Food habits of wolves on barren-ground caribou range

by E. Kuyt

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Food habits and ecology of wolves on barren-ground caribou range in the Northwest Territories

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Contents

List of tables

List of figures

CWS summer assistant Bob Drury holds a litter of four wolf cubs taken from a den along the Thelon River.

The author

Ernie Kuyt is a wildlife biologist with the Canadian Wildlife Service in Fort Smith, Northwest Territories. He has been with CWS since 1960 and has carried out wildlife research and management studies in the Northwest Territories almost continuously since 1957. He received a B.A. from the University of British Columbia in 1957 and graduated with an M.A. from the University of Saskatchewan in Saskatoon in 1970. His Master's thesis was the progenitor for the present report. Mr. Kuyt is a member of a number of scientific and professional societies and is perhaps best known for his work with Whooping Cranes near Fort Smith and his studies of wolves, raptorial birds and other wildlife in the Thelon Game Sanctuary. He has authored over 30 articles in scientific and natural history journals on diverse subjects.

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Thanks are due to charter pilots from Yellowknife, Uranium City and Fort Smith who carried out difficult and often hazardous flying assignments during the field work.

Perspective

Wolves are still present in northern Canada, in contrast to much of southern Canada where wolves are no longer found. With the increase in industrial development in the north and concomitant increases in human population, pressure on northern wildlife resources will increase. The best way to maintain viable wolf populations in northern Canada may be the preservation of some of the large wilderness areas that remain.

The wolf is important for more than aesthetic reasons. It is an important predator on barren-ground caribou, a resource of great value in the economy of northern people. To understand the role of the wolf in its relationship with barren-ground caribou, wildlife managers need to know the wolf's food habits, its movements, as well as other biological factors determining its abundance, such as litter size and mortality of young wolves.

Wolves depend on caribou for food to a large extent, more so in winter than in summer, when smaller prey is often resorted to. Wolves kill calf caribou and animals older than 8 years, primarily.

Many wolves die during their first year of life, particularly in areas where the cubs' parents have trouble finding enough caribou. Thus a greater proportion of wolf cubs die in areas with no caribou than in areas occupied by caribou. This mechanism seems to ensure continued close interrelationships between wolf and caribou, an arrangement which has survival significance for the wolf and probably also for the caribou.

Абстракт
Пищевые привычки волков тундры были исследованы главным образом в 1960-65 годах, хотя некоторая доля работы продолжалась до 1968 года. Исследования производились весною и летом в заповеднике Тселон в Северо-западных территориях, с дополнительной работой в течение зимы на зимних пастбищах карибу на север от Йеллоунайфа в Северо-западных территориях и на восток от Форт-Смита.

Путем проверки меток было установлено, что волки могут покрывать расстояния свыше 200 миль и что их передвижение связано с передвижением карибу в тундре. Зимою волки питаются исключительно карибу; весной и летом они разнообразят свое питание мелкими грызунами, перелетными птицами, яйцами и рыбой, особенно в районах, где карибу временно отсутствуют. Из возрастных групп карибу волки предпочитают телят, но карибу старше 8 лет также подвергаются часто нападениям. Волки режут по меньшей мере в четыре раза больше самок, чем самцов карибу.

Карибу, зарезанные зимой, утилизируются волками полностью; летом остатки их часто предоставляются падалеядным животным и птицам. При нападении волки впиваются в первую очередь в шею карибу. Собственным весом они тянут животных вниз и опрокидывают их.

При максимальном сосредоточении зимующих популяций карибу, территория, приходящаяся на одного волка, достигает 6,9 квадратных миль. Волк в неволе потребляет ежедневно 3,23 фунта бизоньего мяса и жира плюс 0,26 фунта собачьей пищи. Кривая роста молодых волков показывает особенно быстрое развитие маленьких волчат.

Abstract
The food habits of tundra wolves were investigated mainly between 1960 and 1965, although some work continued until 1968. Studies were carried out in spring and summer in the Thelon Game Sanctuary, Northwest Territories, with supplementary winter work on caribou winter range north of Yellowknife, Northwest Territories and east of Fort Smith.

Tag recoveries showed that tundra wolves may migrate over 200 miles and that their movements are associated with those of the barren-ground caribou. During the winter tundra wolves eat only caribou; during the spring and summer they vary their diet by eating small rodents, passerine birds, eggs and fish, particularly in areas temporarily devoid of caribou. Wolves prey on calves more than other age classes of caribou, but caribou of over 8 years are also heavily preyed on. Wolves kill at least four times as many female caribou as males.

Caribou killed in winter are completely utilized by wolves; in summer, parts of carcasses are often left to scavengers. The initial point of attack is the neck, and the caribou is pulled down or knocked down by the impact of the onrushing wolf.

During maximum compression of wintering caribou populations, wolf densities of one wolf per 6.9 square miles were reached. A captive wolf requires 3.23 pounds of bison meat and fat and 0.26 pounds of dog food daily. Mean growth curves illustrate the rapid early growth of cubs.

Résumé
Les habitudes alimentaires des loups des toundras ont surtout été étudiées entre 1960 et 1965, bien qu'une partie du travail se soit poursuivie jusqu'en 1968. Les études ont eu lieu au printemps et en été dans le refuge de gibier de la rivière Thelon; en hiver, on a fait des observations supplémentaires dans l'habitat hivernal du caribou, au nord de Yellowknife (Territoires du Nord-Ouest) et à l'est de Fort Smith.

La récupération d'étiquettes mises à certains sujets a révélé que les loups parcourent des distances dépassant deux cents milles et que leurs déplacements sont reliés à ceux du caribou des toundras. Pendant l'hiver, le loup ne se nourrit que de caribou; au printemps et en été, il varie son régime en mangeant de petits rongeurs, des passereaux, des œufs et des poissons, surtout dans les régions temporairement dépourvues de caribous. Parmi ces derniers, ce sont les petits qui sont la principale proie du loup mais les caribous de plus de 8 ans sont également très souvent chassés. Le loup tue au moins quatre fois plus de caribous femelles que de mâles.

Les loups dévorent en entier les caribous qu'ils tuent l'hiver; en été cependant, des parties de cadavre servent souvent de pâture aux animaux nécrophages. Le prédateur vise toujours le cou, et la proie est renversée sous la force de l'assaut.

Lors des concentrations importantes de caribous dans leur habitat hivernal, on a relevé chez le loup une densité de population allant jusqu'à un animal par 6.9 milles carrés. Un loup en captivité a besoin quotidiennement de 3.23 livres de viande et de gras de bison et de 0.26 livre de pâtée pour chiens. Les courbes moyennes de croissance montrent bien le développement rapide et précoce des louveteaux.

Introduction

Purpose of study

On the basis of caribou studies by Banfield (1954), CWS recommended to federal, provincial and territorial agencies responsible for renewable resources that wolf (*Canis lupus*) populations be reduced in the Northwest Territories to conserve the dwindling stocks of barren-ground caribou (*Rangifer tarandus*). After experimenting in control techniques, CWS undertook the destruction of wolves in the NWT in 1951, with the knowledge that the full effects of wolves and lesser predators upon barren-ground caribou were not adequately known. However, in view of the gravity of the caribou situation, CWS decided control was justified. By 1961 the numbers of wolves taken annually in the NWT had declined considerably and costs per wolf killed had increased. The NWT government relaxed its attempt to reduce the number of wolves on barren-ground caribou range.

In 1957 CWS initiated a study of the wolf as predator on barren-ground caribou, a resource still of great value to the native population. CWS specifically aimed to discover biological factors affecting wolves on barren-ground caribou range and how these factors influenced wolf numbers, and relations to barren-ground caribou populations.

Food studies of wolves on barren-ground caribou range are an important aspect of wolf–caribou studies. There have been few such investigations, and Pimlott (1967) has cited the need for studies of the summer food habits of wolves in tundra regions inhabited by barren-ground caribou. Studies of the food habits, the gross food requirements and the movements of wolves on barren-ground caribou range are reported here.

In 1960, CWS hired me to begin intensive studies in the Thelon Game Sanctuary, about 400 miles northeast of Yellowknife, NWT. I carried out winter studies in 1960 and 1961 in the Beniah Lake area and in 1964 near Bishop Lake and concluded summer field work in August 1965. Some aspects, such as the examination of wolf kills on winter range, were continued until 1968. Unfortunately, as Kelsall (1968) has pointed out, the work began after wolf numbers had been greatly reduced and possibilities for observing wild wolves were limited.

Caribou migration

When wolves and ungulates inhabit the same range, ungulates are usually the main prey of wolves. For this study I needed to know the most often used migration routes of barren-ground caribou, although caribou movements are unpredictable (Kelsall, 1957; 1968). Banfield (1954) describes 19 main caribou herds but indicates that peripheral bands may shift to adjoining herds. Kelsall (1957) refers to the frequently observed overlapping of herds.

Figures 1 and 2 show the general pattern of spring, summer and autumn caribou migration through the study area. For more detailed information about caribou migration in the area refer to Banfield (1954) and Kelsall (1968).

Wolf movements

Tundra wolves, which are almost invariably associated with caribou, accompany the herds over hundreds of miles. Hunters and trappers often observe wolves following caribou on their seasonal migrations. Aerial surveys frequently reveal wolves and wolf trails trending in the same direction as caribou or their trails and also wolves wintering with caribou in forested areas. Conversely, areas where no caribou winter are devoid of wolves. In spring, wolves follow the caribou to the tundra or, sometimes, may even precede them (Critchell-Bullock, 1930; Kelsall, 1960).

Breeding wolves favour areas near tree line south of the Thelon Game Sanctuary. When wolves have reached denning sites there, the caribou continue to calving grounds near Beverly Lake. Although some wolves are found at Beverly Lake, most of the adults remain in the immediate vicinity of their dens further south. Consequently at least 100 miles temporarily separate the calving caribou and the denning wolves. In the autumn the caribou move through the wolf denning areas towards forested areas in the south. By this time the young wolves are able to travel. The wolf families then re-associate themselves with caribou and return with them to winter in forested regions.

Figure 1. General pattern of spring and summer caribou migration.

Figure 1

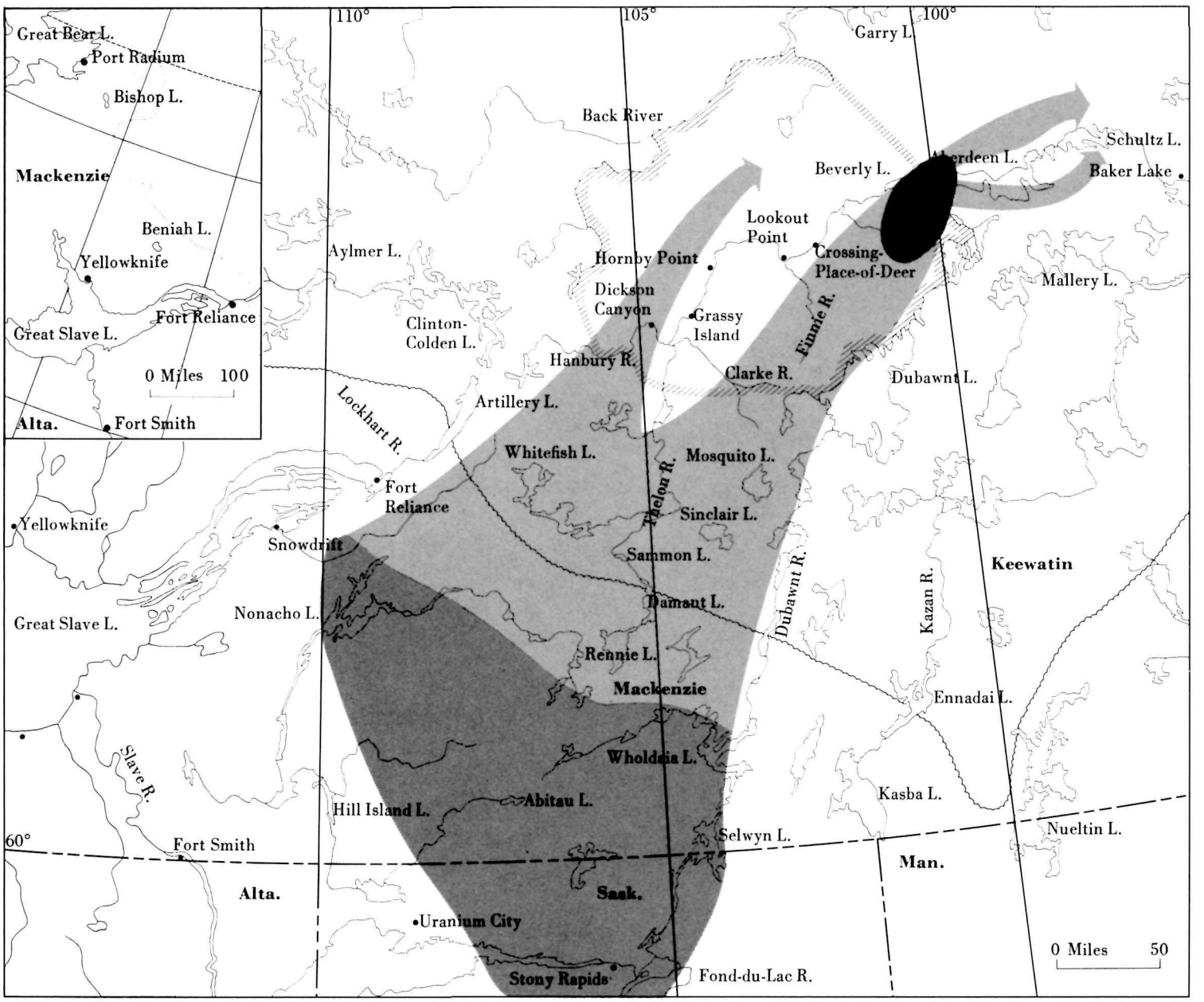
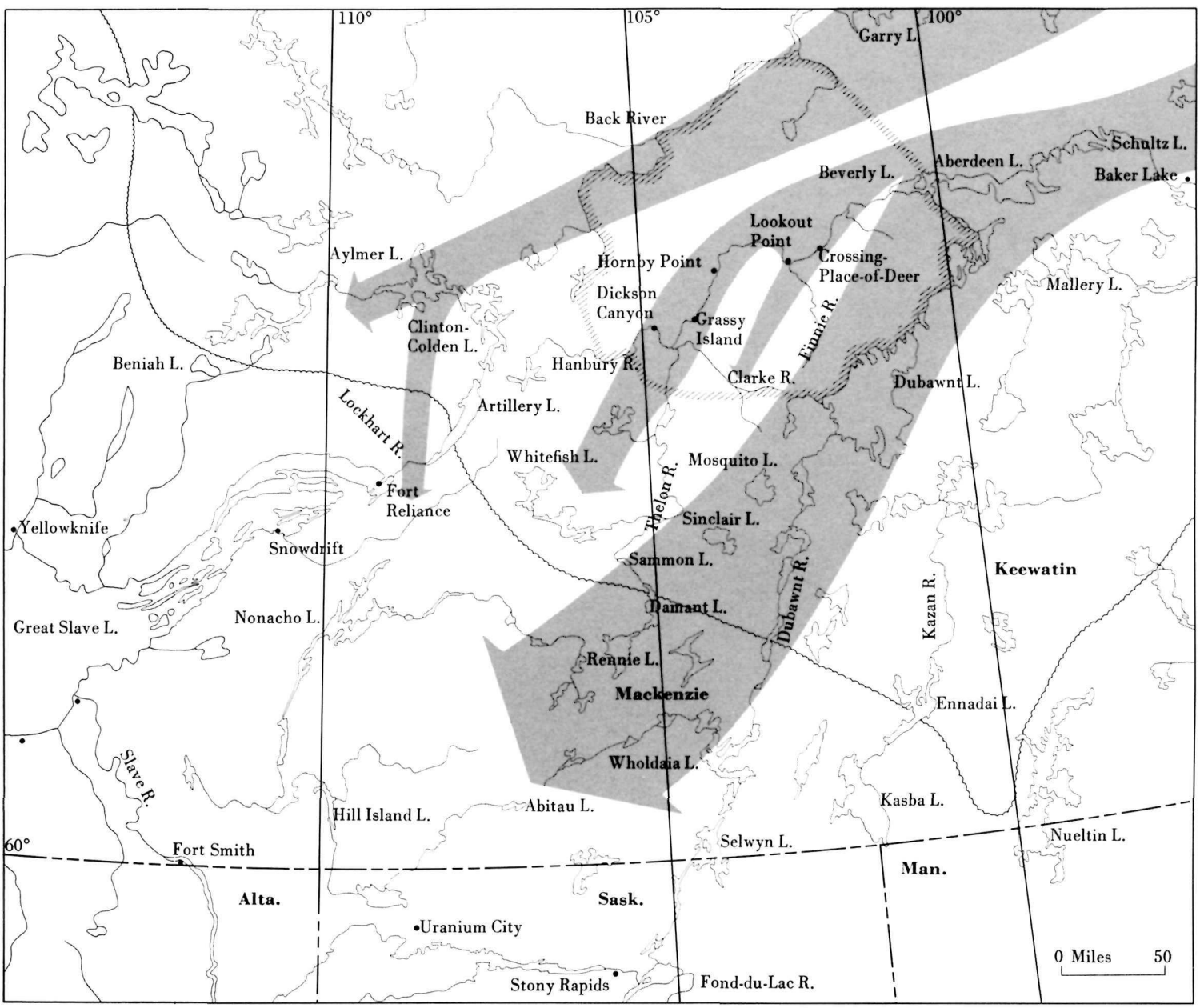


Figure 2. General pattern of autumn caribou migration.

Figure 2



Tree line
Thelon Game Sanctuary

Literature review

General

Clarke (1940) 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

Murie's (1944) was one of the first and most comprehensive studies of the interrelations of wolves and their prey. He found that 69 per cent of the annual diet of Mount McKinley wolves was ungulate prey. Cowan (1947) worked in the Canadian national parks in the Rocky Mountains and found that wolves consumed annually 80 per cent big game and 18 per cent rodents. Thompson (1952) found white-tailed deer (*Odocoileus virginianus*) remains in 97 per cent of 425 wolf scats collected throughout the year in northern Wisconsin, and rodent and lagomorph, including snowshoe hare (*Lepus americanus*), remains 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. He found that smaller animals were more important in summer than in winter. White-tailed deer were the main prey of wolves in Algonquin Park (Pimlott, Shannon and Kolenosky, 1969), with moose (*Alces alces*) and beaver (*Castor canadensis*) of secondary importance. Four wolves introduced in Coronation Island in southeastern Alaska and their offspring fed mainly on black-tailed deer (*Odocoileus hemionus sitkensis*) and the incidence of deer remains in scats increased from 78 per cent in 1961 to 95 per cent in 1964 (Merriam, 1964). Pulliainen (1965) classified domestic animals (chiefly reindeer *Rangifer tarandus tarandus*) and moose as the most important food of wolves in forested areas in Finland. 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, the main food of wolves was caribou and preferably calves. Kelly (1954), Banfield (1954) and Kelsall (1960) found that wolves on barren-ground caribou range preyed almost exclusively on caribou. Mowat's (1948) analysis of 61 wolf scats from denning sites in Keewatin District is the only one available comparable with this study but Mowat indicated that no conclusion may be drawn from his data because it comprised such a small sample. Makridin (1960) provided limited information on summer and winter food habits of arctic wolves in the U.S.S.R. Unfortunately, his food studies are largely unsupported by quantitative data. Pulliainen (1965) discussed food habits of young wolves in captivity.

Movements of caribou and wolves

The migratory movements of barren-ground caribou through the study area were described in detail by Banfield (1954), Kelsall (1957, 1960, 1968) and Thomas, Parker and Kelsall (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) took three wolves from a den near the Back River and ear-tagged and released them. Almost 7 months later a predator control officer killed the three young wolves and two adult wolves near Aylmer Lake, about 185 air miles west-south-west 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) described movements of leg-trapped wolves and of an ear-tagged red wolf (*Canis niger*) which had travelled 125 miles. Banfield (1952) recorded the movements of two ear-tagged wolves in Banff National Park, one of which travelled a minimum distance of 162 miles.

Hunting by wolves

Many biologists have watched wolves pursue caribou, but few have reported a successful hunt. Crisler (1956) witnessed several kills of caribou by wolves and Wilk (*in* Kelsall, 1960) describes one witnessed during the 1957–58 co-operative studies of barren-ground caribou. The latter was the only kill of a caribou by a wolf witnessed during that 18-month study, although up to eight men were in the field simultaneously observing caribou almost daily. Burkholder (1959) provided details of wolves hunting caribou and moose in Alaska. Numerous accounts of wolves hunting moose on Isle Royale were documented by Mech (1966).

Study areas

Typical wolf denning habitat, Sinclair Lake.

Since the two study areas, the Thelon Game Sanctuary and the Bishop Lake–Beniah Lake area (Fig. 1), are similar in many respects, the descriptions of the two areas have been combined.

History

The Thelon Game Sanctuary was established in 1927 for the protection of the musk-ox (*Ovibos moschatus*). This was done on the recommendation of John Hornby who travelled down the Thelon River (Hornby, 1934). In 1956 the sanctuary was reduced in size from 15,000 to 11,200 square miles and its boundaries shifted eastward. For further information on the history of the area, the reader is referred to Clarke (1940).

Indian hunters and trappers still visit the Bishop Lake–Beniah Lake area and mineral exploration and construction of winter roads and mining camps are carried out in the region.

Climate

There do not appear to be great climatic differences between the Thelon River area and the Bishop Lake–Beniah Lake area. Generally speaking, the area is characterized by cold, long winters and short summers with a few hot days. Detailed information about the climate is given in Kendrew and Currie (1955), Bird (1967) and Kuyt (1969).

Geology and topography

Wright (1957), Bird (1967), and Kuyt (1969) may be consulted for information on geology and topography.

Fauna

The mammals and birds which are mentioned here are potential prey or competitors of wolves in, for the most part, the Thelon study area. As I visited the Bishop Lake–Beniah Lake area briefly and only in the winter, I can give little information on the animal life there. Muskoxen are not found in the Bishop Lake–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 I think they are rare in the second study area. Barren-ground grizzlies (*Ursus arctos*) 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 (*Erethizon dorsatum*) and beaver are extremely rare in the Thelon River area (Kuyt, 1965a; 1965b). Arctic hares (*Lepus arcticus*) are sometimes seen on rocky terrain and on eskers, particularly in the Thelon River study area. Ermine (*Mustela erminea*) and wolverine (*Gulo luscus*) 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 (*Alopex lagopus*) 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 (*Vulpes fulva*) have been found denning along the Thelon River. Ground squirrels (*Spermophilus undulatus*) are frequently seen, particularly in sandy areas and on the high banks of the Thelon River. Both collared (*Dicrostonyx groenlandicus*) and brown lemmings (*Lemmus trimucronatus*) are common and subject to periodic fluctuations in numbers. Red-backed voles (*Clethrionomys rutilus*) and masked shrews (*Sorex cinereus*) 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 (*Aquila chrysaëtos*), Bald Eagle (*Haliaeetus leucocephalus*), Gyrfalcon (*Falco rusticolus*) and Peregrine Falcon (*Falco peregrinus*) as well as Rough-legged Hawk (*Buteo lagopus*), Raven (*Corvus corax*) and Herring Gull (*Larus argentatus*) have been observed scavenging. Rock Ptarmigan (*Lagopus mutus*) and Willow Ptarmigan (*Lagopus lagopus*) and the flightless young of many passerine birds constitute potential prey.

Materials and methods

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 and the southern portion of the study area near the tree line are in the Hudsonian Life Zone (Hall and Kelson, 1959). The aerial traveller in winter sees the dark ribbon of the Thelon forests contrasting vividly with the snow and it resembles a green finger-like oasis projecting into the monotonous expanse of the tundra landscape. White spruce (*Picea glauca*) is the predominant tree with black spruce (*Picea mariana*) of lesser importance. Balsam poplar (*Populus balsamifera*) and tamarack (*Larix laricina*) are encountered only in discontinuous clumps along the Thelon and some of its tributaries, especially the Finnie River. Willows (*Salix* sp.) are abundant, particularly along the rivers. Vast expanses of dwarf birch (*Betula glandulosa*) 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 and 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 and lichens form an important part of the flora. The Bishop Lake–Beniah Lake area falls within the Hudsonian Life Zone. Its coniferous forest resembles the southern portions of the Thelon River study area.

Ear-tagging of wolves

We tagged wolves to determine their movements and to relate them to those of barren-ground caribou. We found 11 occupied wolf dens and measured, weighed and ear-tagged 31 cubs. We attached numbered aluminum or brightly-coloured plastic ear tags to cubs of approximately 5 to 7 weeks. One plastic ear tag on a captive wolf in Fort Smith remained intact for two winters. However, some tag loss may occur; predator control officer C. F. Riddle, who recovered five ear-tagged wolves, observed one loose tag.

Food studies of wild wolves

I knew from literature surveys and experience during caribou studies in 1957–58 that predation by wolves is rarely witnessed. Therefore I studied food habits by collecting and analysing wolf scats.

Collection and examination of scats

From 1960 to 1965, I collected 595 wolf scats during spring and summer near active or vacant wolf dens in the Thelon River study area. I recorded where each dropping was found and, in the laboratory, identified and recorded the components.

Reference skeletons and hair of potential prey animals in the area helped me identify the components. The remains of lemmings and voles found in scats were lumped as Microtine rodents. Similarly, we lumped remains of birds except for ptarmigan and geese.

I could not determine the year in which the scats were deposited except for a small number found fresh near occupied wolf dens.

In summer 1965, I observed at least 17 wolves, all of which were associated with dens containing cubs, south of the Clarke River where caribou do not occur in the summer. Clearly, the wolves were utilizing food resources other than live caribou during that time.

I collected wolf scats south and north of the Clarke River in order to compare the summer diet of wolves in areas temporarily devoid of caribou with that of wolves associated with caribou.

Study of captive wolves in Fort Smith (Kuyt, 1969) has shown that cubs' droppings or *milk scats* inside or outside the den are eaten by the cubs' mother at least until weaning. Of the 595 wolf scats I collected during the study 168 were those of cubs. Scats of cubs are much smaller than those of adult wolves. They are always found near dens occupied by cubs and presumably date from when cubs begin to eat solid food. We therefore divided the scat collection into scats of cubs and wolves other than cubs.

Determination of stomach contents

One of the difficulties in the study, particularly in the first few summers, was finding cubs for movement study. Even under undisturbed conditions, wolves are never found in dense concentrations except on caribou winter range. The low wolf numbers in 1960 and 1961 can be attributed to the wolf control program in 1957–58.

I have therefore been reluctant to kill wolves in the denning season for study specimens. I shot five wolves 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 wolves killed in winter were analysed. These include the stomachs of 12 wolves which I killed during the winters of 1960 and 1961 about 125 miles north of Yellowknife, NWT; those of 55 wolves which I killed in February and March, 1964, in the Bishop Lake area, 65 miles southeast of Port Radium, Great Bear Lake; 226 stomachs of wolves killed by C. F. Riddle from 1957 to 1967; and stomachs of five wolves killed in 1960 in the vicinity of Yellowknife. All the wolves had been killed using strychnine baits, and all were taken on caribou range except the five from near Yellowknife.

The caribou meat which I used for 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, I weighed total stomach contents of the 12 Yellowknife wolves to the nearest 5 grams, and separated bait meat and other stomach contents and weighed them on a triple-beam balance. Stomach contents of the 55 Great Bear Lake wolves were examined qualitatively only.

Most of the several thousand wolves killed by predator control officers in the NWT from the beginning of the program until 1968 were taken by C. F. Riddle who operated 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. Riddle examined the 226 wolves superficially and recorded the information on autopsy cards. He did not skin caribou used for baits.

Examination of caribou remains

Summer

We examined 151 caribou remains found in the study areas, including 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 could be determined with certainty in only a few cases. Since caribou rarely remain on the barrens in the winter, the collection of caribou remains reflects summer mortality.

I determined for each carcass the age, using one mandible and the method developed by R. O. Skoog (1955), and the sex, on the basis of length of the jaws (J. McGillis, pers. comm.).

Concentrations of up to six remains were frequently found on such sites as wolf denning areas and wolf routes. Young and Goldman (1944) and Kelsall (1968) have made similar observations. 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.

Winter

During aerial surveys in March 1968 over a concentration of caribou wintering near Abitau Lake, NWT, I examined 17 apparent wolf kills. I flew over the area at intervals of several days and noted that when caribou moved into new areas wolves lagged at least a day behind. I saw no carcasses in these newly-occupied areas. After several days, wolves caught up with the caribou and I frequently saw carcasses, usually on lakes and close to shore. Man was not a predator on caribou there and, even though no attacks were witnessed, I feel confident that the carcasses examined were killed by wolves.

Examination of wolf kills

Fourteen caribou found dead in summer during the present study, were certainly killed by wolves and were sufficiently fresh and intact that much could be learned from them. The point of attack and initial parts eaten of six of the 14 kills (Calf 1, Yearling 2, Cows 3 and 4, Bull 1 and the 1958 kill described in the Appendix) were remarkably similar. In five cases, wolves were in the vicinity and fresh tracks and plucks of caribou hair indicated that a struggle had occurred 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.

Observations on wolf predation

Although freshly killed caribou were found during this study, the act of predation was not witnessed. Patterns of the attacks deduced from tracks and remains are described in the Appendix.

Food studies of captive wolves

Source of captive wolves and history of colony

I kept a colony of from three to 11 captive wolves at Fort Smith in order to observe the feeding behaviour of wolves. Originally, the colony consisted of two cubs, brother and sister, probably of the subspecies *Canis lupus arctos*, caught in 1961 on 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 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 killed 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 killed for study material. The original Axel Heiberg male died after a fight with the Thelon male. One of the two remaining cubs 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 killed. The Thelon male was killed in 1967. The Axel Heiberg female and her 3-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 I destroyed on the day of birth and one which escaped from captivity 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 7 years of age.

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 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 after parturition.

Two litters were born in 1966. Three cubs were born on May 17 to a nulliparous 2-year-old, and four cubs were born on May 24 to a 5-year-old. The 5-year-old had previously whelped in 1963 and 1964 and was the mother of the 2-year-old.

On June 6, 20 days after birth, the three cubs of the 2-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 4 lb. chunk of meat out of the mouth of a 2-year-old male wolf (their mother's brother), carried it away and began to eat it in a corner of the pen. On June 17, these three wolf pups fought for raw bison meat and growled at each other and at the adults while so doing. On June 21 we noted 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 5-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 2-year-old female was nearing the end of her lactating period.

The four cubs born to the 5-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 appeared that only milk scats are eaten. The mother had terminated lactating on July 13, 50 days after parturition.

The same female, then 6 years old, gave birth to six cubs on May 20, 1967. On June 11, I observed the six cubs licking and chewing bison meat although only their deciduous canine teeth and incisors had grown sufficiently to be of any use. On June 20 I noted that some cub scats remained uneaten in the wolf pen. On July 10 the female had ceased lactating.

In summary, five lactating periods lasted more than 34 days in the 2-year-old wolf, 43 days for her mother when 3 years old, 50 days for the same wolf, then 5 years old and 51 days for the same wolf, then 6 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 to 45 days.

If these dates are comparable to those for wild wolves, it may be assumed that cubs at the early age of 1½ months, depend largely or entirely on wild prey.

Type and quantity of food

Most of the food fed to our captive wolves was meat, fat and bones from bison slaughtered or killed by traffic in Wood Buffalo National Park. Commercial dry dog food was used occasionally.

We determined the weight and fat eaten by the wolves, by weighing rejected bones weekly and subtracting their weight from the total weight of meat, fat and bones.

Because our captive wolves usually occupied one compound and were of different ages, I classified them into three age groups to determine the approximate daily meat consumption per wolf. Wolf cubs up to 1½ months depend 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. I arbitrarily assigned the following units to the captive wolves basing the units on daily meat consumption: cubs up to 1½ months (up to July 15) I counted as 0 wolf units, cubs from 1½ months to 4 months (up to September 30) as ½ wolf unit, and wolves older than 4 months as 1 wolf unit. For example, on July 8, 1967 our captive wolf colony consisted of four wolves older than 1 year and five 1-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.

I recorded the approximate amount of meat and commercial dog food eaten for a 3-year period from November 25, 1964 to November 30, 1967 and from this calculated average daily food consumption per wolf unit.

Weighing of captive wolves

Young cubs were weighed to the nearest ounce several times each week for 4 weeks. From the end of their first month to the end of August, the cubs were weighed weekly, then wolves became difficult to handle and weighings were less frequent. On a few occasions, tranquilizers were necessary to obtain weights. I also recorded weights whenever captive wolves were killed.

Results

A wolf den is in the clump of spruce. Sand piles mark three den openings. Hornby Point, Thelon River.

A single cub was found in this den under a clump of spruce. Sinclair Lake.

Ear-tagging of wolves

Nine (29 per cent) of 31 ear-tagged wolf cubs have been recovered; an indication that man's activities are an important mortality factor. 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 a hunter. Seven 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.

Recoveries are numbered and movements are 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 cub from a litter of five, tagged on July 15, 1962, was shot by a hunter north of Schultz Lake in August 1963, 188 air miles east-north-east of the den.

3. A cub from a litter of six wolves, tagged on July 1, 1960 near the Thelon River was killed on December 7, 1965 near Damant Lake or 225 air miles to the southwest.

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, 208 air miles to the southwest.

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, 184 air miles to the southwest.

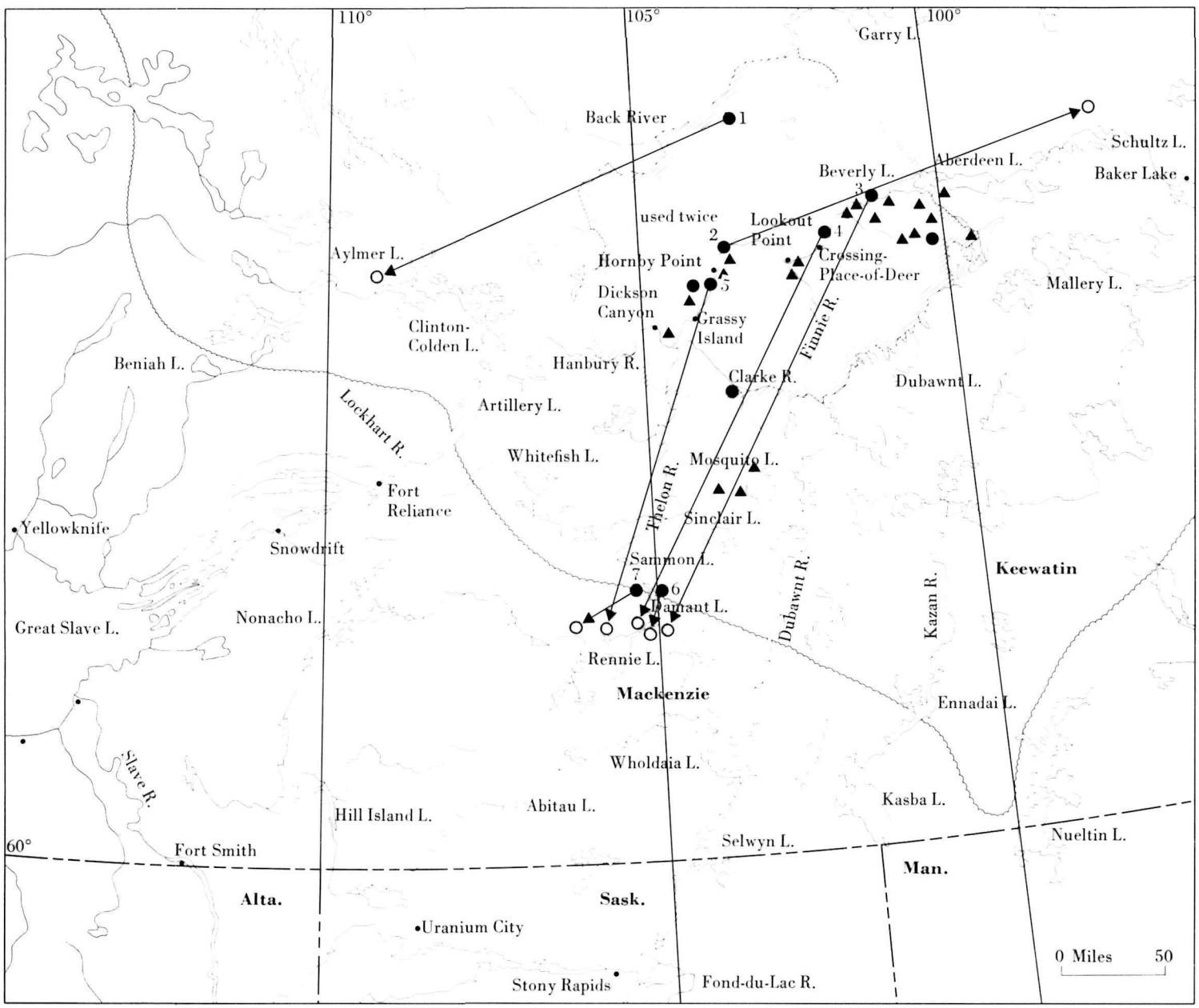
6. A cub, the only one in the litter, tagged on July 21, 1965 near Sinclair Lake was killed on November 1, 1965 near Damant Lake, 16 air miles to the south.

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 to the southwest.

I discovered eight litters of wolves in caribou-occupied areas north of the Clarke River. The litters consisted of six (1960), five (1962, 1965), four (1964, 1965), and three cubs (1960, 1961). A litter consisting

Figure 3. Movements of ear-tagged tundra wolves.

Figure 3



Tree line
Thelon Game Sanctuary
● Wolfdens containing cubs
○ Site of kill of tagged wolves
▲ Wolfdens without cubs

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. Average litter size of wolves denning in caribou-occupied areas was 4.3 and 2.0 cubs in areas devoid of caribou. The means differ significantly at the .05 level. 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. 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.

Food studies of wild wolves

Examination of scats

Table 1 reflects the spring and summer food habits of tundra wolves.

The number of prey items per scat reveals the variety of the wolves' diet (Table 1). There is practically no difference between the two broad age groups – cubs and wolves other than cubs (1.74 and 1.75 prey items per scat). Statistical analysis of the data has shown that a highly significant difference occurs between the means of the number of prey items per scat found in the areas north and south of the Clarke River ($P = 0.001$; $t = 8.256$). This difference is an indication of the greater variety in the diet of wolves temporarily separated from the main prey species.

Caribou—My analysis of scats shows the predominance of caribou in the wolves' diet and this predominance holds true for caribou-occupied areas as well as for areas temporarily devoid of caribou. As droppings cannot be dated accurately and those found in denning areas south of the Clarke River may have been deposited early in the spring when caribou are migrating through those areas, interpretation of the data is difficult.

Thirty-eight per cent of the prey items found in wolf scats were adult caribou remains (Table 1). Analysis of cub scats and scats of other wolves south of Clarke River shows that about 30 per cent of the prey items were caribou remains. The sample of scats of wolves other than cubs, collected north of the Clarke River, where caribou were available for a longer part of the summer, shows that 46.3 per cent of prey items were adult caribou remains. Cub scats from this area were lower in adult caribou remains (30.5 per cent of prey items) but that figure was complemented by calf caribou remains (25.6 per cent of prey items), a much higher percentage than for any of the other three samples: young wolves in the area north of the Clarke River appear to depend heavily on calves. Presumably these were killed by adults or found dead and carried to the dens. In some years many young calves die due to inclement weather, and wolves then have no difficulty obtaining food. Since I found few wolf dens near the main caribou calving grounds at Beverly Lake and consequently few droppings, my data indicate wolves select calves (dead or alive). Adult wolves, associated with dens containing cubs, ate mostly adult caribou; however, the cubs ate a higher proportion of calves.

Muskoxen—Wolves do not prey heavily on muskoxen in the study area.

Nineteen droppings of 595 examined contained remains of muskoxen. I collected them only in 1960 (two scats), 1964 (four scats) and 1965 (13 scats). I collected two of the four 1964 scats at the remains of a 15- to 18-year-old bull muskox found in late July in willow thickets along the Thelon River. Broken branches and dead leaves on the willows, plucks of muskox and wolf hair indicated that the bull had been killed a month earlier, apparently not without a struggle. I collected nine of the 13 scats found in 1965 near an occupied wolf den at the Crossing-Place-of-Deer on the Thelon River, and the remaining four scats 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 summer. I have not seen them south of the Clarke River in that season, nor did Tener and Kuyt (1966) observe them there during a winter survey, when 568 muskoxen were counted within the game sanctuary. No wolves were observed on that survey.

Wolverine—Wolverine are rare in the study area. During five summers in the Thelon Game Sanctuary, I saw wolverine only six times, always along the Thelon River. I found wolverine claws in two wolf scats, both collected near an occupied den on an island in the Thelon River.

Ermine—Ermine are rare in the study area. Because of this they are not important in the wolf's diet. One wolf scat, collected in 1963, contained several bones and hair of 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 in about 1953. It is not clear whether the wolves killed their victim or whether it was found dead and was eaten as carrion. I found wolf hair in seven wolf droppings and the lower first premolar of a wolf in another. Frequent scratching and licking by the wolves during the moult could account for occasional hairs being ingested; however, the one scat with the premolar indicated that the possibility exists that wolves eat their kind.

At wolf dens near Sammon and Sinclair Lake I found what appeared to be several deciduous teeth of young wolves in wolf droppings. They may have been swallowed with the food, when permanent teeth replaced them. Nearby I found skeletal remains of wolf cubs, a further indication

Table 1
Analysis of 1,203 components of 595 wolf scats from spring and summer range of wolves, Thelon River study area, 1960 to 1965. North refers to the area north of Clarke River, where caribou are present during most of wolf denning season. South refers to the area south of Clarke river, temporarily devoid of caribou. No. is the number of scats in which each of the listed components occurred. % is the percentage occurrence in total number of prey items.

	Cubs at dens						Other wolves						All wolves					
	North		South		Total		North		South		Total		North		South		Grand total	
Scat components	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Prey items																		
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
Eggs–unidentified			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 prey items	82	100	210	100	292	99.9	438	100	309	99.8	747	99.7	520	100	519	99.9	1,039	100.2
Total no. of scats	58		110		168		297		130		427		355		240		595	
No. prey items/scat		1.41		1.91		1.74		1.47		2.38		1.75		1.47		2.16		1.75
Non-prey items																		
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	
Total no. of non-prey items																	164	

that cannibalism may have taken place. These teeth were classified as those of *unidentified carnivores.*

The examination of 61 wolf diaphragms showed that approximately 50 per cent of wolves were infected with trichinosis, a further indication of wolves' feeding on wolves or other carnivores such as wolverine, ermine and foxes (Choquette, L. P. E. and E. Kuyt, *unpublished data*).

Arctic fox—I found arctic fox remains in seven wolf scats. I collected four in 1968 near a wolf den on the Kazan River. The den, an enlarged arctic fox den, was vacant when I examined it but had held cubs earlier in the same year (A. H. Macpherson, pers. comm.). Possibly the occupant was killed by wolves, who took over the den. When I returned in 1964, tracks of a single arctic fox indicated that that species was again using the den.

I found the other three wolf scats containing remains of arctic fox 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 so that the fox must have been migrating.

Red fox—Several claws of red fox were recovered from a wolf dropping near Sammon Lake. I saw red foxes several times each summer along the Thelon River and I have found three dens with young there.

Unidentified carnivores—I classified entire or fragmented claws or teeth in this group. There were no remains of unidentified carnivores in cub scats, whereas eight scats of older wolves contained such remains. Adult wolves either do not carry dead carnivores to their dens or, less likely, cubs at dens refuse them.

Arctic hare—I found remains of arctic hare in nine wolf droppings; seven were found north of the Clarke River, along the Thelon, Finnie and Hanbury rivers.

From ground observations and low altitude aerial reconnaissance in winter, early spring and summer, I learned that arctic hare distribution in the Thelon Game Sanctuary varies with season and topography. In late winter and early spring, tracks of hares are common on the willow-clad banks of the rivers where hares are rarely seen in summer. I saw a few hares in summer on eskers, boulder fields and other rocky terrain, chiefly 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 of 595 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 when they were out in the open by simply rushing upwind and running them down. Surprisingly, ground squirrels are not more preyed upon by wolves; 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.

Microtine rodents—Microtine rodents made up 10.5 and 15.9 per cent of prey items in cub scats in areas devoid of caribou and caribou-occupied areas respectively (Table 1). Percentages for wolves other than cubs were 12.3 and 13.7. Their remains occurred with almost equal frequency in the droppings of cubs and other wolves (12 versus 13.1 per cent). The percentages for these 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 mouse hunting by cubs and adults even when caribou were plentiful.

Brown and collared lemmings and red-backed voles occur in the area. Lemmings (especially *Dicrostonyx*) were common in the study area in the summer of 1960. In 1962, the lemming population was reduced 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 lemmings varies from year to year and with location (Macpherson, 1966) so it is difficult to assess their importance in the wolf's diet.

Only caribou remains and those of unidentified birds were more frequently noted than remains of microtine rodents.

Unidentified mammals—Most of those remains were bone chips and occurred more frequently in caribou-occupied areas than south of the Clarke River. Possibly the bone chips were of caribou.

Geese—Wolves are not important predators of geese in the Thelon River study area.

I found three droppings containing goose feathers and, twice, I found parts of legs of Canada Geese (*Branta canadensis*) on wolf dens. A wolf stalking Canada Geese was observed near Grassy Island in 1962. A group of five canoeists on the Thelon River in 1966 accidentally drove a flock of moulters on to shore near Grassy Island, where a wolf, hitherto unseen, caught one of the geese (R. E. Matteson, pers. comm.). Kelsall (pers. comm.) reported that a pilot observed a wolf swimming after flightless Canada Geese on a tundra pond in 1958 in an apparent effort to herd the birds ashore.

White-fronted Geese (*Anser albifrons*) and Canada Geese are common along the Thelon River system where white-fronts breed and both species moult. Canada Geese do not 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 their relative unimportance in the wolf's summer diet, although Willow Ptarmigan are common throughout the

area. One cub scat and 15 adult scats contained ptarmigan (Table 1). Adults are better able to hunt ptarmigan. Table 1 shows that south of the Clarke River ptarmigan are somewhat more important in the wolf's diet than further north.

I saw a wolf chasing two ptarmigan near Mosquito Lake in late July, 1965. The 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—I lumped bird remains (other than those of geese or ptarmigan) which we found in 136 wolf scats (Table 1). Although some were feather shafts of large birds, possibly ducks, most unidentified bird remains were feet and skulls of fledgling passerine birds. At fledging time the feeding calls of these birds are heard everywhere. I do not know whether numbers of passerine birds fluctuated between 1960 and 1968. Wolves south of the Clarke River depended more heavily on small birds (20.4 per cent) than did wolves north of the Clarke River (5.8 per cent). Small birds were especially important in the cubs' diet and in areas devoid of caribou (Table 1).

Eggs—I found egg shell and egg membrane in 36 scats of older wolves and in nine cub scats. Egg remains occurred in 35 droppings from areas temporarily devoid of caribou but only in 10 droppings north of the Clarke River. On several occasions ptarmigan feathers were intermingled with egg shells. All remains were of the thickness of eggs of ptarmigan or duck-sized birds.

Fish—Fish are important in the diet of wolves, where caribou are absent during most of the denning season. Seventeen cub scats and 31 of older wolves contained fish bones and scales whereas north of the Clarke River only eight droppings (all of them of wolves other than cubs) contained fish remains. Only once or twice did I find teeth of fish in droppings, indicating that the wolf had eaten a lake trout (*Salvelinus namaycush*) or northern pike (*Esox lucius*). I also found part of the jaw of a trout or pike and a piece of an unidentified fish skin at wolf dens. No attempt was made to identify 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 (*Coregonus* sp.) are fall spawners; then they gather in schools in shallow waters. Several times in late summer I have seen whitefish trapped in small creeks where they were vulnerable.

Kelsall (pers. comm.) in spring 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 (*Oncorhynchus* sp.) 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.

Arctic Grayling (*Thymallus arcticus*), pike and suckers (*Catostomus* sp.) spawn in early spring in small streams or shallow lakes where they are vulnerable to predation.

Carrion—Several pupal cases of the black blow fly (*Phormia regina*) were found in wolf droppings. Probably the wolves had fed on fly-blown meat. Seven scats contained carrion; all were from wolves other than cubs and all except one were found in caribou-occupied areas north of the Clarke River.

I often encountered dead caribou in the wake of caribou migrations. Some were killed by wolves, others without external wounds may have died from injuries received in crushes. One wolf cannot eat an 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 to decay. In most areas wolves have no difficulty finding live prey in the summer; as the food data (Table 1) suggest, they do not resort often to carrion then.

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 wolf and it seems unlikely that wolves would bother with such small food. Yet wolves in the area temporarily devoid of caribou 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 with fish and small birds, beetles are probably eaten when larger prey is temporarily unavailable.

Hymenoptera—I found remains of Hymenoptera in 10 droppings. These droppings contained parts of bees or wasps which I classified as prey. Their contribution to the wolf's diet is insignificant.

Non-prey items—On occasion, I found in wolf droppings the cuticle of larvae of the caribou warble fly (*Oedemagena tarandi*). Since these larvae were most likely ingested with the flesh of caribou, their remains were classified as non-prey items, as were the pupal cases of blow flies which were part of carrion. Diptera occurred in 10 scats (Table 1).

Grasses and sedges 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 that I collected on a wolf den near Helen Falls on the Hanbury River was a solid mass of grass containing several tapeworms (*Taenia* sp.).

Captive wolves in Fort Smith frequently eat grass even though they are not heavily infested with intestinal parasites. Spruce needles, leaves of ericaceous plants (*Ledum*, *Vaccinium*, *Arctostaphylos*) and Bogmoss (*Spaghnum* sp.) were infrequently found in the droppings of wild wolves. These items and occasional berries are ingested with prey and are classified simply as non-prey.

Of the 595 scats examined, 86 contained what resembled dried clay; several scats were made up of it entirely. It probably consisted mainly or entirely of ash, the excreted waste product resulting from eating meat only, as droppings of captive wolves which had been fed on meat only were identical in appearance and consistency.

The two non-prey items recorded under *Other* (Table 1) were an unidentified piece of metal found in one scat and a No. 4 shot pellet, which may have been in the flesh of a migratory bird, found in another.

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

Specimen no.	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 (*Catostomus* 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 50	Caribou 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 and March, 1964.

No. of stomachs (%)			
	Contents		
Examined	Bait only	Bait and caribou	Other
55 (100)	35 (64)	20 (36)	10* (18)

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

Determination of stomach contents

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 fresh caribou: one held 3 lb. including one kidney, the tongue, larynx, liver and trachea; and the other held 5.75 lb. made up of trachea, tongue, esophagus, heart, liver, lung and one kidney of an adult caribou and a few pieces of discoloured meat and connective tissue (perhaps from an earlier meal). Kelly (1954) found reindeer and caribou tongues in two wolf stomachs. Another stomach examined by him contained an estimated 15 to 18 lb. of caribou including ear, tongue, lip, two kidneys, liver, windpipe, hair and large chunks of meat. The wolf stomach containing 5.75 lb. of caribou also contained a few fragments of bone with a piece of a rifle bullet imbedded in it. Larval tapeworms (*Cysticercus tennuicollis* and *C. tarandi*) found in the caribou meat were indicative of the freshness of the wolf's meal.

I found the sixth wolf, which had been lactating, dead on June 30, 1965 near a wolf den about 25 miles south of Beverly Lake. All ribs on one side had been broken and I believe a grizzly bear killed the wolf. Its stomach contained little food, including several costal cartilages and intervertebral fibrocartilages of a calf caribou.

Wolves collected in winter

Tables 2, 3 and 4 show the results of the analysis of the contents 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 lb. male wolf cub, are noteworthy.

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

A few stomachs contained arctic fox, wolf or wolverine. Most of these predators

had probably died on baits and were eaten by wolves; damaged wolves or arctic fox are sometimes used as bait by predator control officers.

Riddle identified river otter (*Lutra canadensis*) in five wolf stomachs and mink (*Mustela vison*) in one stomach. According to Riddle it is impossible to confuse remains of these furbearers with wolverine hide. Because they are locally rare and water-oriented I do not think that these mustelids would be common prey to wolves, although from low-flying aircraft I have often spotted otter tracks between holes in frozen rivers. Any otter when surprised out of water would be no match for wolves. Since many of the baits are frozen into the ice of lakes and rivers, these furbearers may have fallen victim to the strychnine baits and subsequently were eaten by wolves.

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

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

No. of stomachs (%)					
		Contents			
Examined	Empty	Bait	Caribou	Unidentified	Other
226 (100)	50 (22)	6 (3)	136 (60)	14 (6)	20† (9)

*C. F. Riddle (pers. comm.)

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

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

Specimen no.	Weight (in grams) of stomach contents			
	Total	Bait	Prey	Contents
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

Examination of caribou remains

Spring and summer

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

Table 6 shows the ages of 151 caribou jaws found in spring and summer. The percentage of mortality among caribou up to one year is 33.8, much higher than the 15.1 per cent found by Banfield (1954). Similar discrepancies occur between my data and Banfield's for caribou of 8–9 years and those over 10 years (10.6 per cent versus 4.5 per cent). Banfield's study shows a considerably higher mortality among 2- and 3-year-old caribou than my figures

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

Spring and summer mortality*			Year around mortality†		
Age (years)	No.	Per cent	Age (years)	No.	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)

show. The major difference between Banfield's and my data is that his include hunting by man, so 2- and 3-year-old caribou must have been hunted extensively. The data in Table 6 do not mean that wolves kill a large proportion of calf caribou. Kelsall (1960) examined caribou carcasses and found 56 per cent calves; however, unlike mine, Kelsall's figures are based largely on investigations carried out on caribou calving grounds. Furthermore, Kelsall indicates that some of the calves he reported as wolf kills may have died because of the inclement weather during 1957 and 1958.

Table 6 further shows that mortality except that caused by man is fairly constant except for increases in the 0–1 year, the 8–9 year and over 10 year age classes.

Mortality from all causes, except hunting by man, is lowest among caribou from 4 to 8 years old. This may be because of a low incidence of these four age groups in the caribou population, a reflection of poor calf years. Certainly between 1950 and 1958 calf crops were well below the potential (Kelsall, 1960).

Sex—Seventy-seven of the collection of 151 jaws were from caribou 4 years old and older. Twenty-five of the 77 jaws 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) found a ratio of 35.8 males to 100 females. Kelsall (1960) reported an adult male to female ratio of 60:100. If the 151 jaws are of caribou killed by wolves, as I strongly suspect, female caribou are subject to proportionally higher wolf predation than are males.

Winter

Age—The 17 caribou remains found in winter during aerial surveys are probably the result of wolf predation. Mortality among the 0–1-year-olds (both died at about 9 months) was 11.8 per cent (Table 7), considerably lower than during the summer (33.8 per cent) although still important. Because total mortality among the 0–1-year-olds was expected to be higher than in other age classes, that group would be less available 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) among 9–10-year-old caribou.

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

Age (years)	Female	Unknown	Total	% per age group
0–1		2	2	11.8
1–2	1	1	2	11.8
3–4	2		2	11.8
6–7	1		1	5.9
7–8	1	1	2	11.8
8–9	2		2	11.8
9–10	3		3	17.6
10+	2		2	11.8
Unknown	1		1	5.9
Total	13	4	17	100.2

Sex ratio: 0 males to 100 females

Sex—Also in winter a greater proportion of the carcasses (Table 7) were female caribou than males (0 males to 100 females). A larger sample would be desirable to allow for definite conclusions.

Examination of wolf kills

At only 14 of the 151 caribou remains was there direct evidence that the caribou had been killed by wolves. I considered the similarity in body area attacked and parts of body eaten, the wolf tracks and signs of struggles, and the frequent presence of wolves ample proof. There is a strong correlation between initial parts of a caribou eaten by wolves, as determined from examination of stomach contents and as determined from the examination of wolf kills. No wolf kills were collected south of the Clarke River.

Detailed field notes on the examination of these caribou killed in spring and summer are in the Appendix. 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.

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 kills has shown that the initial point of attack is usually the neck or shoulder; the caribou is pulled down or knocked down by the impact of the onrushing wolf. The wolf then kills the caribou by a crushing bite in the neck.

The shoulder or neck is a better target than the caribou's hind leg. The leg of a running caribou is only a fleeting target and the wolf risks a serious kick whether intentional or accidental; equally important is the fact that the prey might escape. 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 by swimming to the island. None of

Figure 4. Average daily food consumption per captive wolf by month.

the intact known wolf kills provided evidence to show such injury. It is significant that in this instance the caribou escaped.

Seven of the 14 known wolf kills were attacked in the neck area. I believe the remaining seven caribou were killed in the same way but because the carcasses had been largely 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. In that case (Bull 1, Appendix) 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 we found it, and the wolf may have been disturbed sufficiently by our aircraft to cause disruption of its normal feeding behaviour.

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

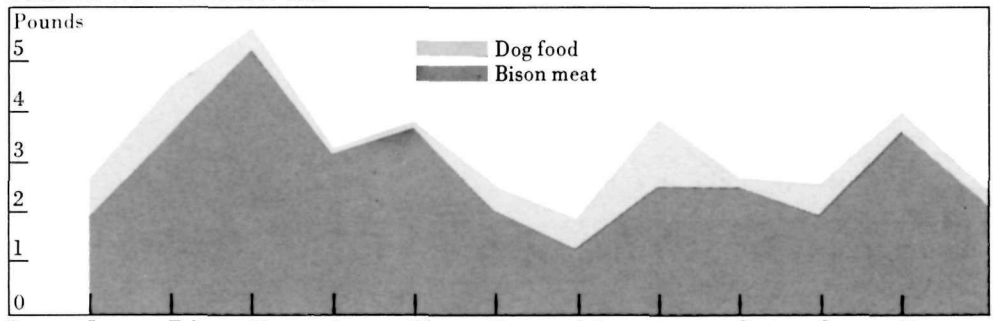
The fleshy upper parts of the caribou's hind leg are also preferred by the wolf but less so than the throat area and the large visceral organs.

Food studies of captive wolves and growth of cubs

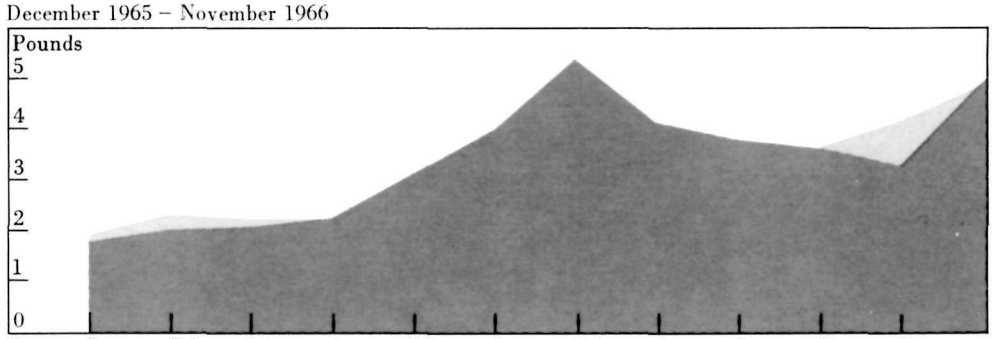
During 3 years (1,101 days) from November 24, 1964 to November 30, 1967, our captive wolves consumed a total of 21,879 lb. of bison meat and fat, and 1,775 lb. of commercial dog food. Total number of wolf units was 6,777; the average number of wolf units per day was 6.2. Based on these figures, the average daily food intake per wolf unit was 3.23 lb. of bison meat and fat and 0.26 lb. of commercial dog food.

Figure 4

December 1964 – November 1965



December 1965 – November 1966



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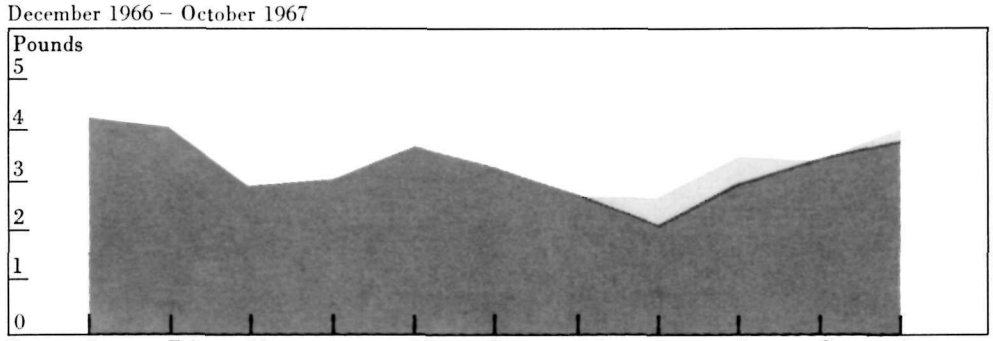


Figure 4 gives the average daily food consumption per wolf by month.

During the feeding studies, the moult patterns and body measurements of all captive wolves were normal. Weights and fat deposits of killed captive animals corresponded closely with those of wolves of the same age and sex killed in the wild.

Growth of cubs

I calculated the mean weekly weights and weekly per cent relative growth rates

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

Weeks/days from birth	Mean weight (lb.) of three males	k
0/3	1.9	
1/3	3.6*	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†	3.9
43/3	82.0†	1.5

*Henceforth mean weight of two males
†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).

Weeks/days from birth	Mean weight (lb.) of two males	k	Mean weight (lb.) 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*	4.4		
39/3			64.0†	3.3
45/3			74.0†	2.4
80/3	81.0*	0.2		

*Weight of one male
†Weight of one female

(Brody, 1945, p. 508; Maher, 1964) 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 (Figs. 5, 6 and 7).

The growth curves illustrate that young wolves grow rapidly at first; then their growth rate drops. The growth curve of Litter 3 (Fig. 7) shows a dip for the end of July. Apparently their daily ration of less than 3 lb. 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 to 24, 1966 and June 15 to 24, 1967 (Figs. 6 and 7). These minor fluctuations probably are related to the cubs' switch from their mothers' milk to meat. The break in the curve of Litter 1 (Fig. 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. Figures 6 and 7 illustrate no differences between the sexes in character or rate of growth.

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

Weeks/days from birth	Mean weight (lb.) of four males	k	Mean weight (lb.) 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*	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†	2.8
46/0	56.0†	3.2		
71/0	80.0‡	2.4	68.0†	1.0

*Henceforth mean weight of three males
†Weight of one wolf
‡Mean weight of two wolves

Figure 5. Mean growth curve of captive wolf cubs, litter 1.

Figure 5

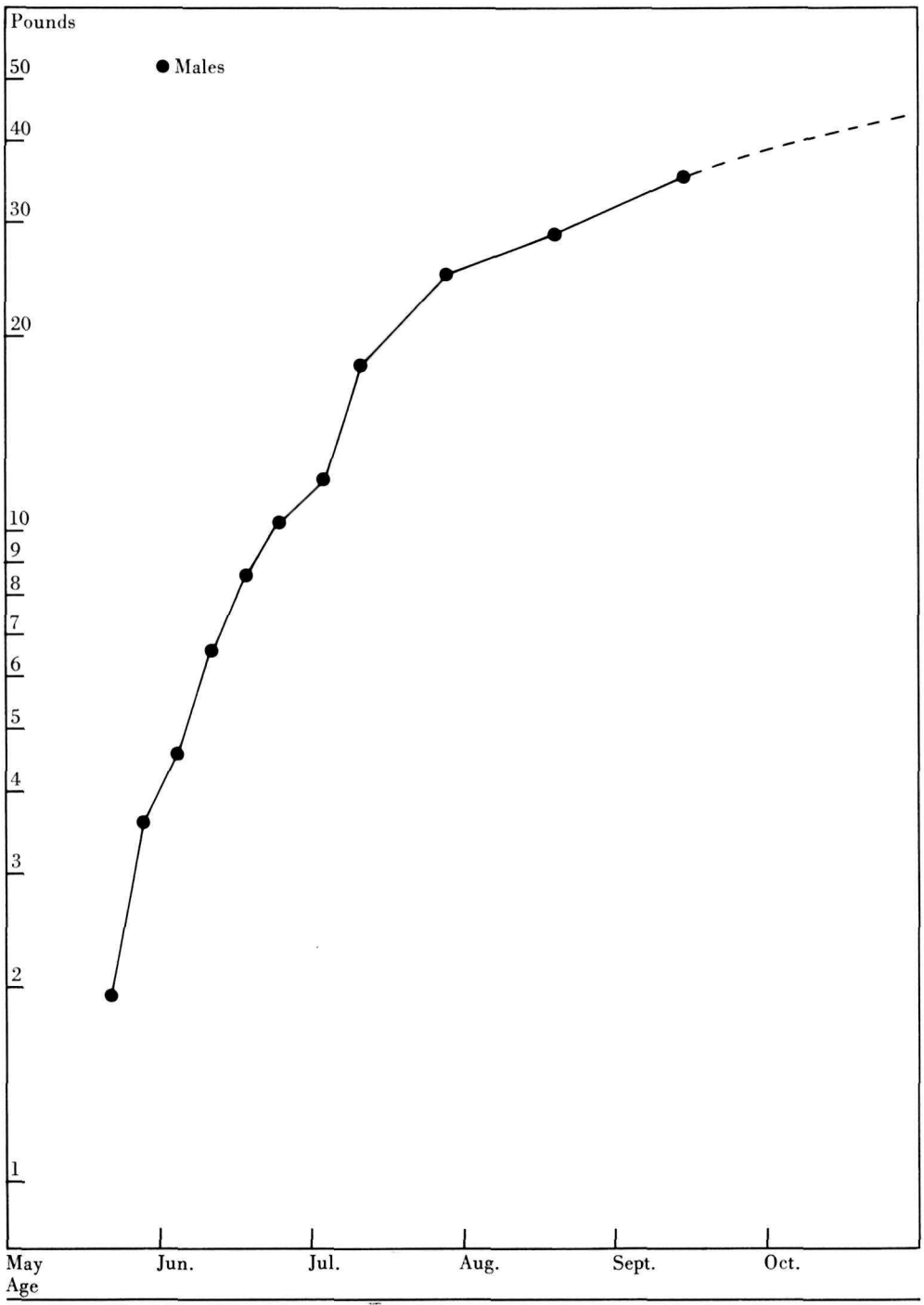


Figure 6. Mean growth curve of captive wolf cubs, litter 2.

Figure 6

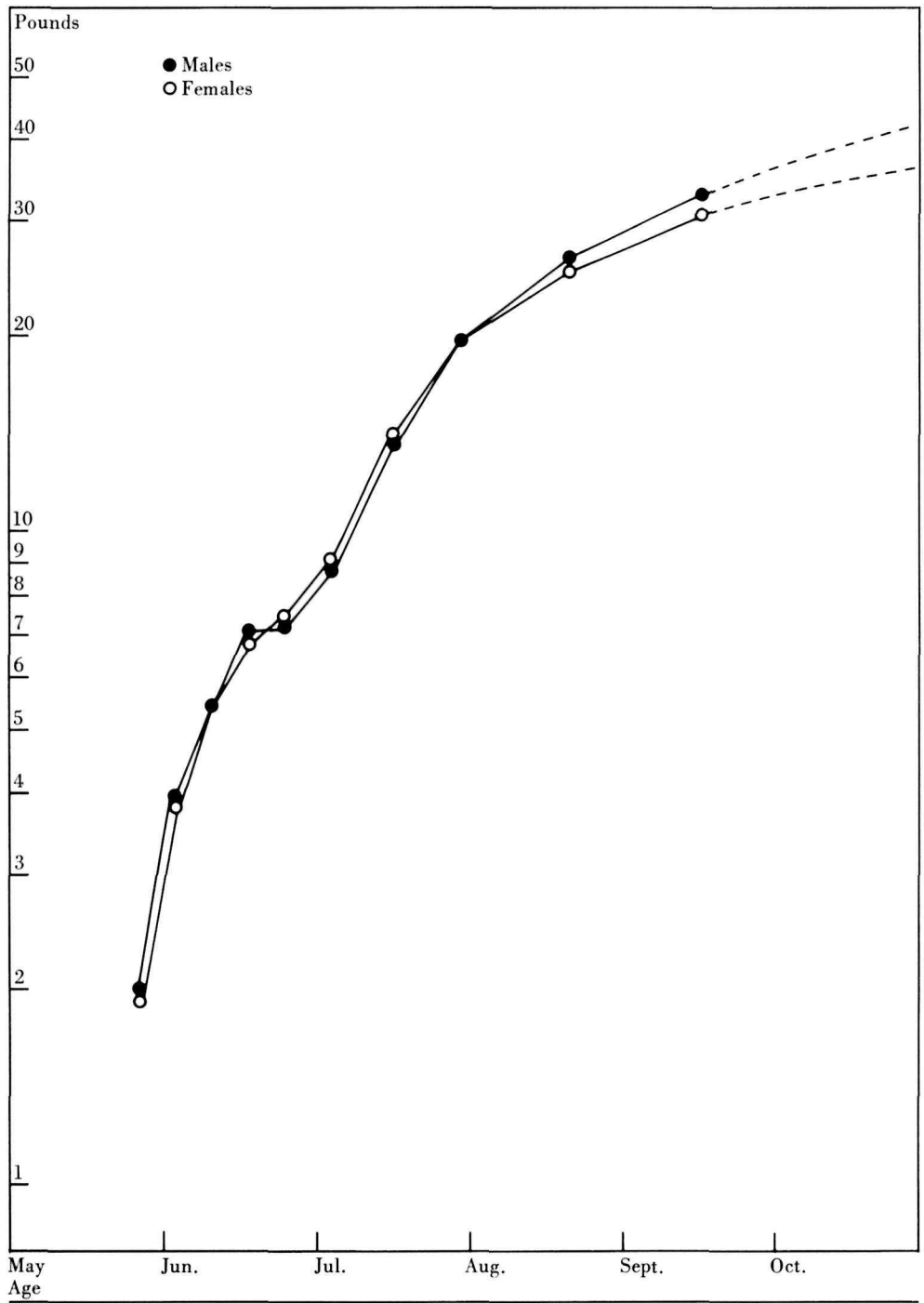
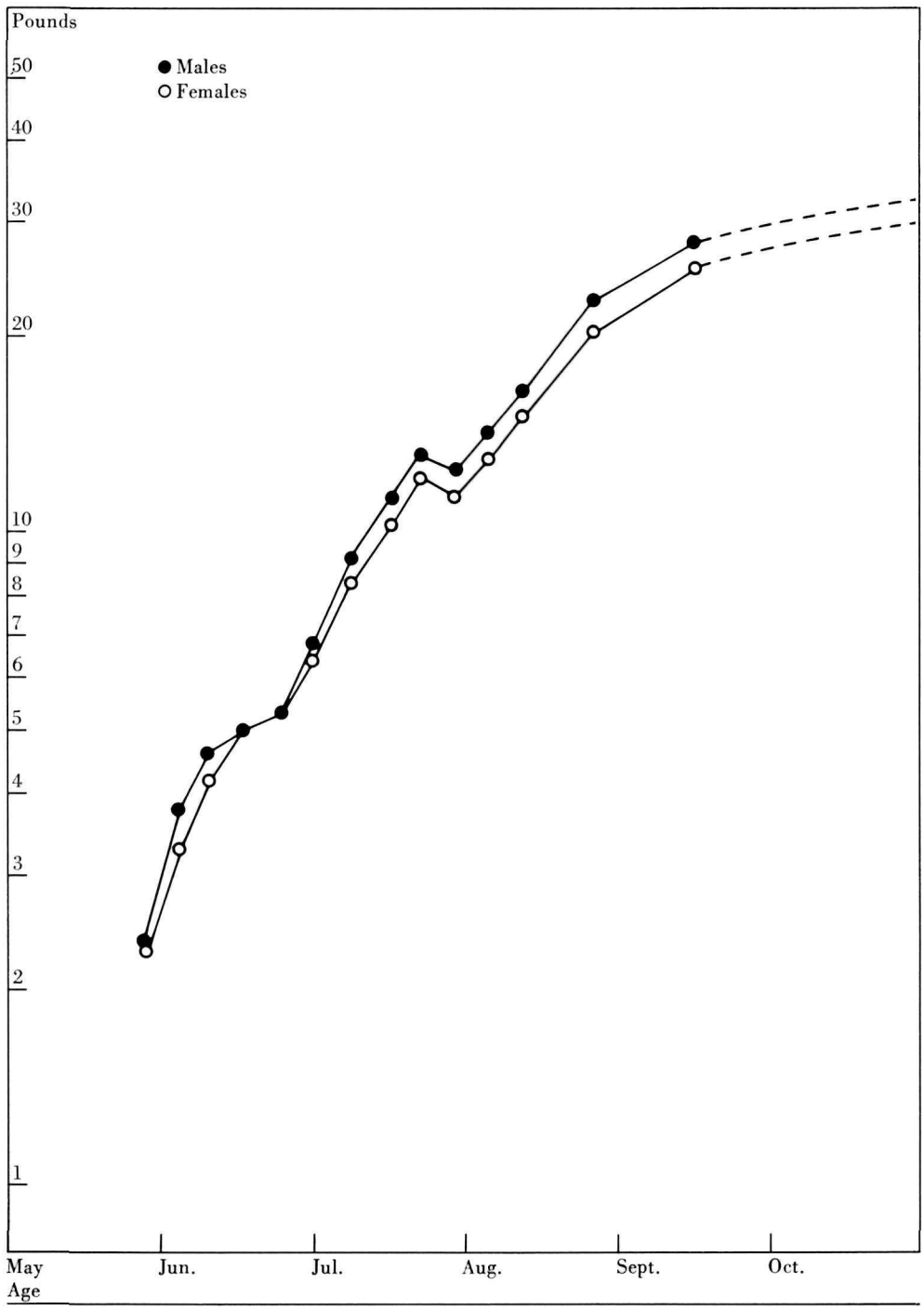


Figure 7. Mean growth of captive wolf cubs, litter 3.

Figure 7



Discussion

Dispersal of wolves from den sites

Each of the nine ear-tagged wolves recovered followed a known caribou migration path (Figs. 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–NWT 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 wolves and confirm the close interrelations between migrating barren-ground caribou and wolves. This bond weakens during the denning season. I found only one wolf den containing cubs in the main caribou calving area and that in 1964. The presence of a second wolf den in the calving area was suspected in 1965, as a 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 2-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 nonbreeding wolves.

In 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 lb. and, unless surprised in their dens, become increasingly difficult to catch prior to tagging. Young wolves should then be able to travel and the wolf families will shortly thereafter follow the migrating caribou. On the winter range the most noticeable aspect of wolf–caribou relationships is that wolves are almost never seen apart from barren-ground caribou. In spring, wolves and caribou return to the tundra. Sometimes wolves return to den sites in advance of the caribou.

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 show that north and south of the Clarke River different numbers of young are raised per pair of breeding wolves. I also observed that the three cubs in one southern litter (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, smaller litters and lighter cubs.

Of 18 pregnant wolves killed by Riddle during the winters of 1965–66 and 1966–67, numbers of embryos varied from 2 to 8 and averaged 5.8. Seven litters produced in captivity averaged 4.0 cubs. I found that wild wolf cubs from this study at about 6 weeks of age averaged 3.5 cubs per litter. Mortality of wolf cubs prior to 6 weeks of age (and possibly some prenatal loss) is therefore decreasing potential litter size from 5.8 to 3.5. The ear-tagging work gives further evidence of high mortality of young wolves after leaving the den site. Seven of the recovered wolves were less than 1 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 NWT. The $40 bounty is paid for wolves of all ages, even for new-born pups, many of which would not live to their first birthday.

Wolf–barren-ground caribou relationships

My 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 denning wolves and their young cubs, is much more varied and depends largely on the availability of smaller prey, including small birds, rodents and fish. Wolves kill approximately equal numbers of caribou of all ages except calves and older caribou. Calves constituted just over one-third of total casualties. It is impossible 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 varies from complete to practically none. I believe that in the few cases where the carcass was abandoned entirely, the wolf must have been driven off by man. Caribou carcasses found in summer are often only partially eaten; before the wolves can return to their kill, mammalian and avian scavengers such as a grizzly bear, wolverine, foxes, Herring Gull, eagles, Rough-legged Hawk, falcons (rarely) and jaegers (*Stercorarius* sp.) will rapidly reduce the carcass.

The dependence of scavengers on 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 believed to subsist solely on birds they catch themselves. 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 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 indicate the temporal importance of carrion to animals customarily feeding on live prey and the role of

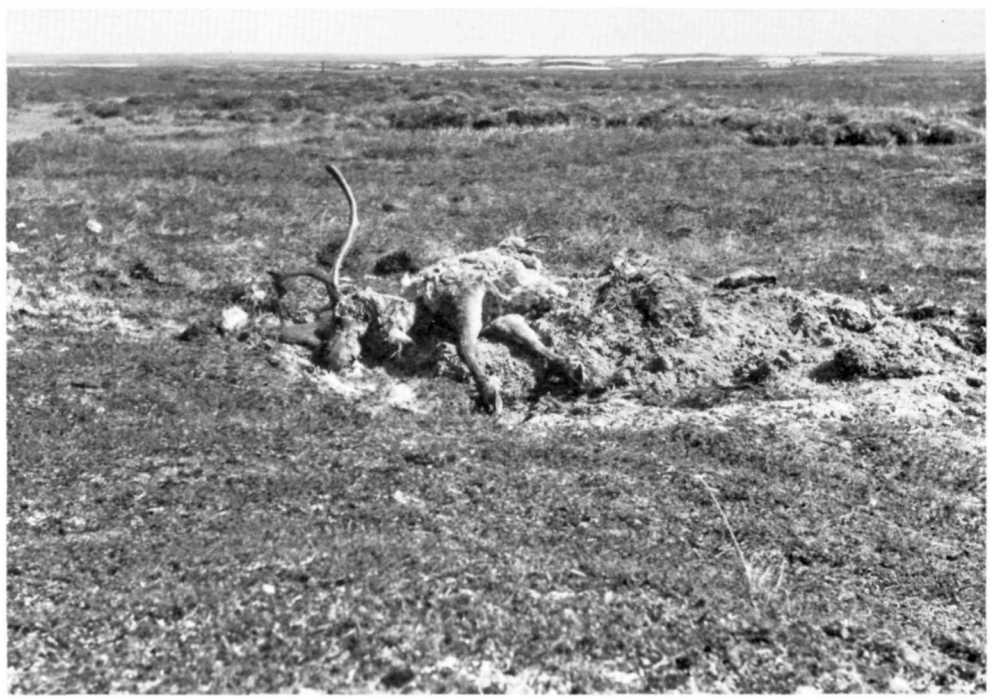
A caribou was killed by wolves here and completely utilized. Abitau Lake.

This bull caribou was probably killed by wolves and partly covered with earth by barren-ground grizzly. Crossing-Place-of-Deer, Thelon River.

the wolf in supplying food to other animals inhabiting its range.

During the denning season I rarely saw wolves in packs large enough to eat a caribou at one meal. Also, food requirements may be less in summer than in winter.

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



Food studies of captive wolves and estimates of food consumption of wild wolves

Our captive wolves thrived on an average daily ration per wolf unit of 3.23 lb. of bison meat and fat and 0.26 lb. 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 3 lb. per wolf compared to about 4 lb. per wolf for the same period in 1966.

The average daily food consumption per wolf by month (Fig. 4) for the periods December 1964 to December 1965 and December 1966 to November 1967 shows a winter high and a summer low of food consumption. The center part of Figure 4 (December 1965 to December 1966) is inconsistent. The captive wolf colony during the summer of 1966 consisted of four adults and seven cubs. I estimated that a wolf cub from 1½ months to 4 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 (Fig. 4, center 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, wild 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) indicated that the energy expended while walking is double that expended while standing and this ratio is approximately the same in relatively large and small animals.

I have observed that wild wolves feeding on freshly killed caribou sometimes pass pieces of undigested hide and cartilage with the droppings. I did not observe that in our captive wolves and consequently I believe that captive wolves are more economical in the utilization of food than wild ones.

Figures 4 to 7 indicate that approximately 3½ lb. of bison meat, fat and dog food daily suffice for captive wolves but growing cubs required more. The daily food fed to our captive wolves would be the minimum requirements for wild wolves.

Taking into consideration the estimates by Maynard (1937) and Brody (1945), wild wolves probably require the equivalent of 7 lb. of bison meat daily or 2555 lb. per year. Kelsall (1960) found the average live weight of 67 caribou to be 163 lb. I estimate that a 163 lb. caribou would provide a wolf with about 110 lb. 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 wolf kills throughout the year. Totalling numbers in each of three age classes (0–1 year, 1–2-year-old and older than 2 years) and weighting data from Table 7 to allow for the larger total in Table 6, I calculated that the total of 23 caribou eaten per wolf annually is made up of five calves, two yearlings and 16 caribou older than 2 years.

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, such as Symington (1965, p. 38) incorrectly quoting Banfield (1954, No. 10B, p. 51).

During the winter, wolf and caribou populations are usually concentrated and trappers and aerial travellers most often see remains of caribou on frozen lakes and rivers. Local and temporal concentrations of wolves and wolf kills are frequently extrapolated to the entire caribou winter range by inexperienced observers. During aerial surveys on March 14, 1968 in the Abitau Lake area I saw 56 different wolves and the remains of 19 caribou killed by wolves in an area of 384 sq miles, giving a density of one wolf per 6.9 sq miles. Undoubtedly some wolves and kills were missed. There were no caribou and no wolves 20 miles from the center of the caribou concentration.

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

A census of the total wolf population in the study area would be difficult and uneconomical. More important than the total population is the effect that it is having on the main prey species, the barren-ground caribou. Since wolves kill many caribou calves, wolves could effectively limit caribou numbers.

Since 1961 predator control positions were reduced from six to one in Mackenzie and Keewatin because the reduced kill of wolves showed that wolf populations had greatly diminished in the previous 10 years. The 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 winter 1965–66 killed 398 wolves, followed by 274 wolves in winter 1966–67. The wolf population then seemed to remain stable, being in balance with the harvest of the predator control officer. His duties were terminated in 1968.

A bounty program effected in the NWT 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.

Even though wolves are being 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 been received of large numbers of wolves.

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

Under the present NWT Game Regulations, the wolf is not classified as a game animal. Changes in the regulations placing the wolf in a more dignified position are desirable. 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 behaviour and ecology of tundra wolves was carried out between 1960 and 1968 in the Thelon Game Sanctuary, NWT, 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, NWT.

2. 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 2-month period when a segment of the breeding population of wolves halts its northward journey south of the caribou calving grounds in order to raise its cubs.

3. Mortality rates of young wolves in the southern part of the breeding area are greater than farther north. Average litter size was 2.0 cubs south and 4.3 cubs north of the Clarke River. Litter sizes were determined when cubs were 5 to 7 weeks old.

4. Examination of 595 spring and summer wolf droppings collected in the Thelon River study area has shown that of 1039 prey 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, a greater average number of different prey 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. Caribou calves are of far greater importance in the diet of wolves in or near caribou breeding areas (67 of 520 prey items or 12.9 per cent) than in the diet of southern wolves (26 of 519 prey items or 5.0 per cent), which utilize small passerine birds, ptarmigan, birds' eggs, fish and insects to a greater extent. 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 north. I found that lemmings and voles were important (133 of 1039 prey items or 12.8 per cent) 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 study area confirms that northern wolves utilize predominantly 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. Caribou are most likely to die as calves. Calves constitute 35.7 per cent of a small sample of 14 spring and summer wolf kills. Calves also constitute 33.8 per cent of 151 remains of caribou which died in spring and summer of all factors, including wolf predation but excluding human hunting. Wolf predation of calves in winter is 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-old and over 10-years-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. 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 kills invariably are completely utilized. During summer, kills are frequently incompletely utilized by wolves primarily because packs are small or non-existent then. A host of valuable mammals and harmless birds scavenge on the remains.

13. Wolf densities as high as one wolf per 6.9 sq miles only occur locally at times of maximum compression of wintering caribou populations.

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

15. I estimate that a wild wolf would eat about 23 average caribou annually.

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Appendix

Detailed field notes from examination of wolf kills

Calf 1
A male calf, still warm, was found near wolf den, Spruce Grove River, July 21, 1960. One wolf was 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.

Calf 2 and Yearling 1
Sex unknown. Found near wolf den July 22, 1961, near southwest end of Aberdeen Lake. Bite marks on necks of both animals. They had died recently. Tracks of two wolves were nearby.

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.

Calf 4
Sex not recorded. Found on August 8, 1963 in same area as calf 3. Tongue, throat of calf had been eaten.

Calf 5 and Cow 1
Sex of calf unknown. Found on August 10, 1964 in same area as calf 3. Caribou were moving south through area. The carcass was partly eaten, including throat and tongue. The cow was 9 years old.

Cow 2
A 4-year-old cow found on August 12, 1964 in the same area as calf 3. The caribou had been killed by a wolf within the previous day or two. Its throat and tongue had been eaten.

Yearling 2
I first saw this animal, a female, 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 plucks 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 ribcage was intact.

Cow 3
Also on June 26, 1965, a 6-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. I noted dried blood on the ground and found the animal's intestine and rumen outside the body and relatively untouched. I observed fresh black wolf droppings. Neck, throat, tongue, part of the intestine and hind leg had been eaten. The front legs and ribcage were untouched, except for bite marks on the left shoulder. One of the caribou's ears was bitten off.

Bull 1
On June 27, 1965 just opposite Lookout Point, I observed from the air a wolf standing beside a dead caribou. I examined the caribou on the ground and found it was a freshly killed 3-year-old bull. Tracks showed that the caribou had been feeding in a sedge swale bordered by birch thickets. The wolf attacked from the thicket and had closed with its prey without a chase. The wolf had stalked the caribou or lain in wait for it and had grabbed it 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 eaten only a small amount of meat from the upper right hind leg and had just broken into the abdominal cavity. On subsequent visits to the site I found that the wolf had not returned.

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 forelegs were almost intact. The caribou had been partly covered by earth, probably by a grizzly bear. One was seen here twice by my assistant who was flying over the area at the time of my ground survey. Two adult wolves and a litter of young were using the den.

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. I saw three wolves slowly walking away from the carcass. An hour later the wolves were still in the vicinity and we landed nearby to examine the kill, an 8–9-year-old cow. Its neck, tongue, throat and intestine had been eaten. The animal had been dragged 25 feet to the place where it was eaten. Tracks and hair indicated that wolves had killed it.

Wolf kill found in 1958
On August 7 when I was studying caribou, I found a cow that had been killed by wolves on 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 in two bounds had caught and killed the cow. 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. The next day, I observed a black wolf 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.

Wounded cow

On August 4, 1957 D.C. Thomas and I found a wounded lactating caribou on an island in the Thelon River near Lookout Point. The caribou had a large fresh wound which may have been made by a wolf in the upper part of a hind leg. The caribou apparently escaped from the predator by swimming. The wounded cow was in poor flesh and was unable to rise when closely approached.

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