965 near a wolf den about 25 miles south of Beverly Lake. Its stomach contained only a small amount of food, including several costal

cartilages and intervertebral fibro-cartilages of a calf caribou.

ii. Wolves collected in winter

Tables 2, 3 and 4 summarize results of the examination of stomachs of 12, 55 and 226 wolves killed on caribou winter range. For comparison, Table 5 shows the results of the examination of the stomachs of five wolves poisoned on range not used by caribou. The great variety and quantity of food eaten by specimen EK 211160, a 57-pound male wolf cub, are noteworthy.

It is evident that caribou constitute the staple food of wolves. Practically all wolves killed on strychnine baits will have varying amounts of poisoned meat in their stomachs. Since predator control officer Riddle does not skin the meat used for baits, it is impossible to determine from his reports (Table 4) whether the caribou meat found in 136 wolf stomachs was bait meat or not.

A small number of stomachs contained remains of arctic fox, wolf and wolverine. It seems certain

Table 2. Analysis of stomach contents of 12 wolves killed on caribou winter range north of Yellowknife, winter 1960 and 1961.

Specimen number	Weight (in grams) of stomach contents			Contents
	Total	Bait	Prey	
EK 223604	450			Mostly bait, several black spruce cones.
EK 223605	550	400	150	Wolverine.
EK 223606	725	720	5	Ptarmigan.
EK 223607	225			Mostly bait, rest carrion, including sucker (<u>Catostomus</u> sp.).
EK 223608	125	20	105	Wolverine hide.
EK 171611	1025	1025		Bait only.
EK 171612	950	600	350	Caribou hide and hair.
EK 132612	1300	500	800	Caribou.
EK 132613	2575	900	1625	Caribou.
			50	Red Fox.
EK 132615	275			Mostly bait.
EK 132616	450	250	200	Caribou, few ptarmigan feathers.
EK 13361	375	125	250	Caribou.

Table 3. Analysis of stomach contents of 55 wolves killed on caribou winter range near Great Bear Lake, February-March, 1964.

Number of stomachs examined	Number of stomachs containing:		
	Bait only	Bait and caribou	Other
55	35 (64%)	20 (36%)	10* (18%)

* Ptarmigan and/or unidentified birds (8), mouse (1), wolverine (1 stomach).

Table 4. Analysis of stomach contents of 226 wolves killed on caribou winter range in southeast Mackenzie District from 1957-1967.*

Number examined	Empty	Number of stomachs containing:			
		Bait	Caribou	Unidentified	Other
226	50 (22%)	6 (3%)	136 (60%)	14 (6%)	20** (9%)

* Data from C. F. Riddle.

** Includes arctic fox (7), otter (5), wolf (4), wolverine (2), mink (1), and fish (1 stomach).

Table 5. Analysis of stomach contents of five wolves killed near Yellowknife on range not used by caribou, winter 1960.

Specimen number	Weight (in grams) of stomach contents			Contents
	Total	Bait	Prey	
EK 124601	975	975		Entirely bait.
EK 124602	825			Mostly bait, some garbage.
EK 124603	1350	1340	10	Snowshoe hare.
EK 23460	1050	850	200	Fish (wolf killed near fish camp).
EK 211160	3325	1050	695	Snowshoe hare.
			75	Ptarmigan.
			50	Spruce grouse.
			200	Muskrat.
			25	Red squirrel.
			5	Fish.
				Pieces of leather, rags and spruce twigs.

that most of these predators had died on baits and were eaten by wolves. It is known that damaged wolves or arctic fox are sometimes used as bait by predator control officers.

Otter and mink were identified by Riddle in five and one stomachs respectively. Confusion of remains of these furbearers with parts of the hide of wolverine is, according to Riddle, not possible. It seems unlikely that these locally rare and water-oriented mustelids would be common prey to wolves, although on the basis of track observations from low-flying aircraft, I have noted that otter travel extensively on ice between holes in frozen rivers. Any otter, when surprised out of the water, would be no match for wolves. Since many of the baits are frozen into the ice of lakes and rivers, there remains a possibility that these furbearers may have fallen victim to the strychnine baits and were subsequently eaten by wolves.

Only the 10 stomachs containing ptarmigan and the stomach containing mouse reflect with certainty the utilization of live prey other than caribou by wolves on caribou winter range.

c. Examination of caribou remains

i. Spring and summer

Age

There is only indirect evidence that the collection of 151 caribou mandibles (Table 6) represents summer mortality caused by wolves. The present sample reflects the age and sex composition of caribou dying in spring and summer of all causes (predation, diseases, accidents, weather), excluding human predation. Because of reasons given earlier (location of remains near wolf dens), I believe that a large proportion of the sample represents mortality by wolves.

Results of the examination of 151 caribou jaws found in spring and summer are tabulated (Table 6). The present study shows a much higher (33.8 per cent versus 15.1 per cent) mortality among caribou up to one year than found by Banfield (1954). A similar observation can be made for caribou 8-9 years and 10+ years old (10.6 per cent versus 4.5 per cent). Banfield's study shows a considerably higher mortality among two- and three-year-old caribou

Table 6. Caribou spring and summer mortality by age in areas not hunted by man, compared with year-round mortality of all causes including hunting by man.

Spring and summer mortality*			Year-round mortality**		
Age (years)	N	Per cent	Age (years)	N	Per cent
0 - 1	51	33.8	1	44	15.1
1 - 2	9	6.0	2	51	17.5
2 - 3	11	7.3	3	60	20.5
3 - 4	10	6.6	4	22	7.5
4 - 5	8	5.3	5	23	7.9
5 - 6	5	3.3	6	12	4.1
6 - 7	5	3.3	7	15	5.1
7 - 8	8	5.3	8	17	5.8
8 - 9	16	10.6	9	13	4.5
9 - 10	7	4.6	10	12	4.1
10+	16	10.6	11	13	4.5
Unknown	5	3.3	12	10	3.4
Total	151	100.3		292	100.0

* Present study.

** Data from Banfield (1954).

than my figures show for mortality of caribou, excluding hunting by man. The major difference between Banfield's and my data is that the former include hunting by man. It is certain, therefore, that during Banfield's study two- and three-year-old caribou were hunted extensively by man. On the basis of Table 6 only, it cannot be said that wolves kill a large proportion of calf caribou. Kelsall (1960) in examining caribou carcasses found an even greater percentage of calves (56 per cent). In contrast to the present study, however, Kelsall's figures are based largely on investigations carried out on caribou calving grounds. Inclement weather during 1957 and 1958 appeared to have caused large calf losses and Kelsall indicates that some of the calves reported by his field men as wolf kills may have died of other causes.

Table 6 further shows that mortality, except that caused by man in age classes other than calves, is fairly constant except for an increase in the 8-9 year and older than 10-year age classes.

Mortality from all causes, except hunting by man, is lowest among the 4-8 year age classes.

It is possible that this is because of a low incidence of those four age groups in the caribou population, a reflection of a series of poor calf years. Certainly between 1950 and 1958, calf crops were well below the potential for barren-ground caribou (Kelsall, 1960).

Sex

Seventy-seven of the collection of 151 caribou remains were of caribou considered to be four years of age and older. Twenty-five of these were damaged so that their sex could not be determined. Nine of the remaining 52 were males and 43 were females; a sex ratio of 20.9 males to 100 females. Banfield (1954) in studying the herd composition of caribou, found a ratio of 35.8 males to 100 females. More recently, Kelsall (1960) reported an adult male:female ratio of 60:100. If the sample of 151 jaws reflects wolf predation, as it is strongly suspected, it appears that female caribou are subject to proportionally higher wolf predation than are males.

ii. Winter

Age

It has been explained (p. 31) that the 17 caribou remains found in winter during aerial surveys are probably the result of wolf predation. Mortality among the 0-1 year age class (at time of death about nine months old) although still important was 11.8 per cent (Table 7), considerably lower than during the summer (33.8 per cent). Because total mortality in the 0-1 year age class was expected to be higher than in other age classes, the availability of that group would be less in winter than in the preceding summer. Although caribou mortality is fairly evenly distributed in the small sample, there is a somewhat higher mortality (17.6 per cent) in the 9-10 year age class than in the other age classes.

Sex

The winter remains show a greater proportion of carcasses of female caribou than males (0 males to 100 females) as did the summer caribou remains. A larger sample would be desirable to allow for definite conclusions.

Table 7. Age and sex of 17 caribou killed by wolves on caribou winter range, Abitau Lake, N.W.T., March 1968.

	Female	Unknown	Total	Per cent
0 - 1 year		2	2	11.8
1 - 2 year	1	1	2	11.8
3 - 4 year	2		2	11.8
6 - 7 year	1		1	5.9
7 - 8 year	1	1	2	11.8
8 - 9 year	2		2	11.8
9 - 10 year	3		3	17.6
10+ year	2		2	11.8
Unknown age	1		1	5.9
Total	13	4	17	100.2

Sex ratio: 0 males to 100 females.

d. Examination of wolf-killed caribou

Of the 151 caribou remains found in spring and summer, only at 14 was there direct evidence that they had been killed by wolves. The similarity among the 14 caribou carcasses in body area attacked, parts of body eaten, the evidence of attack by wolves in the form of tracks and signs of struggles, and the frequent presence of wolves are considered ample proof that

these caribou were the prey of wolves. There is a strong correlation between the initial parts of a caribou eaten by wolves (as determined from examination of stomach contents) and the results of the examination of wolf-killed caribou. No similar material was collected from the area south of the Clarke River.

Detailed field notes on the examination of these caribou killed in spring and summer are in Appendix A. The 14 caribou were composed of the following age and sex categories:

- 5 calves (one male, sex of other four not recorded) - 35.7 per cent;
- 2 yearlings (one female, sex of one not recorded) - 14.3 per cent;
- 2 bulls (3 and 8-9 year old) - 14.3 per cent;
- 5 cows (4, 6, 8-9, 9 year old, age of one not known) - 35.7 per cent.

e. Observations of wolf predation on caribou

Murie (1944), Crisler (1956) and Kelsall (1968) have described examples of success and failure of the rarely witnessed caribou hunts by wolves.

My examination of wolf-killed caribou has shown that the initial point of attack of wolves is usually the

neck or shoulder of the caribou. That area is bitten by the wolf and the caribou pulled down or knocked down. The wolf then seizes the neck or shoulder and kills the caribou by a crushing bite in the neck.

The shoulder or neck target appears to be a much better locus of attack for a wolf than the caribou's hind leg. The leg, in a rapidly running caribou, can only be a fleeting target and, in case of a near miss by the wolf, might produce a serious blow or kick, whether intended by the caribou or accidental. Certainly of equal importance to the wolf, this might also result in the escape of its prey. A wounded caribou found in 1957 on an island in the Thelon River, had been bitten in the upper part of a hind leg. The animal may have escaped from a predator by swimming to the island. None of the intact caribou known to have been killed by wolves showed such injury. It is significant that in this instance the caribou escaped. Impact in the shoulder or neck area, should the wolf's teeth miss their target, in all likelihood would result in the caribou being knocked over by the onrushing wolf. Seven of the 14 known wolf-killed caribou found in the present study were killed in that manner. I believe the remaining seven caribou were killed in the same way but because of the extent to which the carcasses had been eaten, it was not possible to be certain.

Initial feeding of wolves

The throat area, including the tongue, had been eaten or bitten on all but one of the 14 caribou killed by wolves. Sometimes these parts are eaten immediately after the caribou's death but once (Bull 1, Appendix A) a small amount of flesh from a hind leg was eaten initially. As in the case of Calf 1, the bull had been killed recently, perhaps minutes before being found by us, and the wolf may have been disturbed by the survey aircraft sufficiently to cause disruption of its normal feeding behaviour.

After eating the tongue and adjacent parts of the fresh kill, the wolf usually breaks into the caribou's abdominal cavity and pulls out the intestine and stomach, apparently to facilitate reaching the preferred liver, kidneys, heart and lungs. The intestine is frequently eaten in winter but in the summer it is often left intact. The stomach is rarely eaten although our captive wolves in Fort Smith readily ate the washed stomach of bison. The contents of the caribou's stomach are probably disagreeable to the wolf's taste.

The fleshy upper parts of the caribou's hind leg are also preferred by the wolf but apparently less so

than the throat area and the large visceral organs. It was reported earlier (p. 27, p. 60) that the stomach of a wolf killed on July 16, 1963 near Aberdeen Lake, contained a kidney, the tongue, larynx, trachea and liver of a freshly dead adult caribou and that another wolf, taken on August 11, 1963, had eaten the tongue, trachea, esophagus, heart, liver, one kidney and lung of a caribou which had died recently.

3. Food studies of captive wolves and growth of cubs

a. Food consumption by captive wolves

During three years (1,101 days) from November 24, 1964 to November 30, 1967, our captive wolves consumed a total of 21,879 pounds (9933 kg) of bison meat and fat, and 1,775 pounds (806 kg) of commercial dog food. Total number of wolf-unit days (p. 35) was 6,777, the average number of wolf units per day was 6.2. Based on these figures, the average daily food intake per wolf unit was 3.23 pounds (1466 g) of bison meat and fat and 0.26 pounds (118 g) of commercial dog food. The average daily food consumption per wolf unit by month is in Figure 4.

During the feeding studies, all captive wolves exhibited normal moult patterns and body measurements. Weights and fat deposits of sacrificed captive animals corresponded

closely with those of wild-caught wolves of the same age and sex.

b. Feeding habits of captive cubs

On June 8, 19 days after birth, the five cubs born on May 20, 1964, began eating a mixture of commercial dogmeal, chopped meat and milk. On June 18, less than a month after their birth, these cubs were chewing on frozen meat. On June 19, two of the five cubs were separated from the rest of the litter and taken along on field studies in the Thelon study area. From that day to the middle of August they were fed a mixture of boiled fish and dogmeal. The mother stopped lactating on or about July 2; 43 days from birth of the cubs.

Two litters were born in 1966. Three cubs were born on May 17 to a nulliparous two-year-old, and four cubs were born on May 24 to a five-year-old. The five-year-old had previously whelped in 1963 and 1964 and is the mother of the above-mentioned two-year-old.

On June 6, 20 days after birth, the three cubs of the two-year-old wolf were first observed chewing on meat, and less than a week later the cubs readily quit their underground den when the older wolves were being fed. On June 13, two of the cubs pulled a four-pound chunk of meat out of the mouth of a two-year-old male wolf (their mother's full brother), carried it away and

began to eat it in a corner of the pen. On June 17, these three wolf pups fought over the possession of raw bison meat and growled while so doing, at each other and at the adults. On June 21 it appeared that the three cubs were becoming increasingly dependent on meat. They howled and appeared fretful and excited but calmed down when fed raw meat. Two of the cubs dug out of their pen earlier that day and one managed to get into the lactating five-year-old's pen and was seen contentedly sucking milk from her, apparently more abundantly supplied than the cub's mother. It appears that at approximately 34 days from whelping the two-year-old female was nearing the end of her lactating period.

The four cubs born to the five-year-old female on May 24, 1966 fed on a large piece of raw meat on June 24. Two days later I observed them fighting over meat and on June 28 they also howled prior to being fed. Their mother stopped eating puppy scat on the same day. It appears that only "milk scats" are eaten. The mother had terminated her lactation period on July 13, 50 days after giving birth to her cubs.

The same female, now six years old, gave birth to six cubs on May 20, 1967. On June 11, the six cubs were observed

licking and chewing on bison meat although on that date only the deciduous canine teeth and incisors had grown sufficiently to be of any use. On June 20 it was noted that some cub scats now remained uneaten in the wolf pen. On July 10 the female had ceased lactating.

In summary, five lactating periods lasted 34+ days in the two-year-old wolf, 43 days for her mother when three years old, 50 days for the same wolf, then five years old and 51 days for the same wolf, then six years old. These dates are similar to those given by Ognev (in Pulliainen, 1965) who states that the female wolf suckles her young for 35-45 days.

If these dates can be extrapolated to lactation periods of wild wolves, it may be assumed that cubs at the early age of approximately a month and a half, depend largely or entirely on wild prey.

c. Growth of cubs

The mean weekly weights and weekly per cent relative growth rates (Brody, 1945, p. 508; Maher, 1964) were

calculated for three litters of cubs born in 1966 and 1967 in our compound in Fort Smith (Tables 8, 9, and 10). Growth curves for the three litters were plotted (Figures 5, 6 and 7).

The growth curves illustrate the rapid early growth of young wolves followed by a reduction in the rate of growth. The growth curve of Litter 3 (Figure 7) shows a dip for the end of July. Apparently their daily ration of an average of less than three pounds (1360 g) of bison meat per wolf without added dog food was insufficient to maintain the growing cubs.

The growth curves show points of inflection for the periods June 18-24, 1966, and June 15-24, 1967 (Figures 6 and 7). These minor fluctuations probably are related to the change in the cubs' diet from their mothers' milk to meat which took place during those periods (pp. 77-79). The break in the curve of Litter 1 (Figure 5) is not as pronounced as in the other two. Litter 1 consisted of only three male cubs. Perhaps the effects of a change from milk to meat on a small litter are not as pronounced as on a larger litter. The growth curves of Litters 2 and 3 show no apparent differences in character or growth rate between the sexes.

Table 8. Mean weekly weights and weekly per cent relative growth rates (k) of captive wolf cubs (Litter 1, born May 17, 1966).

Age (weeks/days from birth)	Mean weight (lbs.) of three males	k
0/3	1.9	
1/3	3.6 ^a	63.9
2/4	4.6	21.4
3/4	6.6	36.1
4/4	8.6	26.5
5/4	10.4	19.0
6/6	12.0	11.1
7/6	18.0	40.5
10/3	24.5	11.9
13/4	28.0	4.2
17/3	34.5	5.4
37/3	75.0 ^b	3.9
43/3	82.0 ^b	1.5

a henceforth mean weight of two males.

b weight of one male.

Table 9. Mean weekly weights and weekly per cent relative growth rates (k) of captive wolf cubs (Litter 2, born May 24, 1966).

Age (weeks/days from birth)	Mean weight (lbs.) of two males	k	Mean weight (lbs.) of two females	k
0/3	2.0		1.9	
1/4	3.9	58.5	3.8	60.7
2/4	5.4	32.5	5.4	35.1
3/4	7.0	25.9	6.7	21.6
4/4	7.1	1.4	7.4	9.9
5/6	8.7	15.8	9.0	15.2
7/4	13.5	19.8	14.0	25.8
9/3	19.5	25.2	19.5	17.8
12/4	26.0	9.2	24.8	7.7
16/3	32.5	5.8	30.0	4.9
35/3	75.0 ^a	4.4	---	---
39/3	---	---	64.0 ^b	3.3
45/3	---	---	74.0 ^b	2.4
80/3	81.0 ^a	0.2	---	---

a weight of one male.

b weight of one female.

Table 10. Mean weekly weights and weekly per cent relative growth rates (k) of captive wolf cubs (Litter 3, born May 20, 1967).

Age (weeks/days from birth)	Mean weight (lbs.) of four males	k	Mean weight (lbs.) of two females	k
1/0	2.4		2.3	
2/1	3.8	40.2	3.3	31.6
3/0	4.6	22.3	4.2	28.1
4/0	5.0	8.3	5.0	17.4
5/0	5.3	5.8	5.3	5.8
6/0	6.8 ^a	24.9	6.4	18.9
7/0	9.1	29.1	8.4	27.2
8/1	11.1	17.4	10.3	17.8
9/0	13.0	18.4	12.1	18.8
10/0	12.4	-4.7	11.3	-6.8
11/0	14.0	12.1	12.9	13.2
12/0	16.2	14.6	15.0	15.1
14/0	22.2	15.8	20.0	14.4
17/0	27.2	6.8	25.0	7.4
42/0	---	---	51.0 ^b	2.8
46/0	56.0 ^b	3.2	---	---
71/0	80.0 ^c	2.4	68.0 ^b	1.0

a henceforth mean weight of three males.

b weight of one wolf.

c mean weight of two wolves.

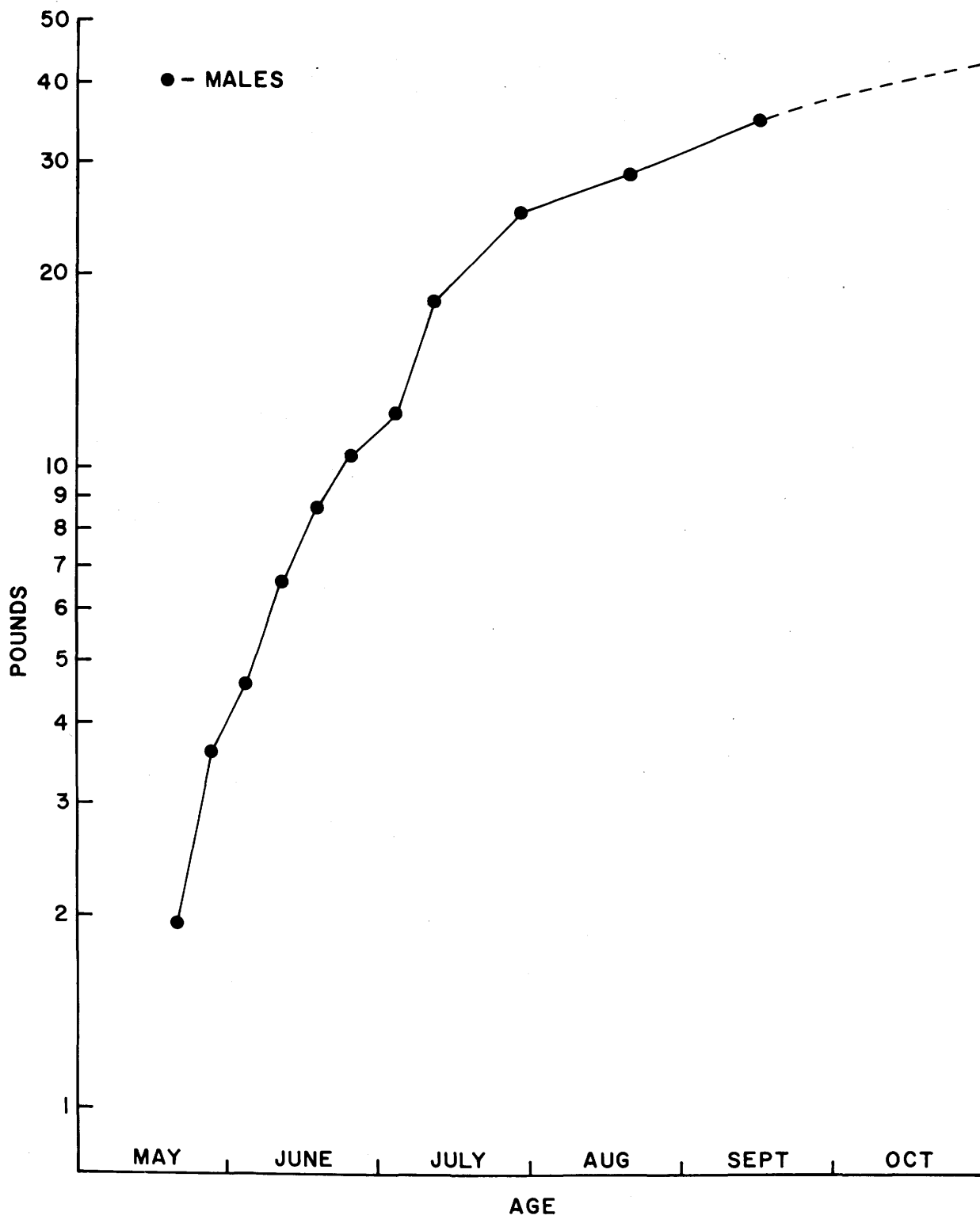


Figure 5 - MEAN GROWTH CURVE OF CAPTIVE WOLF CUBS, LITTER I.

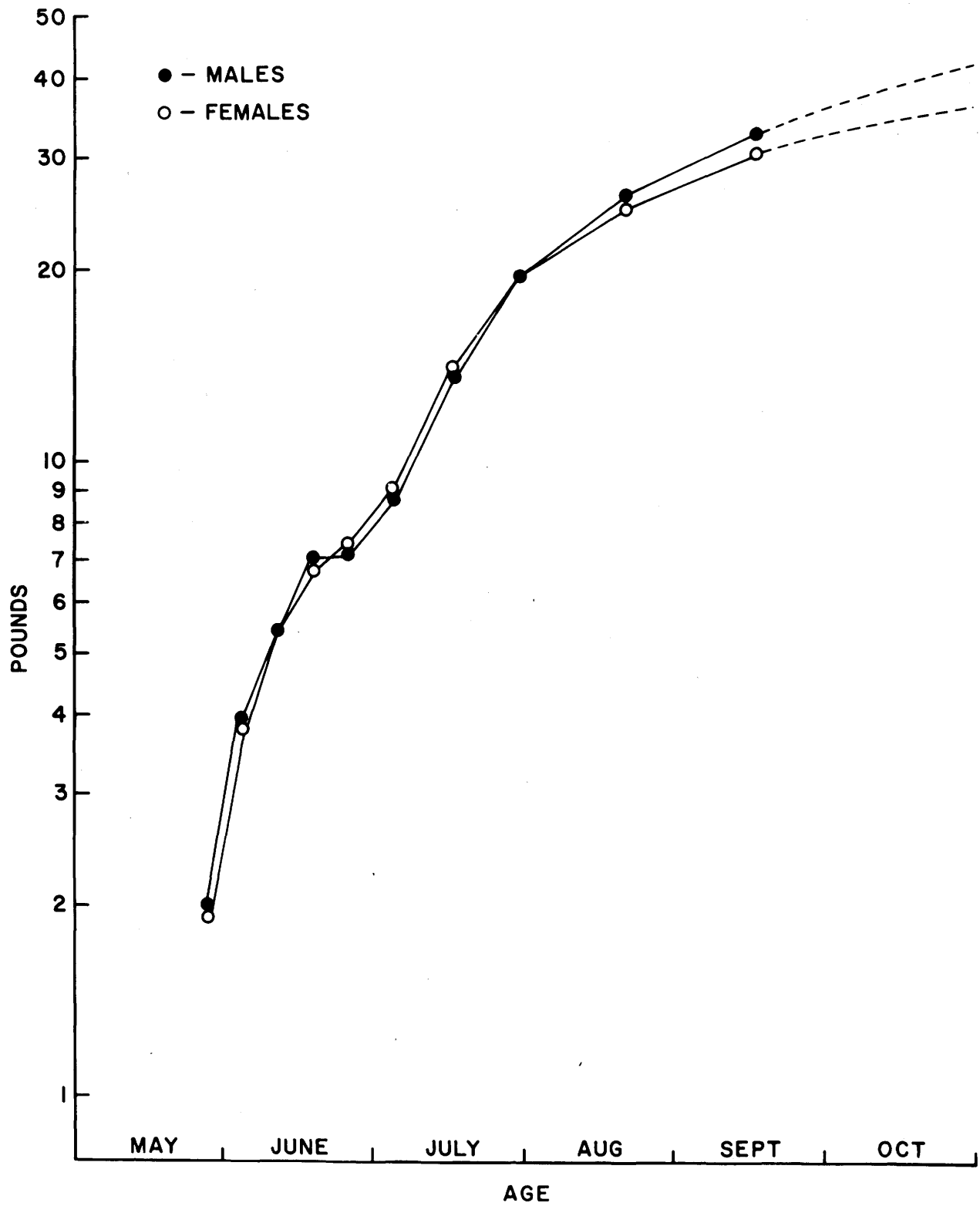


Figure 6 - MEAN GROWTH CURVE OF CAPTIVE WOLF CUBS, LITTER 2.

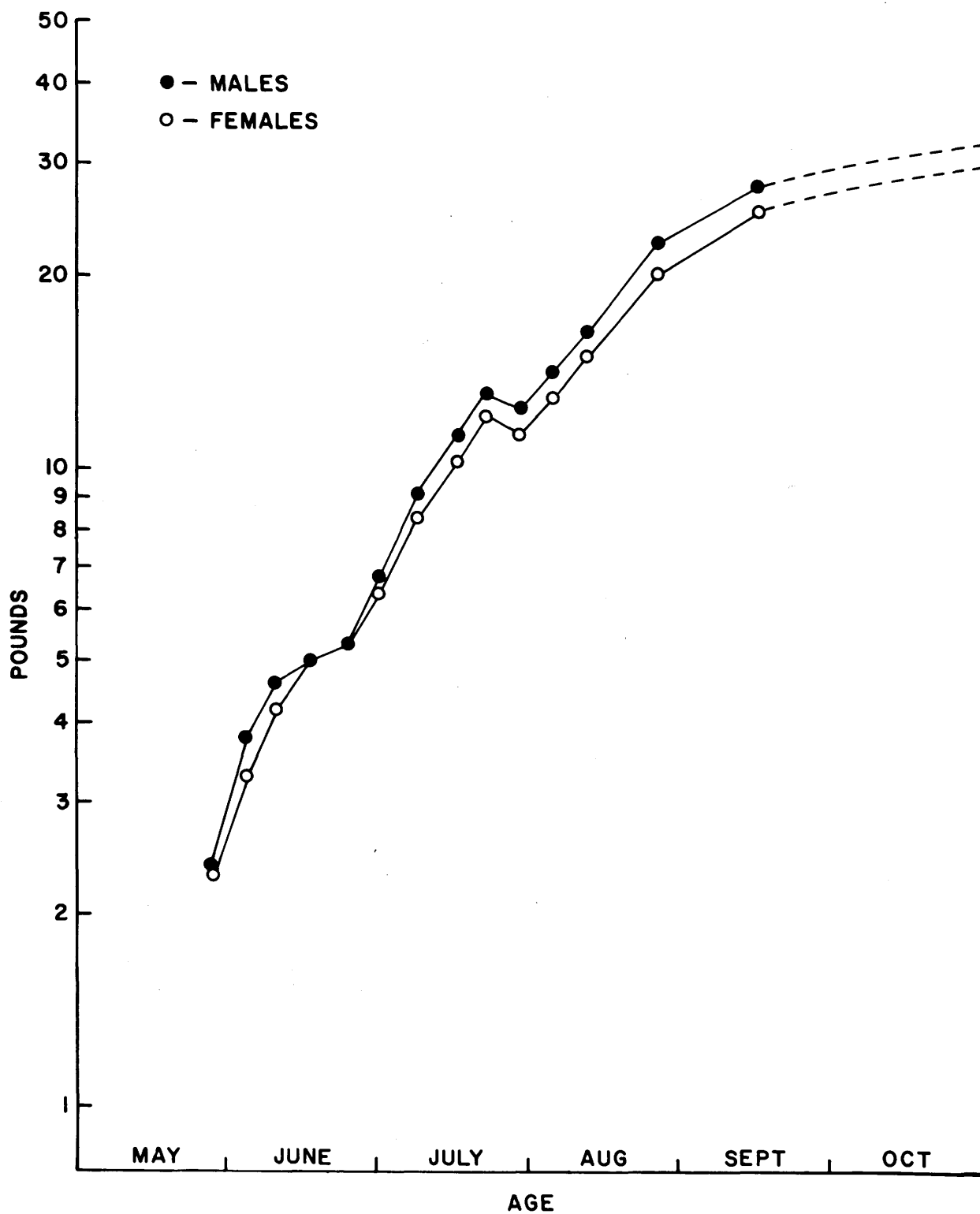


Figure 7 - MEAN GROWTH CURVE OF CAPTIVE WOLF CUBS, LITTER 3.

DISCUSSION

1. Dispersal of wolves from den sites

The results of the wolf ear tagging work show that three different travel routes may have been taken by the nine recoveries. All three routes are known caribou migration paths (Figures 1, 2 and 3). The movements of four ear-tagged cubs and of the tagged 5½-year-old wolf fall within the autumn migration path of the large caribou herd which calves near Beverly Lake and winters near the Saskatchewan-Northwest Territories border. The litter of three ear-tagged cubs apparently followed the late summer or autumn caribou migration up the Back River towards Clinton-Colden and Aylmer Lakes. The 14-month-old wolf probably followed the post calving migration of caribou towards Schultz Lake where it was shot by a Baker Lake Eskimo.

These records add considerably to our knowledge of the movements of tundra-raised wolves and confirm the close interrelations between migrating barren-ground caribou and their attendant wolves. This relationship is loosened during the denning season. The only wolf den containing cubs in the main caribou calving area was found in 1964. The presence of a second wolf den in the calving area was suspected in 1965 as a dead wolf which had been lactating

at death was found 20 miles west of the den which had contained cubs in 1964. The five wolves shot during the study in caribou-occupied areas were all young males, possibly yearlings or two-year-old wolves. Similarly, the tagged wolf shot by a hunter from Baker Lake was a 14-month-old male. These observations lead me to believe that most of the wolves seen with caribou during and after the calving period are non-breeding wolves.

During August when caribou are returning to the south, they pass through the wolf denning areas. By the middle of August, wolf cubs weigh more than 15 pounds and, unless surprised in their dens, become increasingly difficult to catch prior to tagging. Young wolves should then be able to travel well and undoubtedly wolf families leave their den sites at that time and follow the migrating caribou. On the winter range wolf-caribou relationships are most noticeable in that wolves are almost never seen other than in association with barren-ground caribou. With the coming of spring, wolves and caribou return to the tundra. Sometimes, as has been pointed out, wolves in returning to den sites may move ahead of the caribou.

2. Mortality of young wolves

It is unfortunate that more wolf dens containing cubs were

not found during the study. The size of the 11 litters found shows that there are differences in number of young raised per pair of breeding wolves north and south of the Clarke River. Relevant to the difference in wolf litter size is our observation that the cubs in one of the southern litters of three (Sammon Lake) averaged several pounds lighter than northern cubs of the same age. In the area of Sammon Lake and nearby Sinclair Lake, skulls and other skeletal remains of young wolves were found near den sites. This material was not found near den sites north of the Clarke River. Shortage of the main food species (caribou) in the southern area during part of the denning season was probably responsible for mortality, resulting in smaller litters and lighter cubs.

Of eighteen pregnant wolves killed by Predator Control Officer Riddle during the winters of 1965-66 and 1966-67, numbers of embryos varied from two to eight with an average of 5.8. The number of cubs in seven litters produced in captivity averaged 4.0 per litter. Litter size of wild wolf cubs from this study at about six weeks of age averaged 3.5 cubs per litter. Mortality of wolf cubs prior to six weeks of age (and possibly some pre-natal loss) is therefore decreasing the potential production of young per family per year from 5.8 to 3.5. Further evidence of high mortality of young wolves after

leaving the den site is found in the results of the ear tagging work. Seven of the recovered wolves were less than one year old, one was 14 months old and only one wolf, 5½ years when killed, could be regarded as adult.

In view of the high mortality of young wolves, it is of interest to reflect on the wolf bounty program currently in effect in the Northwest Territories. The \$40 bounty is paid for wolves of all ages, even for new-born pups, a high percentage of which would not live to their first birthday.

3. Wolf - barren-ground caribou relationships

Food studies have confirmed that barren-ground caribou constitute the main food of wolves on caribou range. Whereas the winter diet of wolves consists almost exclusively of caribou, the summer diet of wolves, particularly that of denning wolves and their young cubs, is much more varied and depends to a large degree on the availability of smaller prey animals, including small birds, rodents and fish. Mortality due to wolves amongst age classes of caribou is fairly evenly distributed except mortality of calves and of older age classes of caribou. Calves constituted just over one-third of total casualties. It is not possible to state what proportion of calves killed by wolves would have survived in the absence of wolves. It has already

been pointed out that many calves eaten by wolves probably died during periods of harsh weather and that wolves in these cases performed services as scavengers.

Utilization of the caribou carcass has been observed to vary from complete utilization to practically none. It is believed that in the few cases where the carcass was abandoned entirely by the wolf, disturbance by man was chiefly responsible. Caribou carcasses found in summer are often only partially eaten by wolves. Before the wolves can return to their kill, mammalian and avian scavengers, such as grizzly bear, wolverine, foxes, herring gull, eagles, rough-legged hawk, falcons (rarely) and jaegers, will rapidly reduce the carcass.

The dependence of scavengers on the utilization of caribou (including those killed by wolves), temporal and seasonal as it may be, is an aspect of wolf ecology that has not been adequately studied. In early spring, I have seen peregrine falcons feeding on discarded intestines of barren-ground caribou, although these birds are generally known to subsist solely on live-caught birds. A predator control officer informed me that on occasion he has poisoned "falcons" (presumably gyrfalcons) near the tree line in the middle of the winter on strychnine wolf baits. I have also found remains of a young gyrfalcon, apparently killed by a

wolf while the bird was feeding on a leg of a caribou in close proximity to a wolf den. These examples may be indicative of the temporal importance of carrion to animals customarily feeding on live prey and of the role of the wolf in supplying food to other animals inhabiting its range.

Wolves during the denning season are only rarely seen in packs large enough to eat a caribou at one meal. Food requirements may also be less in summer than in winter and alternate food species are used.

Complete utilization of the kill is usual in winter. The large wolf packs and greater food requirements are factors which are probably responsible. During surveys in February-March 1968 in the Abitau Lake region, where caribou were wintering in a dense concentration, we frequently found caribou carcasses. Most of them were fully utilized with only bits of hide and bone remaining. Particularly the carcasses of calves born in the previous year were reduced to bits of hide and rumen contents which even ravens no longer visited.

4. Food studies of captive wolves and estimates of food consumption by free-ranging wolves

Our captive wolves have thrived on an average daily ration per wolf unit of 3.23 pounds of bison meat and fat and

0.26 pounds of commercial dog food but from Figures 4 and 7 it appears that food fed in 1967 from the middle of June to the middle of September was close to a subsistence ration only. During that period the daily total food intake was close to three pounds per wolf compared to about four pounds per wolf for the same period in 1966.

The average daily food consumption per wolf by month (Figure 4) for the periods December 1964-December 1965 and December 1966-November 1967 shows a winter high and a summer low of food consumption. The centre part of Figure 4 (December 1965-December 1966) is inconsistent. The age composition of the captive wolf colony during the summer of 1966 consisted of four adults and seven cubs. It was estimated (p. 39) that a wolf cub from 1½ months to four months of age would eat about half as much as an adult wolf. Perhaps Figure 4 is an indication that the estimate is not quite realistic and that the cubs would each be eating more than half of an adult wolf's daily ration.

There also is some evidence (Figure 4, centre and lower graph) that during the mating season (February 15 to March 30) wolves' food requirements drop somewhat or are at lower levels than during the remainder of the year. No breeding took place in 1965.

It is difficult to relate the information obtained from captive wolves to the conditions prevailing in the wild. Even though the captive wolves in Fort Smith had ample room for exercise, free-roaming wolves undoubtedly use more energy in their daily activities than our confined wolves. Maynard (1937) states that the daily energy requirement of the horse or man at hard work is approximately double the maintenance need. Brody (1945), expressing this in a different way, indicates that the ratio energy expense of walking over energy expense of standing equals 2 and that this ratio is approximately the same in relatively large and small animals.

It has been observed in the field that wild wolves feeding on freshly-killed caribou sometimes pass pieces of undigested hide and cartilage with the droppings. That has not been observed in our captive wolves and consequently it appears as if wild wolves are less economical in the utilization of food than are captive wolves.

From Figures 4-7, it appears that approximately $3\frac{1}{2}$ pounds of food daily (bison meat, fat and dog food) suffice to maintain captive wolves with additional food required for growing cubs. The daily food rations fed to our captive wolves must be regarded as the minimum requirements for free-living wolves.

Taking into consideration the estimates by Maynard (op. cit.) and Brody (op. cit.), free-ranging wolves probably require the equivalent of about seven pounds of bison meat daily or 2555 pounds per year. Kelsall (1960) found the average live weight of a sample of 67 caribou to be 163 pounds. I estimate that a 163-pound caribou would provide a wolf with about 110 pounds of usable meat. On that basis, and assuming that the food values of bison and caribou meat are the same, a wolf would eat about 23 average caribou annually. We could further assume that Tables 6 and 7 reflect age composition of caribou killed by wolves throughout the year. Totalling numbers in each of three age classes (0-1 year, 1-2 years and older than 2 years) and weighting data from Table 7 to allow for the larger total in Table 6, it can be calculated that the total of 23 caribou killed per wolf annually is made up of five calves, two yearlings and 16 caribou older than 2 years.

5. Wolf density

High densities of wolves would naturally result in large numbers of caribou killed. The sight of many carcasses on frozen lakes and rivers would remain uppermost in travellers' minds and could easily give rise to exaggerated stories of wanton killing, compounded

by unfortunate misquotations in the literature (Symington, 1965, p. 38).

During the winter, wolves and caribou are usually found in concentrated populations and it is during that time that remains of caribou on frozen lakes and rivers are most often seen by trappers and aerial travellers. Local and temporal concentrations of wolves and of caribou killed by them are frequently misinterpreted by inexperienced observers and extrapolated to the caribou winter range as a whole. During aerial surveys on March 14, 1968 in the Abitau Lake area, I saw 56 different wolves and the remains of 19 caribou carcasses killed by wolves in an area of 384 square miles, giving a density of one wolf per 6.9 square miles. Undoubtedly, some wolves and kills were missed. Twenty miles from the centre of the caribou concentration there were no caribou and no wolves.

Pimlott (1967) has summarized the densities of wolf populations estimated by other workers. These densities vary from 111 to 10 square miles per wolf for general range. Only one figure for winter range (10 square miles per wolf) is given (Cowan, 1947). A high wolf density of one wolf per 6.9 square miles as found at Abitau Lake could only occur at times of maximum winter compression of the prey population.

An estimate of the total wolf population in the study area cannot be given. A census would be difficult and uneconomical. A more important consideration than the total wolf number is the effect the present wolf population is having on the main prey species, the barren-ground caribou. It may be argued that since it has been shown that wolves kill many caribou calves, wolves may well constitute an effective limiting factor of caribou.

Since 1961, predator control activities in Mackenzie and Keewatin Districts have been much reduced and in the area where formerly six predator control officers worked, only a single one remains. The change was implemented in 1961 because a much reduced kill of wolves showed that wolf populations had greatly diminished in the previous 10 years. The single remaining predator control officer killed just over 200 wolves annually between 1961 and 1965. He then moved his main camp south to the tree line and in 1965/66 killed 398 wolves, followed by 274 wolves in 1966/67. At the present, it appears that he is harvesting a segment of the wolf population without making any serious inroads into the population.

A bounty program now in effect in the N.W.T. removed 635 wolves from October 1965 to September 1967. Of this number, 289 (46 per cent) were killed on barren-ground

caribou range as compared to 672 killed in that period by the predator control officer on a much smaller area. It is extremely unlikely that the wolf bounty program is bringing about any appreciable change in the wolf population, although it must be stated that this program was re-introduced for welfare purposes.

It is of interest to note that even though at present wolves appear to be harvested only on a small scale, there have not been any recent accounts of excessive killing of caribou by wolves, and few reliable reports have lately been received of large numbers of wolves observed.

On the other hand, barren-ground caribou have increased in number since 1959 (Kelsall, 1968) in the face of an apparently stable wolf population. It appears that the present number of wolves is not a serious factor in caribou mortality. Current work in Alaska (T. A. McGowan, pers. comm.) has shown that termination of wolf control and protection of wolves in the area occupied by an increasing caribou population have not brought about a decline in caribou numbers.

Under the present N.W.T. Game Regulations, the wolf is not classified as a game animal. It is hoped that changes in the Game Regulations may soon be made placing

the wolf in a more dignified position than it now holds.
Under proper management, this unique northern mammal will
remain an integral part of our forests and barren grounds.

SUMMARY

1. A study of the feeding ecology of tundra wolves was carried out between 1960 and 1968 in the Thelon Game Sanctuary, N.W.T. and in adjoining areas to the south. Winter collections were obtained from the tree line area south of the Sanctuary and from the Bishop Lake-Beniah Lake area north of Yellowknife, N.W.T.
2. The results of wolf tagging studies in the area of the Thelon Game Sanctuary indicate close interrelations between tundra wolves and migrating barren-ground caribou. These wolves are found in close association with barren-ground caribou throughout the year with the exception of about a two-month period when a segment of the breeding population of wolves halts its northward following of the major caribou herds in order to raise its young.
3. There is some evidence that mortality rates of young wolves in the southern part of the breeding area are greater than of young wolves raised farther north. Average litter size of southern wolves was 2.0 cubs per litter and average size of litters from north of the Clarke River was 4.3 cubs per litter. Age of these young wolves was estimated at 5 to 7 weeks.

4. Examination of 595 spring and summer wolf droppings collected in the Thelon River study area has shown that of 1039 food items, 395 (38.0 per cent) were remains of adult caribou and 93 (9.0 per cent) were remains of calf caribou. Clearly, caribou constitute the main prey species of tundra wolves in spring and summer. In areas temporarily devoid of caribou (south of the Clarke River), a greater average number of different food items per dropping (2.16 as compared to 1.47 for areas north of the Clarke River) is indicative of the resident breeding wolves' greater dependence on prey species other than caribou. Because of their greater availability in the northern areas, calf caribou are of far greater importance in the diet of northern wolves (67 of 520 food items or 12.9 per cent) than in the diet of southern wolves (26 of 519 food items or 5.0 per cent).

Small passerine birds, ptarmigan, birds' eggs, fish and insects are utilized to a much greater extent by the southern wolves than by the wolves occupying areas north of the Clarke River. Muskox and arctic ground squirrel were not found in droppings of southern wolves as muskox do not occur in the south and ground squirrels are less common there than in the northern part of the study area. Lemmings and voles were found to be an important (133 of 1039 food items or 12.8 per cent) item

in the diet of wolves, whether caribou were present or not.

5. The examination of a small number of stomachs of wolves killed during the summer in the northern part of the area under study, confirms these wolves' predominant utilization of caribou.
6. Examination of stomachs of wolves killed on caribou winter range in forested areas shows that caribou are the staple diet of wolves and that other live prey is taken only rarely.
7. Heaviest mortality of caribou is experienced by calves. Calves constituted 38.4 per cent of a small sample of 13 known spring and summer wolf kills. Calves also constituted 33.8 per cent of 151 remains of caribou found to have died in spring and summer of all factors, including wolf predation but excluding human hunting. Wolf predation of calves in winter is still important (11.8 per cent) although considerably decreased from the summer rate.
8. Mortality amongst age classes of caribou other than calves is relatively constant with the exception of the 8-9 year-old and older caribou. A high mortality (10.6 per cent) in the 8-9 year and 10⁺-year-old groups occurs

in the sample of 151 caribou remains found in spring and summer and believed to represent mortality due to wolves. Somewhat higher mortality in 9-10 year-old caribou than among other caribou occurs in the small sample of 17 wolf kills found in winter (17.6 per cent).

9. Female caribou are subject to heavier wolf predation than are male caribou.
10. Mechanics of wolves' attacks on caribou as deduced from caribou remains are described. The neck region of the prey is the favourite locus of attack by wolves.
11. The flesh of the neck and the throat, the tongue, liver, heart, kidneys and lungs of the caribou are preferred by the wolf.
12. Winter wolf-killed caribou invariably are completely utilized. During the summertime, caribou carcasses are frequently incompletely utilized by wolves primarily because of the small size of packs in the summer. A host of harmless or valuable mammals and birds scavenge on the remains of caribou left by wolves.
13. Wolf densities as high as the observed density of one wolf per 6.9 square miles are only of local and temporal occurrence and take place only at times of maximum

winter compression of wintering caribou populations.

14. Captive wolves were maintained on an average daily ration per wolf of 3.23 pounds of bison meat and fat and 0.26 pounds of commercial dog food. These rations sufficed for the maintenance of adult wolves and for reproduction and moulting but additional food was required for growing cubs.

15. It is estimated that a free-living wolf would eat about 23 average caribou annually.

LITERATURE CITED

- American Ornithologists' Union. 1957. Check-list of North American Birds, Fifth Edition, 1957. 691 p.
- Banfield, A. W. F. 1952. The range of individual timber wolves (Canis lupus). J. Mammal. 34(3):389-390.
- Banfield, A. W. F. 1954. Preliminary investigation of the barren-ground caribou (2 parts). Can. Wildl. Serv., Wildl. Mgmt. Bull. Ser. 1, No. 10A and 10B.
- Banfield, A. W. F. 1959. The distribution of the barren-ground grizzly bear in northern Canada. Nat. Mus. Can. Bull. 166:47-59.
- Bird, J. B. 1967. The physiography of Arctic Canada. Johns Hopkins Press, Baltimore, 336 p.
- Brody, S. 1945. Bioenergetics and growth. Reinhold Publishing Corporation, New York, 1023 p.
- Burkholder, B. L. 1959. Movements and behavior of a wolf pack in Alaska. J. Wildl. Mgmt. 23(1):1-11.
- Clarke, C. H. D. 1940. A biological investigation of the Thelon Game Sanctuary. Nat. Mus. Can. Bull. 96 (Biol. Ser. No. 25), 135 p.
- Cowan, I. McT. 1947. The timber wolf in the Rocky Mountain National Parks of Canada. Can. J. Res. D, 25:139-174.
- Crisler, L. 1956. Observations of wolves hunting caribou. J. Mammal. 37(3):337-346.
- Critchell-Bullock, J. C. 1930. An expedition to sub-arctic Canada, 1924-25. Can. Field-Natur. 44(9):207-213.
- Dice, L. R. 1952. Larger units of community classification, Ch. XX in L. R. Dice, Natural Communities, U. of Mich. Press, Ann Arbor.
- Fernald, M. L. 1950. Gray's Manual of Botany, 8th edition, Amer. Book Co. 1932 p.
- Francis, C. S. 1960. Wolves feeding on water bugs and minnows. Blue Jay, XVIII (3):139.

- Hall, E. R. and K. R. Kelson. 1959. The mammals of North America, Vol. I and II. Ronald Press Co., New York, 1083 p.
- Hornby, J. 1934. Wild life in the Thelon River Area, Northwest Territories, Canada. Can. Field-Natur. 48(7):105-111.
- Kelly, M. W. 1954. Observations afield on Alaskan wolves. Proceedings 5th Alaska Sc. Conf., pp. 1-8.
- Kelsall, J. P. 1957. Continued barren-ground caribou studies. Can. Wildl. Serv., Wildl. Mgmt. Bull. Ser. 1, No. 12.
- Kelsall, J. P. 1960. Co-operative studies of barren-ground caribou, 1957-58. Can. Wildl. Serv., Wildl. Mgmt. Bull. Ser. 1, No. 15.
- Kelsall, J. P. 1968. The migratory barren-ground caribou of Canada. Can. Wildl. Serv. Monogr. No. 3.
- Kendrew, W. G. and B. W. Currie. 1955. The climate of central Canada, Queen's Printer, Ottawa, 194 p.
- Kuyt, E. 1962. Movements of young wolves in the Northwest Territories of Canada. J. Mammal. 43(2):270-271.
- Kuyt, E. 1965a. Three mammal records from the Thelon Game Sanctuary, N.W.T. Blue Jay, XXIII (3):134-135.
- Kuyt, E. 1965b. Additional notes on recent occurrence of mammals in the Thelon Game Sanctuary, N.W.T. Blue Jay, XXIII (4):173.
- Kuyt, E. 1966. Further observations on large Canada geese moulting on the Thelon River, Northwest Territories. Can. Field-Natur. 80(2):63-69.
- Macpherson, A. H. 1966. The abundance of lemmings at Aberdeen Lake, District of Keewatin, 1959-63. Can. Field-Natur. 80(2):89-94.
- Maher, W. J. 1964. Growth rate and development of endothermy in the snow bunting (Plectrophenax nivalis) and Lapland longspur (Calcarius lapponicus) at Barrow, Alaska. Ecology, 45(3):520-528.
- Makridin, V. P. 1960. The arctic wolf and the control of it. (Transl. from Russian). Krasnoyarski Rabochiy, Krasnoyarsk, U.S.S.R., 73 p.

- Maynard, L. A. 1937. Animal nutrition. McGraw-Hill Book Co. New York and London. 483 p.
- Mech, L. D. 1966. The wolves of Isle Royale. U.S. Dept. Int., U.S. Natl. Park Serv. Fauna Ser. No. 7.
- Merriam, H. R. 1964. The wolves of Coronation Island. Proceedings 15th Alaska Sc. Conf. pp. 1-7.
- Mowat, F. M. 1948. Report on field studies of the barren-land wolf. Typewritten report in files of Can. Wildl. Ser. Ottawa. 36 p.
- Murie, A. 1944. The wolves of Mount McKinley. U.S. Dept. Int., U.S. Natl. Park Serv. Fauna Ser. No. 5.
- Pimlott, D. H. 1967. Wolf predation and ungulate populations. Am. Zool. 7:267-278.
- Pimlott, D. H., J. A. Shannon and G. B. Kolenosky. 1969. The ecology of the timber wolf in Algonquin Provincial Park. Ont. Dept. Lands and Forests Res. Rep. (Wildlife) No. 87. 92 p.
- Pulliainen, E. 1965. Studies on the wolf (Canis lupus L.) in Finland. Ann. Zool. Fenn. 2:215-259.
- Scott, W. B. 1958. A checklist of the fresh water fishes of Canada and Alaska. Royal Ontario Museum Publication, 30 p.
- Skoog, R. D. 1956. Range, movements, populations and food habits of the Steese-Fortymile caribou herd. M. Sc. thesis, U. of Alaska.
- Stenlund, M. H. 1955. A field study of the timber wolf (Canis lupus) on the Superior National Forest, Minnesota. Minn. Dept. Cons. Tech. Bull. No. 4.
- Symington, F. 1965. Tuktu, the caribou of the northern mainland. Queen's Printer, Ottawa, 92 p.
- Tener, J. S. 1960. The present status of the barren-ground caribou. Can. Geog. J., 60(3):98-105.
- Tener, J. S. 1965. Muskoxen in Canada. Can. Wildl. Serv. Monogr. No. 2.
- Tener, J. S. and E. Kuyt. 1966. Muskoxen survey, Thelon Game Sanctuary. Typewritten report in files of Can. Wildl. Serv. Ottawa. 4 p. and map.

- Thomas, D. C., G. R. Parker and J. P. Kelsall. 1968. Population estimates of barren-ground caribou on the Canadian Mainland from 1955 to 1967. Can. Wildl. Serv. Progress Note No. 3., February 1, 1968.
- Thompson, D. Q. 1952. Travel, range and food habits of timber wolves in Wisconsin. J. Mammal. 33(4): 429-442.
- Wright, G. M. 1957. Geological notes on eastern district of Mackenzie, Northwest Territories. Geol. Surv., Canada. Paper 56-10.
- Young, S. P. and E. A. Goldman. 1944. The wolves of North America. Am. Wildl. Inst. Washington, D.C. 636 pp.

APPENDIX A

Detailed field notes on examination of wolf-killed caribou.

1. Calf 1. Found near wolf den, Spruce Grove River, July 21, 1960. A male calf, still warm, one wolf seen nearby. The calf was skinned in order to discover wounds. The calf's skull had been penetrated by the wolf's canine teeth and there were additional small bite marks on the side of the neck.
2. Calf 2 and Yearling 1. Sex unknown. Found near wolf den July 22, 1961, near S.W. end of Aberdeen Lake. Bite marks on necks of both animals. They had died recently. Tracks of two wolves were nearby.
3. Calf 3. Sex unknown. Found in wake of southward caribou migration past Lookout Point, Thelon River on August 5, 1963. The calf had its throat and tongue eaten and had bite marks on the side of its neck. Holes in the pelvic region may have been caused by avian scavengers.
4. Calf 4. Sex not recorded. Found on August 8, 1963 in same area as No. 3. Tongue, throat of calf had been eaten.

5. Calf 5 and Cow 1. Sex of calf unknown. Found on August 10, 1964 in same area as No. 3. Caribou were moving south through area. The carcass was partly eaten, including throat and tongue. The cow was nine years old.
6. Cow 2. A four-year-old cow found on August 12, 1964 in the same area as No. 5. The caribou had been killed by a wolf within the previous day or two. Its throat and tongue had been eaten.
7. Yearling 2. This animal, a female, was first seen from the air on June 26, 1965 near a small lake just east of the mouth of the Dubawnt River. Two herring gulls and a rough-legged hawk were feeding on the carcass. The animal had died recently. The neck, tongue, throat, hind legs and intestine had been partially eaten. There were numerous signs of a struggle and tufts of caribou winter hair and dried blood indicated that the caribou had been attacked and dragged about. The rumen had been removed from the body cavity and was relatively untouched. The rib cage was intact.
8. Cow 3. Also on June 26, a six-year-old cow was found near Esker Lake. A wolf was seen in the vicinity and about 25 herring gulls, providing the same service as ravens in the winter time, acted as an "indicator

species" by drawing my attention to the dead caribou. Examination revealed tufts of caribou hair and some wolf hair scattered on the tundra and marks where the caribou had been worried or dragged about. Dried blood was found on the ground and the animal's intestine and rumen were found outside the body and relatively untouched. Fresh black wolf droppings were also observed. Neck, throat, tongue, part of the intestine and hind leg had been eaten. The front legs and rib cage were untouched, except for bite marks on the left shoulder. One of the caribou's ears was bitten off.

9. Bull 1. On June 27, 1965 just opposite Lookout Point, a wolf was observed from the air standing beside a dead caribou. The caribou was examined on the ground and was found to be a freshly-killed three-year-old bull. The caribou had been feeding in a sedge swale bordered by birch thickets. The wolf had made its attack from the thicket and appeared to have closed with its prey without a chase. The wolf had stalked the caribou or lain in wait for it and had grabbed the caribou by the neck and pulled or knocked it down. One of the cervical vertebrae was fractured as a result of the wolf's attack. That or the consequent loss of blood killed the caribou. The wolf had only eaten a small amount of meat from the upper right hind leg and had just broken into the abdominal cavity. Subsequent

visits to the site of the kill showed that the wolf had not returned.

10. Bull 2. On June 29, 1965, an 8-9 year-old bull was found several hundred yards from a wolf den near the Crossing-Place-of-Deer. Tongue, throat and intestine had been eaten, caribou hair and some wolf hair was scattered about while the caribou's rumen, which was outside the body, and its forelegs were almost intact. The caribou had been partly covered by dirt, probably by a grizzly bear. A large bear was seen here twice by my assistant who was covering the area from the air at the same time as my ground survey. Two adult wolves and a litter of young were using the den.

11. Cow 4. On June 29, 1965, while we were flying over the area just west of the mouth of the Dubawnt River, the presence of herring gulls indicated a dead caribou. Three wolves were seen slowly walking away from the carcass. An hour later the wolves were still in the vicinity and a landing was made nearby in order to examine the dead caribou. It was an 8-9 year-old cow. Its neck, tongue and throat had been eaten as well as the intestine. The animal had been dragged 25 feet to the place where it was eaten. Tracks and hair indicated that this too, had been a wolf kill.

12. Wolf kill found in 1958. When the author was engaged in caribou studies in 1958, a cow caribou, killed by wolves was found on August 7 along the bank of the Thelon River, about 50 miles downstream from Lookout Point. A single caribou calf was observed standing in the river nearby and on the shore we found a freshly-killed lactating caribou. At least two adult white wolves and two young cubs were seen nearby. Tracks in the sand revealed that the cow and her calf had walked along the river where the cow had been attacked by a wolf. The wolf had waited in the willows and after two bounds had caught the cow and killed it. There were bite marks on the neck of the caribou. One hind leg had been bitten off entirely by the wolf by severing the caribou limb at its articulation with the acetabulum.

On the following day, a black wolf was observed near the site of the kill. Only bits of hide, a few pieces of ribs and some dried blood remained. The five wolves in the area had eaten the rest or carried it away.

13. Wounded cow. On August 4, 1957, D. C. Thomas and the author found a wounded lactating caribou on an island in the Thelon River near Lookout Point. The caribou had a large fresh wound in the upper part of a hind leg, which may have been made by a wolf. The caribou

apparently escaped from the predator by swimming. The wounded cow was in poor flesh and was unable to rise when closely approached.

APPENDIX B

Scientific names of animals and plants mentioned in text.

1. Mammals (Nomenclature as in Hall and Kelson, 1959)

Masked shrew	<i>Sorex cinereus</i>
Snowshoe hare	<i>Lepus americanus</i>
Arctic hare	<i>Lepus arcticus</i>
Arctic ground squirrel	<i>Spermophilus undulatus</i>
Red squirrel	<i>Tamiasciurus hudsonicus</i>
Beaver	<i>Castor canadensis</i>
Northern red-backed mouse	<i>Clethrionomys rutilus</i>
Muskrat	<i>Ondatra zibethicus</i>
Brown lemming	<i>Lemmus trimucronatus</i>
Collared lemming	<i>Dicrostonyx groenlandicus</i>
Porcupine	<i>Erethizon dorsatum</i>
Gray wolf	<i>Canis lupus</i>
Red wolf	<i>Canis niger</i>
Arctic fox	<i>Alopex lagopus</i>
Red fox	<i>Vulpes fulva</i>
Barren-ground grizzly bear	<i>Ursus arctos</i> *
Ermine	<i>Mustela erminea</i>
Mink	<i>Mustela vison</i>
Wolverine	<i>Gulo luscus</i>
River otter	<i>Lutra canadensis</i>
Moose	<i>Alces alces</i>

* Nomenclature as in Banfield (1959)

Barren-ground caribou	<i>Rangifer tarandus</i>
Muskox	<i>Ovibos moschatus</i>

2. Birds (Nomenclature as in A.O.U. Check-list 1957)

Canada goose	<i>Branta canadensis</i>
White-fronted goose	<i>Anser albifrons</i>
Rough-legged hawk	<i>Buteo lagopus</i>
Golden eagle	<i>Aquila chrysaëtos</i>
Bald eagle	<i>Haliaeetus leucocephalus</i>
Gyr Falcon	<i>Falco rusticolus</i>
Peregrine falcon	<i>Falco peregrinus</i>
Spruce grouse	<i>Canachites canadensis</i>
Willow ptarmigan	<i>Lagopus lagopus</i>
Rock ptarmigan	<i>Lagopus mutus</i>
Herring gull	<i>Larus argentatus</i>
Common raven	<i>Corvus corax</i>

3. Fishes (Nomenclature as in Scott, 1958)

Lake trout	<i>Salvelinus namaycush</i>
Arctic grayling	<i>Thymallus arcticus</i>
Northern pike	<i>Esox lucius</i>

4. Plants (Nomenclature as in Fernald, 1950)

White spruce	<i>Picea glauca</i>
Black spruce	<i>Picea mariana</i>
Tamarack	<i>Larix laricina</i>
Balsam poplar	<i>Populus balsamifera</i>
Dwarf birch	<i>Betula glandulosa</i>