The Ecology of the Timber Wolf (*Canis lupus* Linn.) in Southern Manitoba - Wilderness, Recreational and Agricultural Aspects.

by

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THE ECOLOGY OF THE TIMBER WOLF (*Canis lupus* Linn.) IN SOUTHERN MANITOBA - WILDERNESS, RECREATIONAL AND AGRICULTURAL ASPECTS.

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ABSTRACT

The ecology and recreational value of timber wolves (*Canis lupus*) in the Wallace Lake area and the extent of wolf predation on cattle in agricultural regions of Manitoba were examined during 1973-1975 in an effort to evaluate the ecological, recreational and economic status of wolves in Southern Manitoba.

A population of approximately eleven wolves occupied the 563 km^2 Wallace Lake study area resulting in a density of one wolf per 51 km^2. Examination of 203 wolf scats from the study area showed that moose, white-tailed deer and beaver comprised 89.5% of the wolves' diet. Beaver was the primary prey species during summer while moose and deer were utilized heavily during the winter. There was no shift in the wolves' diet to young ungulates during the summer.

Post-mortem examinations of 21 wolf carcasses collected by trappers from scattered locations throughout Southern Manitoba revealed the majority were in good nutritional condition with light parasite loads and few pathologic abnormalities. Sixteen of 20 wolves aged were less than one year old.

A questionnaire survey of 126 summer visitors to the Wallace Lake study area indicated a large majority was interested in hearing and seeing wolves, and 73.6% would have been willing to participate in organized programmes on wolf biology had these been available.

A questionnaire mailed to 1,059 cattle owners yielded a 49.2% return. Of those, 19% had lost livestock to predators of all species during the last five years. Only 1.8% had lost a total of 19 calves and one sheep, attributable to wolf predation during 1973-74. It was concluded that livestock losses to timber wolves in Manitoba were minimal.

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INTRODUCTION

The timber or grey wolf (*Canis lupus* Linn.) at one time had a circumpolar distribution in the Northern Hemisphere. It was found in all Northern Hemisphere habitat types with the exception of certain desert areas in the western and south-western regions of the United States and tropical rain forests (Goldman, 1944). In North America the wolf's range extended from the High Arctic Islands to the southern end of the Mexican Plateau (Goldman, *ibid*.). Wolves now occupy approximately half of their former range in North America (Theberge, 1973). The remnant populations outside Canada and Alaska are very small and geographically limited.

Men and wolves have seldom co-existed peacefully. The wolf is a predator of large mammals and this has led to conflicts, either real or imagined, with man's utilization of game animals and husbandry of domestic livestock. The belief that wolves prey on humans has also contributed to the fear and hatred that man has felt for the wolf. As a result, wolves have been exterminated in much of their former range.

As in other areas of North America, the wolf in Manitoba has been subjected to bounty and poison campaigns in an attempt to lower the population and hence the presumed conflict with man. In Manitoba wolves have been restricted primarily to the boreal forest "wilderness area" of the province with small outlying populations existing in Riding Mountain National Park and Spruce Woods Provincial Park. Wolves are occasionally seen in agricultural Manitoba. Although there is no longer a provincial bounty on the wolf, it is still classified as a predator and is therefore unprotected throughout the year except in wildlife refuges and Riding Mountain National Park.

In recent years the public attitude toward predators has changed. Increases in both the sport-hunting value and the commercial value of predators have resulted in increased hunting and trapping pressures. At the same time, the aesthetic and intrinsic values of predators have been recognized and the wolf has become a symbol of "wilderness". Because of their increased aesthetic and commercial values, there is now a greater need for "management" of wolves and other predators than for control. Management of predators requires information on the biology of the species, on their effects on agricultural operations and on their effects on other wildlife species.

Few data have been collected on wolves in Manitoba except in Riding Mountain National Park where a detailed study of wolf ecology is presently being conducted as part of a large mammal systems study (Carbyn, pers. comm.). Records of track occurrences, rough population estimates and some reports of predation on livestock have been presented in regional reports by the Manitoba Department of Renewable Resources and Transportation Services (R.R.T.S.). This, however, is not an adequate basis for making management decisions of potential biological and economic impact on wolf populations.

I undertook this study to provide some basic data on the ecology of timber wolves in Manitoba. The primary objective of my study was to examine the ecology of timber wolves in the Wallace Lake area. The secondary objective was to examine some aspects of the relationship between man and wolves. This involved evaluating: 1) the effects of wolves on cattle-rearing operations in agro-Manitoba and 2) the attitudes of tourists in a wilderness area (Wallace Lake) to wolves. The data collected in this study were used to formulate recommendations for a wolf management policy for Manitoba.

LITERATURE REVIEW

Timber wolves evolved as pack-hunting predators of large animals. They possess physical and behavioral characteristics which have adapted them to this niche. The adaptations which enable them to capture large ungulates render them inefficient as hunters of small animals. Studies in North America have shown that timber wolves depend on large ungulates for their primary food source. Although wolves consume a wide variety of small mammals, birds, fish, invertebrates and vegetation, beaver (*Castor canadensis*) is the smallest species they prey on regularly. There is a large recent body of literature concerning the interaction of wolves with moose (*Alces alces*), deer (*Odocoileus sp.*) and beaver.

Pimlott *et al*. (1969) observed that wolf food habits studies in North America have shown that there is an "optimum prey species" in every area. That is, one species provides the majority of the wolves' diet. They suggested that a combination of prey characteristics such as density, escape and defence capabilities and habitat physiography determine the "optimum prey species" of an area.

Wolves concentrate on the smallest or easiest prey to catch when two or more species of large prey inhabit the same area (Mech, 1970). Peterson (1955) found that wolves preyed more heavily on white-tailed deer (*Odocoileus virginianus*) than on moose in the St. Ignace Island area of

Ontario. Despite the fact that moose were much more abundant, he found that their remains occurred in only 36% of the scats collected while deer remains were found in 57%. Cowan (1947) reported that mule deer (*Odocoileus hemionus*) contributed more to the diet of wolves in Jasper and Banff National Parks than the deer population size would suggest. He found that deer kills were approximately half as numerous as elk (*Cervus canadensis*) kills although only about one third as many deer as elk were seen. Pimlott *et al*. (1969) also found that deer were the preferred food of wolves in Algonquin Park, Ontario.

The feeding habits of timber wolves shift with changes in prey populations (Murie, 1944; Voigt *et al*. 1976) and also with the seasonal availability of prey. When one prey species becomes scarce or unavailable, such as beaver do during the winter, they concentrate on other species. An important seasonal change in the diet of wolves is the shift from adult to infant ungulates during the summer.

FOOD HABITS OF WOLVES

MOOSE

The wide distribution of moose in North America has made them the primary ungulate prey of wolves in many areas. Moose is also an important game species, a situation which has led to real and imagined conflicts between humans and wolves over the utilization of moose.

The importance of moose to the diet of wolves depends upon the availability of alternate food sources. Murie (1944) found that barren-ground caribou (Rangifer tarándus) was the major food source of wolves in Mount McKinley National Park and moose remains were identified in only nine of 1,174 scats. Cowan (1947) noted that while moose were fifth in abundance in the total game population of Jasper and Banff National Parks, they were the third item in importance in the wolves' diet (7% of 420 scats). Pimlott et al. (1969) expected that moose would be the predominant food item following a decline in the deer population in the Marten River area of Ontario. However, the occurrence of moose remains in scats was only 17% while deer was 42%. Burkholder (1959) observed a pack of 10 wolves in Alaska for six weeks and found that, of 22 kills, 14 were caribou and eight were moose. Stephenson and Johnson (1972) and Stephenson (1975a) found that moose were the primary prey of wolves in south-central Alaska.

The wolves in Isle Royale National Park in Michigan rely on moose and beaver for their food supply. Moose are the only ungulates found on the island. Mech (1966) found moose remains in 75.9% of 438 summer scats and Shelton (1966) found that moose comprised 86% of summer food items occurrences. Beaver remains were found in approximately 11% of the summer scats collected during these studies. The summer predation pattern on Isle Royale changed in the early 1970's due to an increased beaver population and a decrease in moose productivity.

Beaver became the principal food source for the wolves during the summer, occurring in 76% of the scats examined in 1973 (Peterson, 1975). Moose have remained the major winter food source for the wolves.

Selection of Moose

Mech (1966) found that the predation efficiency (per cent of moose "tested" that were killed) of wolves on Isle Royale was 7.8%. Shelton (1966) found the total predation efficiency of wolves on Isle Royale over five years (his study and Mech's) was 8.1%. The low predation efficiency of wolves suggests that they must search out moose which are more vulnerable to predation than the majority of the population. A number of factors including age, sex, debilitating conditions, winter severity and range conditions have been found to influence the suceptibility of moose to predation by wolves.

Predation by wolves is usually concentrated on calves and relatively old moose. Studies of the summer food habits of wolves have shown that calves often comprise the majority of moose eaten during that season. Mech (1966) found that 75% of identifiable occurrences of moose remains were calves. Pimlott _et al_. (1969) found that calves comprised 88% of the occurrences of moose remains. Frenzel (1974) also found a very high proportion of calf remains in summer wolf scats.

Moose, especially calves, were a major item in the summer diet of wolves in south-central Alaska (Stephenson, 1975a).

Because it is impossible to discern whether food items found in scats are obtained through predation or scavenging, it is difficult to determine the significance of this high occurrence of calf remains. If the wolves are feeding on dead calves or calves that would have died of other causes they would not affect the population significantly. However, if they were preying on young animals which would otherwise survive, they could be a significant limiting factor.

LeResche (1968) found that in one area in Alaska the greatest mortality among moose calves occurred during the first five months after birth. During that time, 56% of the calf crop was lost. The greatest mortality, approximately 26%, occurred within two weeks of parturition. Causes of mortality included drowning, entrapment by vegetation, abandonment, injuries inflicted by the mother and predation. Gasaway et al. (1977) estimated calf mortality in another area of Alaska to be 40 - 50% from parturition to six weeks and 60 - 70% by six months of age. They believed wolf predation to be the most probable cause of this high mortality rate.

Moose between the ages of one and seven years are usually not affected by wolf predation (Mech 1966). Winter studies have shown that calves and older animals (eight years and older) bear the brunt of wolf predation. Burkholder (1959) determined the ages of seven moose killed by wolves and found that six were calves and one was a yearling. He did not notice any selection for age among 14 caribou killed by the same pack during the observation period. Mech (1966) found that calves composed 15% of the moose population on Isle Royale during his three year study. However, calves comprised 36% of 50 observed winter kills and approximately 47% of 36 kills made by the large pack of 15 wolves. No wolf-killed moose between the ages of one and seven years were found. Moose eight years and older comprised 46% of the winter kills. Shelton (1966) in a later study, examined 28 kills made by the large pack and found that 79% were eight years or older. Fourteen per cent of these kills were calves despite the fact that he estimated that calves made up approximately 17% of the late winter population. This low representation of calves may be explained by the fact that in 1962 he missed at least three kills (probably calves) by the big pack. Wolfe and Allen (1973) found that 32% of the 44 wolf-killed moose they examined, also on Isle Royale, were calves.

Mech (op. cit.) and Shelton (op. cit.) found a strong selection for female moose on Isle Royale during February and March (67% and 65% respectively), assuming the sex ratio was even. Shelton (ibid.) reported that the sex ratio of all adult moose killed or eaten by wolves, including those found in spring, summer and fall, was 18 males: 19 females.

Furthermore, the sex ratio of all remains, young and adult, for which sex could be determined, was 23 males: 25 females. On the basis of this information, Mech (1970) suggested that wolf predation on bull moose was concentrated during some period other than February and March. Wolfe and Allen (1973) however, did not find this selection for cows in later studies on Isle Royale. Stephenson and Johnson (1972) found that five of nine wolf-killed moose they examined in Alaska were adult females but that adult females were the most abundant group in their study area.

Debilitating factors such as malnutrition, parasites and pathological conditions may increase the vulnerability of moose. It is difficult to find evidence of physical disabilities in wolf-killed animals because the carcass is usually completely consumed or nearly so by the time it is discovered. As Mech (1970) pointed out, it is also difficult to determine the effect of various debilitating factors on vulnerability when the incidence of these factors in the population is unknown.

Moose are subject to a wide range of diseases and parasites, many of which seem to have been acquired in North America from contact with livestock and native deer of the genus *Odocoileus* (Anderson and Lankester, 1974). Sylvatic echinococcosis is common in Canada and the northern United States wherever moose and wolves co-exist. Anderson and Lankester (*ibid.*) briefly reviewed the literature on

Echinococcus granulosus and found general agreement that increasing numbers of pulmonary hydatid cysts increase an animal's vulnerability to predators and other stresses. Mech (1970) found a much higher rate of infection in a small sample of wolf-killed moose than in animals that died of other natural causes.

Mech (*ibid*.) reported that 21% of 61 wolf-killed moose on Isle Royale had moderate or severe granulomatous lesions in the manibular region which may have been the result of actinomycosis or food impaction. Although the effect of such infection in moose is unknown, Murie (1944) found that it was an important factor in predation in Dall sheep (*Ovis dalli*) between two and eight years of age.

Peek *et al*. (1976) found that all mortality appeared to be concentrated on calves, yearlings and the oldest animals in a Minnesota moose population. Cerebrospinal nematodiasis (*Parelaphostrongylus tenuis*) was found to be the cause of death in 23 of 34 moose which died of natural causes. Moose which died of nematodiasis were under five years of age. Peek *et al*. (*ibid*.) suggested that the presence of this parasite in the population might alter the age structure of wolf-kills by predisposing relatively young moose to predation.

Mech (1970) suggested that malnutrition, as evidenced by fat-depleted femur marrow, may increase the vulnerability of moose to wolf predation. The marrow of eight of 54 wolf-killed adult moose on Isle Royale was fat-depleted. Studies in Alaska have not shown a strong selection for malnourished moose. Stephenson and Johnson (1972) and Stephenson (1957b) found that the majority of moose taken by wolves were in relatively good nutritional condition. Franzmann and Arneson (1976) found that the marrow fat content of moose killed accidentally and by wolves during the winter was very similar. The marrow fat content of these groups was significantly greater than that of moose which starved to death during the same period. Their data suggested that wolves selected moose from the entire population and did not rely on moose under nutritional stress.

Effect of Winter on Predation

Moose have physical and behavioral adaptations to snow cover. Their long legs assist in their browsing habit and are an obvious advantage in thick snow cover. Coady (1974) concluded that adult moose are relatively unimpeded by snow thicknesses up to 70 cm. Snow thicknesses greater than 90 cm severely restrict movement and can be critical. Calves are less able to cope with thick snow cover because of their shorter legs.

During the winter, moose are in a negative energy balance due to the low quality of browse available during that season (Gasaway and Coady, 1974). Thick and/or hard snow can add to this stress by reducing the availability of low-growing browse species and restricting movement so that more energy is expended moving to feeding areas than is derived from the ingested food (Coady, op. cit.).

Several authors have recorded the effect of severe winters on moose populations. MacLennan (1975) reported heavy mortality in Saskatchewan following the severe winter of 1970-71. Gasaway et al. (1977) reported a general and precipitous decline in the Alaskan moose population during the winter of 1965-66 which had near-record snow accumulation.

The pattern of wolf predation on moose changes during severe winters with more than 70 cm of snow. Moose of all age classes become more vulnerable but most noticeable are calves and young adults from one to six years of age. Peterson and Allen (1974) found that unusually thick snow cover resulted in an increased rate of predation and less complete utilization of kills. Of 193 wolf-killed moose, 31% were calves when snow thicknesses were less than 76 cm. However, when the snow thickness was greater than 76 cm the proportion of calves rose to 49% of 76 kills (Peterson and Allen, ibid.). They found that during the severe winters of 1969, 1971 and 1972, 38% of 42 adult moose killed by wolves were from one+ to three+ years of age while in other years on Isle Royale (with less snow) this age class represented only 12% of 113 kills. Stephenson (1975b) reported that during the severe winter of 1971-72, calves comprised 56.1% of the wolf-killed moose located but had made up only 15.8% of the autumn 1971 population. This suggests that calf mortality increases significantly only during very severe winters.

Peterson and Allen (1974) suggested several possible explanations for increased calf vulnerability under these conditions. Both moose and wolves use shorelines extensively because travelling is easier there than inland, resulting in more contacts between the two species. Cows and calves are separated occasionally when the cow goes inland to feed while the calf remains near the shore. When a cow-calf pair is tested by wolves, the cow guards the rear and the calf is forced to break trail thereby expending a great deal of energy. The ability of cows to protect their calves may also be reduced by winter stress. Calves are the first age group to be affected by malnutrition which reduces their vigor and increases their vulnerability. Stephenson (1975b) reported that the marrow fat content of eight adult wolf-killed moose averaged 75.8% while that of 14 calves averaged 21.8%.

Stephenson (1975b) found that the average age of adult moose taken by wolves during two average winters was 10.6 years while hunter-killed moose averaged about six years which suggested that the wolves selected moose which were slightly older than the population average. During the severe winter of 1971-72 however, the mean age of adult wolf-killed cows and bulls was 8.6 and 3.0 years respectively. Hunter-killed adult cows and bulls in 1971 averaged 6.7 and 3.2 years respectively. This suggested that younger animals were more vulnerable during that severe winter.

Wolves and moose differ greatly in their abilities to travel in specific snow conditions. The static weight-load of moose has been found to vary from 420 g / cm^2 to over 1000 g / cm^2 (Nasimovich, 1955; Kelsall and Telfer, 1971). Coady (1974) found that the foot load decreased from fall to spring due to seasonal loss of body weight. Peterson and Allen (1974) conducted compaction tests to determine the weight-load that best simulated the track depth of moose and found that the average value was 230 g / cm^2. Wolves have a much lower weight-load. Nasimovich (op. cit.) found standing weight-loads of 89 to 114 g / cm^2 and Peterson and Allen (1974) found that a weight-load of approximately 100 g / cm^2 best simulated track depths of wolves. The long legs of moose give them an advantage in thick snow cover of low density but wolves are supported by crusts through which moose break.

Pruitt (1959) described a "snow shadow effect" caused by vegetation along shorelines which results in a band of relatively thick soft snow extending up to 90 meters out from the shore. As this snow is thicker and softer than the snow farther out on the lake it may give the wolves an advantage over their prey when contact occurs there. Pruitt (ibid.) also noted that a "snowfence effect" caused by shoreline vegetation results in thicker softer snow cover for a variable distance inland than is found under normal forest cover. This might also give the wolves an advantage if the prey attempted to move inland after contact occurred.

The increased vulnerability of moose during severe winters appears to be due to a combination of the effect of weather on their health and vigor and a restriction of their escape and defense capabilities by thick snow. Although studies by Stephenson (1975b), Stephenson and Johnson (1972) and Franzmann and Arneson (1976) showed that wolf-killed moose were usually in better condition nutritionally than moose that were winter-killed, severe winters reduce the nutritional level and hence increase the vulnerability of the entire population. In extremely thick snow cover (over 70 cm), the fact that the weight-load of wolves is less than half that of moose could become a critical factor. Furthermore, until the snow becomes dense enough to support a moose, each increase in density is to the wolf's advantage. Mech (1966) noted that when pursuing a moose, most of the wolves followed single file in the trail of the moose. This enables the wolves to conserve energy while the moose is forced to exert valuable energy breaking the trail. These factors plus the increased contact along shorelines probably account for increased predation rates during severe winters.

Malnutrition due to thick snow and restricted browse intake can have a long term effect on moose susceptibility to wolf predation. Gasaway and Coady (1974) noted that pregnant cows undergo a period of greatly increased energy demands from early March until parturition. Malnutrition during this fetal period results in calves which are of subnormal size at birth and suffer long-term retardation in growth and development (Peterson, 1975).

Peterson (ibid.) found that on Isle Royale the percentage of one to six year old wolf-killed moose rose from 5% to 22% from the early 1960's to the late 1960's and increased to 53% in the early 1970's. This mortality pattern continued even in winters of below average snow thicknesses. Most of these moose were in average physical condition. Since most of these moose were born after winters in which nutritional hardship was apparent, Peterson suggested that malnutrition during the fetal period affected their later development so that they were susceptible to wolf predation during age classes when Mech (1966) found that most moose were "invulnerable" to wolves.

Effects of Wolf Predation on Moose Populations

The question whether or not wolves can control or limit populations of moose or other "big game" species is the core of much conflict between man and wolves. Various studies have shown that wolf predation can be a major mortality factor and under certain conditions may be the primary factor limiting moose populations.

Pimlott (1967a) postulated that predators may have effectively controlled ungulate populations before humans altered the environment. He suggested that deer and moose did not evolve intrinsic mechanisms of population control to prevent their exceeding their food supply because they had very efficient predators. Pimlott (ibid.) considered that the forest ungulates and their predators evolved in relatively stable environments that could not support high density prey populations.

Cowan (1947) reported that survival rates of elk, deer, moose and sheep were nearly identical in wolf-inhabited and wolf-free areas. He believed that range condition was the critical limiting factor. The prey: predator ratio in Cowan's study area was very high - approximately 300 to 400 head of "big game animals" per wolf. He noted that the wolves were not able to remove the injured and diseased animals from the population let alone prevent populations from increasing.

Mech (1966) and Shelton (1966) concluded that the wolves on Isle Royale were controlling the moose population below the level at which the food supply would become the limiting factor. The wolf: moose ratio in these studies was approximately 1:30. Both authors noted that continuing forest maturation would eventually reduce the amount of available browse and hence cause a reduction in both moose and wolf populations.

The beneficial effects of intensive wolf predation on Isle Royale were evidence by high productivity and the absence of starvation in the moose population. The twinning rate is a sensitive indicator of a moose population's productivity. Data presented by Mech (1966) and Shelton (1966) indicated an extremely high twinning rate of approximately 32%. Since wolves arrived on Isle Royale the moose population has remained relatively stable and has not exhibited the extreme increases and decreases found in the 1930's and 1940's which were due to depletion of the food supply (Mech *op. cit.*).

Pimlott *et al.* (1969) noted the beneficial influences of wolf predation on the Isle Royale moose population but criticised the conclusion reached by Mech (1966) and Shelton (1966) that wolves were controlling the moose population. The criticisms of Pimlott *et al.* (*op. cit.*) were based on three weaknesses in the facts. Firstly, the moose population may have been underestimated. Secondly, Mech and Shelton obtained their estimates of annual adult mortality by projecting the rate of kill of adults during their winter study period. Pimlott *et al.* (*ibid.*) suggested that fewer adults were killed in the summer when calves were most vulnerable. Thirdly, the conclusion that the population was stable was based primarily on the observation of calves in late winter.

Peterson (1975) reported that the wolves on Isle Royale have not imposed a limit on moose density independent of the food supply and other environmental factors. Browse production in the most recent burn (1936) has declined, forcing the moose to increase their use of areas of more mature forest which are marginal habitats. However, despite the decreasing carrying capacity, the moose population increased during the 1960's. A series of severe winters beginning in 1969 has increased the stress on the moose populations. As a result of these conditions, the productivity of the moose has declined and there is more evidence of malnutrition. Peterson (ibid.) noted a twinning rate of only 14% from 1966 through 1973, a significant decline from that reported by Mech (1966) and Shelton (1966). Peterson (op. cit.) also reported several deaths due to malnutrition in 1971, 1972 and 1974.

As mentioned previously, the pattern of wolf predation on Isle Royale has shifted during the 1970's so that a greater proportion of young adult moose were taken. The wolves responded to the increased vulnerability of moose functionally by an immediate increase in kill rate and numerically by an increase in wolf density (Peterson, 1975). Peterson (ibid.) stated that although the mid-winter moose population has not declined significantly since 1969, the low calf production and survival and high winter mortality due to predation suggest that a decline in the moose population is very possible. In addition to an increased predation rate, the wolves were killing young moose before they could contribute to the population. Peterson (ibid.) noted that the degree of control exerted by wolves depends ultimately upon the browse supply and winter severity which affect the vulnerability of moose to predation as well as their productivity.

Workers in Alaska have found that wolves can have a controlling effect on moose populations when moose survival and productivity are reduced by severe winter conditions and/or declining habitat conditions. Rausch (1969) noted that the best correlation of moose population fluctuations appeared to be with winter range and climatic extremes rather than with hunting or wolf predation. Rausch et al. (1974) suggested that when severe winters result in population decreases, wolves may accelerate the decrease by preying intensively on the younger age classes as shown by Peterson (1975). Bishop and Rausch (1974) stated that a combination of wolf predation and hunting have probably prevented the recovery of the Nelchina Basin moose population following a decline due to severe winters.

Gasaway et al. (1977) studied the effects of wolf predation on a moose population in interior Alaska. The moose population in the Tanana Valley increased from the 1940's until the mid-1960's due to a combination of factors - an increased food supply resulting from fires, cessation of market hunting, initiation of a predator control program and a long series of mild winters. The population declined during the severe winters of 1965-1966 and 1966-1967, recovered slightly and then crashed during the winter of

1970-1971 when up to 50% of the population may have died. The population continued to decline through 1975.

The wolf population in the area increased following the cessation of the predator control program and remained high while the moose population declined. This resulted in a wolf : moose ratio of approximately 1 : 15 in 1975. A ratio of approximately 1 wolf : 43 ungulates existed when Dall sheep and caribou were included but these species were limited to the mountainous southern half of the area. Therefore moose was the only ungulate prey available in half the area.

Gasaway et al. (ibid.) found that high rates of calf and adult mortality precluded population growth. Hunting, range conditions and disease were not limiting the population. They found that low reproductive rates and neonate mortality were not responsible for the low population. Surveys showed that summer and winter calf mortality increased during the 1970's. The greatest increase in calf mortality occurred between June and November. Calf mortality in a group of 48 collared cows was estimated to be 68% by five months of age in 1975. This information suggested that predation was the most significant factor influencing calf survival and hence population growth.

Following much political controversy, the wolf population in the study area was reduced by approximately 60% during the winter of 1975-76. This resulted in very low wolf densities in the Tanana Flats where moose were the only available ungulate prey.

Calf survival was much higher through November, 1976 and similar to the rates observed during the early 1960's when the population was increasing. The increased rate of calf survival was presumed due to reduced wolf predation.

Gasaway et al. (ibid.) concluded that the moose population had reached a critically low point due to severe winters. This decline was hastened by sport hunting which took an estimated 15-20 percent of adult moose in 1973. Once the moose population reached that critical low point, wolves were able to regulate it and cause further declines.

WHITE-TAILED DEER

White-tailed deer is the major prey species of timber wolves in most areas of North America where the two species co-exist. Thompson (1952) and Stenlund (1955) found that deer were the staple food of wolves in Wisconsin and Minnesota. Later studies by Mech et. al. (1971b), Frenzel (1974) and Van Ballenberghe et al. (1975) showed that deer was the primary prey of wolves in northeastern Minnesota. Pimlott et al. (1969) found that deer was the principal prey of wolves in the Algonquin Park area of Ontario. Deer remains were found in 80% of 1435 summer scats and in 90% of 50 winter scats collected in Algonquin Park. Deer comprised 42% and 59% of summer scats collected in the

Marten River and Pakesley areas respectively near Algonquin Park. Despite the importance of beaver in their summer diet, wolves could not exist in these areas if moose and especially deer were not available to them (Pimlott et al. ibid.).

Voigt et al. (1976) found that due to a decline in deer population, beaver became the principal summer food of wolves in the three areas studies by Pimlott et al. (op. cit.). The occurrence of deer remains dropped from 76% in 1963 to 33% in 1972 in Algonquin Park while in the Pakesley area it was only 11% from 1964 through 1967. In 1969 the occurrence of deer hair in 220 summer scats in the Marten River area as 1%. This change in the feeding habits of wolves resulted from a decreased availability of deer while the beaver population remained fairly high or increased. Because beaver are not available during the winter, Voigt et al. (op. cit.) suggested that a continued decline in the deer population would result in lower wolf densitites in the Algonquin Park area.

Selection of Deer

As with moose, wolf predation on deer is selective. Mech and Frenzel (1971) noted that wolves had a low success rate in capturing deer during the winter. Only one chase of 14 which were observed was successful (6.7%). This was similar to the kill rate of moose found on Isle Royale (7.8%)

by Mech (1966). The low success rate suggests that most deer are relatively invulnerable to wolf predation or conditions of the hunts are usually not favorable to the wolves. Vulnerability to wolf predation depends on age, physical disabilities, snow conditions and habitat condition.

Fawns usually comprise a major proportion of the deer fed upon by wolves during the summer. Thompson (1952) found fawn remains in approximately 45% of the summer scats which contained deer hair. Fawn hair comprised 71% of deer occurrences between 1 July and 30 September in the Algonquin Park area (Pimlott et al. 1969). Voigt et al. (1976) found that fawn hair comprised 81% of the occurrences of deer hair after 31 May in the same area.

Van Ballenberghe et al. (1975) documented the seasonal importance of fawns to wolves and the changes in the wolves' diet over the summer. Prior to the fawning period, adult deer comprised 77% of the food item occurrences. From mid-June until mid-July, deer remains were found in 81% of the scats and of those, 48% were fawns. The occurrence of deer declined after mid-July to less than 50% and only approximately 33% of the deer occurrences in scats were fawns. Van Ballenberghe et al. (ibid.) suggested that the abrupt decrease in deer and fawn consumption was due to decreased numbers or vulnerability of fawns and increased utilization of other food sources.

It is difficult to determine the effect on deer populations of heavy utilization of fawns during the summer by wolves because the proportion of fawns consumed as carrion is unknown as is the proportion of fawns which would have died of other causes even if wolves had not taken them. Pimlott et al. (1969) suggested that if much of the predation on fawns is non-compensatory it could have a substantial limiting effect on deer populations.

Cook et al. (1971) studied fawn mortality in a wildlife refuge in Texas, Of 81 radio-collared fawns, 58 died during the study and 93% of this mortality occurred within 32 days of parturition. Coyote (*Canis latrans*) predation accounted for 50% of the fawn deaths. Cook et al. (ibid.) suggested that predation by coyotes on fawns was the major factor stabilizing this deer population. They also noted that disease could be an important regulating factor both as an independent mortality factor and as a predisposing factor in predation. White et al. (1972) stated that: "Heavy predation on newborn ungulates apparently represents one of the most important loss factors and evolutionary forces in many populations."

Wolf predation during the winter is concentrated on deer older than five years. Pimlott et al. (1969) aged 331 wolf-killed deer and found that 17% of them were fawns, 25% were one to four years old and 58% were five years or older. This age distribution differed significantly from that of

275 deer killed by cars or collected for research purposes in Algonquin Park of which 20% were fawns, 67% were one to four years old and only 13% were five years or older. The age distribution of the latter group was similar to that of hunter-killed deer inside Algonquin Park. Mech and Frenzel (1971) found an abnormal age distribution among wolf-killed deer in northeastern Minnesota. Wolf-killed deer were significantly older (average of 4.7 years) than hunter-killed deer with an average age of 2.6 years. The age distribution of 433 hunter-killed deer was: fawns 26%, one to four years 64% and five years and older 10%. Both authors noted that fawns may be under-represented in these studies since their small carcasses may be consumed more completely making them difficult to locate.

Mech and Frenzel (ibid.) offered two possible explanations for the increased vulnerability of deer over five years of age. Firstly, the deer are in the final half of their life span and their alertness and fitness may be expected to decline. Secondly, Kelsall (1969) found that the weight-load on track increased in deer, at least up to 4.5 years. Therefore older deer would probably sink deeper into snow than young animals and their escape would be impeded.

Wolf predation appears to be selective for female fawns and adult male deer. Mech and Frenzel (1971) found a higher proportion of females (59%) in fawn wolf-kills than in adults (46%) while the sex ratio of hunter-killed fawns was even. Pimlott *et al*. (1969) did not separate fawns from adults but found that males comprised 57% of 257 sexable wolf-kills in Algonquin Park. This differed significantly from the expected 50 : 50 sex ratio. Mech and Frenzel (*op. cit*.) found that in a wilderness area wolves preyed more heavily on adult males (71%) than on adult females (39%). Hunter-killed deer also contained a higher percentage of males (66%) presumably due to their greater movement during the rutting season which overlapped the hunting season. In the hunted area wolves killed a significantly higher percentage of adult does (56%) than in the wilderness area. This was due presumably to the effect of hunters on the sex ratio of the deer population. Kolenosky (1972) found that the sex ratio of wolf-killed deer (250 males : 100 females) was significantly different from that of hunter killed deer (92 males : 100 females), during the same period. He suggested that this was the result of bucks wintering on the fringe of the areas used by does and fawns. Since predation was disproportionately heavy along this edge, more bucks were taken by wolves.

Mech and Frenzel (1971) suggested that does may normally be less susceptible to predation than bucks. Kelsall (1969) found that does had lower weight-load-on-track than bucks at all ages due to lower body weight and similar track area. Bucks may also be more susceptible to predation because of their poorer condition following the rut.

Mech and Frenzel (*op. cit.*) found that the incidence of dental and jaw abnormalities and pathological conditions of the lower limbs was significantly higher in wolf-killed than in hunter-killed deer. A high percentage of fawns (13%) and yearlings (84%) killed by wolves during mid and late winter exhibited delayed tooth replacement. This suggested that either they were born later than usual or were suffering from some nutritional deficiency. The incidence of pathological abnormalities increases with age and probably increases the vulnerability of deer over five years old.

Effects of Winter on Predation

The vulnerability of deer to predation is increased by thick snow cover conditions (Mech *et al.* 1971a). Kolenosky (1972) noted that the hunting success rate of wolves (based on track interpretation) rose from 25% during a winter when the maximum snow thickness was approximately 36 cm to 63% the following winter when the snow thickness was approximately 51 cm in January. These authors and Pimlott *et al.* (1969) also noted that deer carcasses were not completely consumed initially as they were during average winters. Pimlott *et al.* (*ibid.*) suggested that the palatability of individual deer might affect the degree of consumption. Although Kolenosky (*op. cit.*) found that wolves periodically returned to their kills and ultimately consumed them, Mech *et al.* (*op. cit.*) found that many were abandoned. It appears, therefore, that when prey animals are relatively easily obtained the degree of utilization decreases.

Deer are restricted in movement by snow thicknesses of 40 cm or more. Wolves are better supported in snow than deer because of a lighter "weight-load-on-track". Peterson and Allen (1974) found that a weight-load of approximately 100 g / cm^2 best simulated the track depth of wolves. Verme (1968) found that a weight-load of approximately 211 g / cm^2 best simulated the track depth of deer. This difference in track load may become a critical factor in thick snow cover. Mech et al. (1971a) suggested that a general decline in fitness of the deer population and a tendency for deer to congregate on lakes where wolves have the advantage, along with the relatively lighter track-load of wolves, may explain the increased vulnerability of deer during winters with thick snow cover.

Effects of Wolf Predation on Deer Populations

The question whether or not wolves can control or reduce deer populations is a very old one - often tinged with intense emotionalism. Young (1944) recorded several gory accounts of the slaughter of deer by wolves, especially in winter "yards". Criddle (1925) described the destructive effect of wolves on deer during severe winters in Manitoba. This question has still not been fully answered, but recent studies have shown that wolves can reduce deer populations especially during winters with thick snow conditions.

A number of studies have shown conclusively that wolves prey heavily on fawns. Pimlott (1967a) suggested that if much of this fawn mortality were non-compensatory, that is, if most of the fawns would survive if there were no wolf predation, then a dense wolf population may constitute a potent limiting factor.

The white-tailed deer is at the northern edge of its range in most of Canada and winter stress is a definite limiting factor. The northward extension of the deer's range followed land-clearing and logging operations which created suitable habitat. Changing land-use practices, fire prevention and forest maturation have reduced the extent and quality of deer habitat in many areas.

The limiting effect of severe winters on deer populations is increased by the fact that deer become more vulnerable to wolf predation during periods of thick snow. Mech et al. (1971a) and Kolenosky (1972) found that during winters with "normal" snow cover, the estimated kill rate of wolves was approximately one deer per wolf per 18 days. However, during periods of thick snow cover, Mech et al. (op. cit.) found that this kill rate almost doubled. Kolenosky (op. cit.) found that the success rate of wolves killing deer was approximately 250% greater during a winter with thick snow.

Pimlott (1967a) suggested that, on the basis of studies done in Algonquin Park, wolves may not be capable of controlling deer at a ratio exceeding 100 deer per wolf. Furthermore, "predation by wolves may cease to be an important limiting factor when densities of deer exceed 20 per square mile." Pimlott et al. (1969) stated that while their data suggested that wolf predation was a major mortality factor affecting deer in Algonquin Park they were not detailed enough to determine whether wolves were the "primary mortality factor that is limiting the deer population." Pimlott (1967a) did note that wolf predation may have prevented major eruptions in the deer population in the park.

Thompson (1952) found that wolves with a density of one per 40 - 50 square miles did not prevent an over-population of deer from developing in one county in Wisconsin. The rate of increase may have been slower than in wolf-free areas but the magnitude was similar.

Mech (1970) stated that "the single, unqualified question of whether or not predators control the numbers of their prey cannot, in my opinion be covered by any broad generality." Mech (ibid.) reached a tentative conclusion that "wolf predation is the major controlling mortality factor where prey-predator ratios are 24,000 pounds of prey per wolf or less, but that at higher ratios wolf predation cannot keep up with annual reproduction: it then becomes only one of several other contributing mortality factors and cannot be considered a primary controlling influence." Mech (ibid.) used the ratio of "pounds of prey per wolf" to integrate data from wolf studies dealing with such prey species as deer, moose and caribou.

BEAVER

Beaver is an important secondary food source for wolves over much of its range. Beaver, which usually weigh between 15 and 35 kg when full grown (Banfield, 1974) is the smallest animal that is important in the wolf's diet.

The significance of beaver seems to depend upon their abundance and the availability of the wolf's primary prey - the large ungulates. Murie (1944) found that beaver, which were widely distributed but not abundant in Mount McKinley National Park, occurred in only .15% of the wolf scats he collected. Rausch (1967) stated that beaver form an important part of the wolf's diet in southeastern, southcentral and interior Alaska.

Cowan (1947), working in the Rocky Mountain Parks of British Columbia and Alberta, found that beaver comprised an important part of the wolves' diet in certain areas. Overall, beaver remains occurred in 7% of the scats he collected (1.5% in the winter and 17% in the summer), but at one den, 42% of 60 pup scats were composed entirely of beaver. This exceeded the importance of deer and elk combined. That den was located in an area where the beavers had killed most of the aspen and were forced to travel far from their ponds in search of food, making them easy prey for predators.

Van Ballenberghe <u>et al</u>. (1975) found that beaver was of secondary importance to wolves in northeastern Minnesota, occurring in 9.4% of 637 scats. Beaver was found in 9.7% of the summer scats. This figure approximates Peterson's (1955) findings of 10.5% occurrence in 76 scats in Ontario. Van Ballenberghe et al. (op. cit.) reported that locally beaver was very important to wolves as it occurred in 45.4% of 60 scats found at one rendezvous site.

Detailed quantitative studies in central North America have provided the best insight into wolf-beaver relationships. Work in the Algonquin Park area of Ontario and on Isle Royale has shown that beaver comprises a major portion of the wolf's diet.

Pimlott et al. (1969) found that white-tailed deer, moose and beaver were the principal items in 1,435 wolf scats collected in Algonquin Park from 1958 to 1962. Their percent frequencies of occurrence were 80.5, 8.5 and 7.1 respectively. Of fifty scats collected during the winter of 1962-63, 45 (90%) contained deer hair, three (6%) contained moose hair and two (4%) beaver hair.

Voigt et al. (1976) reported on further summer wolf food habits studies in these three areas. The frequency of occurrence of beaver hair in Algonquin Park increased from approximately 7% in the summer of 1963 to 55% in the summer of 1972. This was accompanied by a decrease in the occurrence of deer hair from 76% to 33%. Similarly in the Marten River area, the occurrence of beaver increased from 37% to 74% in

1969. Beaver hair was the predominant item (75%) in scats collected in the Pakesley area from 1964 to 1967.

The deer population in the Algonquin Park area has declined since the severe winters of 1958-59 and 1959-60, while the beaver population has fluctuated but remained at a relatively high level. Beaver were found to be three to four times more abundant in the Pakesley area than in Algonquin Park. Beaver has become the primary summer food of wolves in these three areas, presumably because of the decreased availability of deer (Voigt *et al*, *ibid*.).

The beaver population reached a peak on Isle Royale about 1948 and then declined rapidly in the early 1950's (Shelton, 1966). He believed that this decline was caused mainly by epizootic tularemia (*Francisella tularensis*) which affected all areas adjacent to Lake Superior at that time. By 1966, the population had partially recovered from its low point (Shelton, *ibid*.).

The importance of beaver to wolves on Isle Royale has increased dramatically since the early 1960's. Mech (1966) found beaver remains in 10.8% of the 438 scats he collected and Shelton (*op. cit*.) found beaver in 11% of 475 scats. (16% of summer scats). Moose was the primary food item occurring in 75.9% and 86% of the scats respectively. Peterson (1975) reported that the beaver population on Isle Royale had approximately doubled from 1962 to 1973. Beaver remains were found in 76% of the scats collected in 1973 and accounted for 50% of the prey occurrences in 554 summer scats. Beaver had therefore become a principal food source during the open water season. Peterson (*ibid.*) attributed the increased wolf density on Isle Royale partially to the dense beaver population especially as moose calf production was generally low. The availability of beaver is a major factor influencing pup survival (Mech, 1977).

The effect of wolf predation on beaver populations is not well understood. Cowan (1947) believed that predators could not prevent a beaver population from increasing as long as an adequate food supply was "safely available." The wolf population on Isle Royale which had increased from approximately 28 in 1966 to at least 41 in 1975 did not prevent the beaver population from doubling between 1962 and 1973 (Peterson, 1975). Factors such as low water levels or a food shortage which adversely affect beavers would predispose them to predation. Under such conditions, predation might be the immediate cause of a population decline.

MATERIALS AND METHODS

STUDY AREA

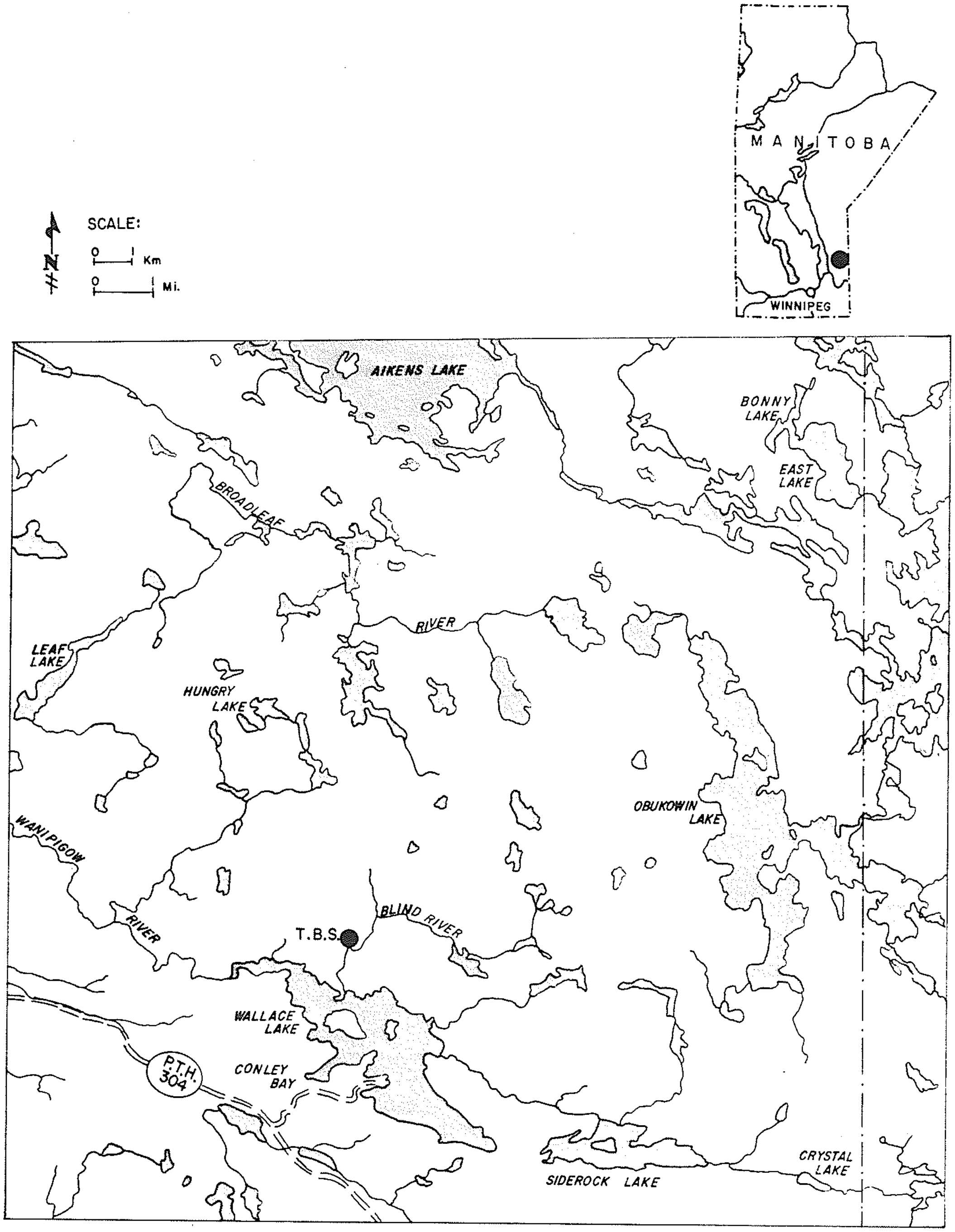
The study area is in southeastern Manitoba, east and north of the town of Bissett (Fig.1). It lies between Wallace Lake to the south and Aikens Lake to the north, the Broadleaf River to the west and the Ontario Border to the east (50^{o} 59'N to 51^{o} 11'N and 95^{o} 9' 15"W to 95^{o} 30'W), an area of approximately 563 km^2. Is is part of the Nelson River Drainage Basin. All the field work was done in this area. The base of operations for the study was the Taiga Biological Station (TBS).

Weir (1960) stated that the study area is in the Precambrian Drift Plain area of the Precambrian Shield. The Precambrian Drift Plain lies along the Ontario border east of Lake Winnipeg. The terrain is rolling to hilly and the surface deposits consist of varying amounts and thicknesses of glacial drift with abundant rock outcrops. These glacial drift deposits are predominantly of granitic materials. Bogs and lakes cover 40% to 60% of the surface area. The altitude in this area varies between 304 and 395 metres above sea level.

The geology of the study area was examined by Russell (1948). His study indicated that the bedrock structure of the area consists of Precambrian grey biotite granite.

The dominant soil types of this area are Podzol and Grey Wooded soils. Both soil types are derived from coarse-grained

Figure 1. Map of study area showing its location in Manitoba


MANITOBA
WINNIPEG
SCALE:
0 Km
0 Mi.
AIKENS LAKE
BONNY LAKE
EAST LAKE
BROADLEAF
RIVER
LEAF LAKE
HUNGRY LAKE
OBUKOWIN LAKE
WANIPIGOW
RIVER
BLIND RIVER
T.B.S.
WALLACE LAKE
CONLEY BAY
P.T.H. 304
CRYSTAL LAKE
SIDEROCK LAKE

crystalline rocks. Podzol soils form under a cover of coniferous forest and are typically found in jackpine-covered areas. Grey Wooded soils develop in areas predominantly covered by deciduous forest. Podzol and Grey Wooded soils are found in association over large areas of the Precambrian Shield.

The climate of Manitoba can be described as continental. Summer temperatures in the Wallace Lake area are warm (average July temperature is 18.3 to 18.9 degrees C.) and winter temperatures are cold (average January temperature is -33.7 to -34.2 degrees C.). Annual precipitation averages between 508 mm and 533 mm. Annual snowfall averages from 1397 mm to 1524 mm and the snow cover usually remains from November to April.

According to Rowe (1972), Wallace Lake is in the ecotone between the Northern Coniferous and the Lower English River sections of the Boreal Forest Region of Canada. Black Spruce (Picea mariana) is the dominant species in the Northern Coniferous section. It is associated with jack pine (Pinus banksiana) on the poorly-drained lowlands. The spread of jack pine has been favoured by frequent fires which are probably responsible for the scattered representation of white birch (Betula papyrifera). White Spruce (Picea glauca) balsam fir (Abies balsamea), trembling aspen (Populus tremuloides) and balsam poplar (Populus balsamifera) form mixed stands in river valleys, around some lakes and on southfacing slopes. The Lower English River section of the Boreal Forest is characterized by mixed stands of trembling aspen, balsam poplar and white spruce which provide the chief forest cover on well-drained sites. Balsam fir, white birch and jack pine are also present. Jack pine is common on the sandier sites but also extends to clay and silt soils after fire. Black spruce and larch (Larix laricina) occupy shallow bogs. Green ash (Fraxinus pennsylvanica), American elm (Ulmus americana) and bur oak (Quercus macrocarpa) are found on riverine sites. Mixed stands of conifers and hardwood with early seral stages of plant succession, which are the most productive ungulate habitat, were found mainly along water bodies on the periphery of the study area.

Human activity in the study area was limited to light trapping, prospecting and tourism. Most of the tourist activity is concentrated around the campground on Wallace Lake although parties of canoeists or snowmobilers may be encountered along the major travel routes.

METHODS

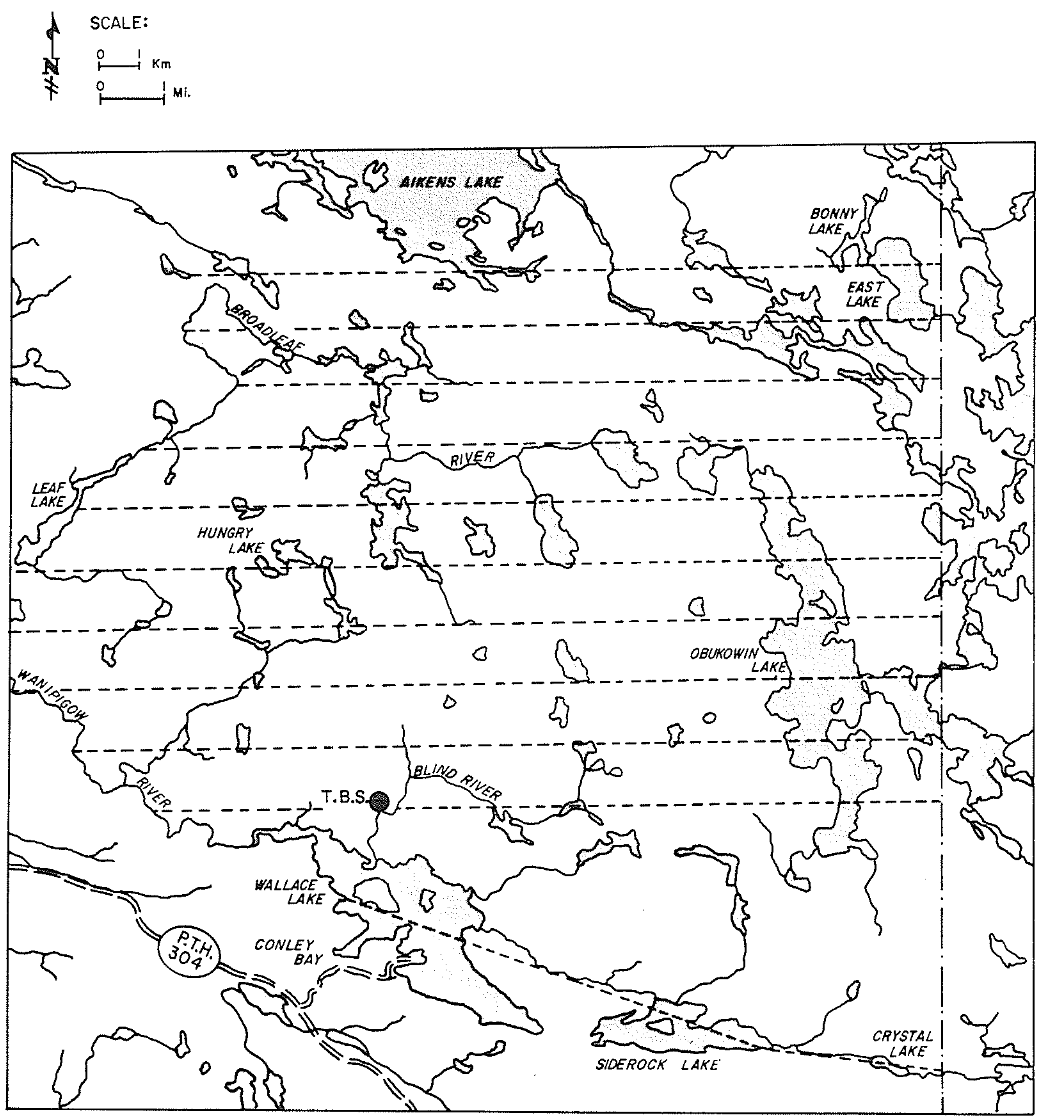
The study period extended from May, 1973 to June, 1975. It was subdivided into four "biological" seasons: Break-up (April), Summer (May to October), Freeze-up (November) and Winter (December to March) in order to clarify the food habits of the wolves which varied according to the season.

Populations

Aerial surveys and ground observation were used in an attempt to determine the size of the wolf and ungulate populations within the study area. The aerial surveys were carried out during the winter when observation conditions were optimal. Survey flights were flown east to west at 1.6 km intervals over the study area (Fig.2). These flights took place at the pleasure of the weather and when an aircraft could be obtained. Because of these factors, they could not be made at the regular intervals I would have preferred. There were six flights during the winter of 1973-74. They were on 17 and 18 December, 1973 and 13, 14 18 and 26 February 1974. In the second winter the first flight was not made until 10 February 1975. I then flew on 12, 20, 24, 26 February and 3 March. A total of 18.8 hours were flown in 1973-74 and 12.5 hours in 1975.

The survey flights were all flown at approximately 131 kilometers per hour at an altitude of 242 to 303 metres. They were done between 1000 hours and 1500 hours so that the sun would be high enough to reduce shadows to a minimum. Particular attention was paid to frozen water bodies and open areas where timber wolves were most visible. I made note of all timber wolves and other animals as well as tracks seen on these flights. The occurrence of black or light-coloured wolves was noted along with pack size to assist in differentiating between packs. Whenever a carcass

Figure 2. Map of study area showing aerial survey lines.


SCALE:
Km
Mi.
AIKENS LAKE
BONNY LAKE
EAST LAKE
BROADLEAF
RIVER
LEAF LAKE
HUNGRY LAKE
OBUKOWIN LAKE
WANIPIGOW
RIVER
T.B.S.
BLIND RIVER
WALLACE LAKE
CONLEY BAY
P.T.H. 304
SIDEROCK LAKE
CRYSTAL LAKE

was sighted, we attempted to land in order to inspect it. This was seldom possible however, due to slush and snow conditions. During the first winter, a PA-18 Piper Super Cub was used. All but one of the flights in the second winter were flown in a PA-12 Piper Cub. A Cessna 180 flew one survey when the PA-12 was unavailable. On this flight my wife acted as a second observer.

I also used "howling" as a technique to locate packs and determine pack size. Pimlott (1960) and Joslin (1966, 1967) used this technique with great success in Ontario. I howled three or four times at approximately 30 second intervals and waited for a response. Then after three or four minutes this was repeated. I did this at various times and locations throughout the study whenever low wind velocities and/or foreknowledge that wolves were nearby made success possible.

I conducted a search for wolf dens in the spring of 1974 and again in 1975. The area between Siderock Lake and the Ontario border was selected for this search because the rough terrain and close proximity to water matched criteria described by Mech (1970) for den sites.

Food Habits

The feeding habits of timber wolves were determined by analyzing scats (faeces) collected throughout the year. I also analyzed the stomach contents of trapped wolves to provide additional information on feeding habits.

Scats were collected on the roads, trails and portages in the Wallace Lake area. I travelled these routes as often as possible in the summer and winter, both to be able to date the scats and to keep track of the wolves' movements. A total of 231 wolf scats were collected during the study: 127 in 1973, 67 in 1974 and 37 in 1975. Of these 34.6% were found on Provincial Road 304 while the remaining 65.4% were found in the bush or on frozen water bodies. The scats were collected in paper bags with the following information recorded: location, date, vegetation, probable age of scat, and collector.

I usually found scats deposited singly. However, on three occasion I collected groups which were deposited in an area where the wolves had rested while consuming deer or moose carcasses. These 28 scats were composed entirely of deer or moose hair. Because my sample sizes were relatively small, these clumped samples biased the results. Therefore, I omitted these samples from my calculations leaving a sample size of n = 203.

Few scats were collected in November of both years because I was isolated at the Taiga Biological Station during freeze-up. I was absent from the area during break-up in 1974 and 1975 so few scats were collected in April and May of these years. With the exception of nine days in June, I concluded my field work in April, 1975. Therefore, the scat sample for summer 1975 was incomplete and the results can only be used to indicate the continuing importance of beaver as a food source for wolves during that season.

Before analysis, the scats were autoclaved at 8.6 - 9.1 kg steam pressure and a temperature of 117° C. for one hour to reduce the possibility of contracting parasites, primarily *Echinococcus sp.* (Lubinsky, pers. comm.). Frenzel (1974) also recommended autoclaving wolf scats before laboratory analysis. At the time of autoclaving, the data from the bags were transferred to cards upon which the results of the analysis were recorded.

The method used in scat analysis followed that of Fichter *et al.* (1955) and Pastuck (1974). After autoclaving, the scats were soaked overnight in water to soften and then washed with tap water in two strainers (7.1 and 23.6 mesh per cm^2) to remove extraneous material. I then placed the material from both strainers on a numbered paper towel and allowed it to dry. The samples were examined individually by segregating them into their components. Because of the possibility that viable *Echinococcus sp.* might still be present, the samples were dampened with alcohol and a surgical mask and gloves were worn during the examination.

I assembled a reference collection of potential food items to facilitate identification of the ingested materials. Samples of hair from potential prey species in the Wallace Lake area were obtained. Museum study skins and skeletons were available and literature was referred to as needed. The manual by Adorjan and Kolenosky (1969) was used for comarison of hair scale impressions.

Scat contents were identified by comparing teeth, claws and hairs with the reference collection. Hairs were identified by the following criteria: general morphology, colour banding and cuticular scales. The cuticular scales were examined by preparing hair impressions as described by Van Zyll de Jong (1966). These impressions were then compared with reference material and the literature for identification.

The percent volume of each food item was estimated visually after it was identified and segregated. Using a method similar to that of Knowlton (1964), each occurrence was classified as either a major item (M.I.) or not a major item. This was done to show the relative importance of each item to the wolves' diet. For example small bits of vegetation were found in almost all the scats. If these were discussed on the basis of their frequency of occurrence, their importance would be greatly exaggerated since they occupied only a very small volume in the samples.

I used the following definitions to indicate the relative importance of food items which were ingested:

Frequency of occurrence (F.O.):

The number of food samples (scat or stomach) in which a particular food item appeared.

Percent frequency of occurrence:

$$\frac{\text{Frequency of occurrence}}{\text{number of food samples}} \times 100$$

Major Item (M.I.):

A food item which comprised 40% or more by volume of a food sample on the basis of visual estimate.

Frequency of occurence as a major item:

The number of food samples in which a particular food item appears as a major item.

Percent frequency of occurrence as a major item:

$$\frac{\text{Frequency of occurrence as a major item}}{\text{number of food samples}} \times 100$$

When two items in one food sample occurred as a major item, each was tabulated as one-half of an occurrence to maintain the integrity of the sampling unit and to limit the sum of the percentage frequencies of occurrence as a major item to 100%.

The stomach contents of all the wolf carcasses I collected were examined. Thirteen carcasses had identifiable material remaining in the stomach. Analysis of the stomach contents presented some problems not encountered in scat analysis. Most of the wolves examined were trapped, and because of the varying lengths of time spent in the trap before death, digestion had progressed to varying degrees. Also, some of the material was probably bait. Therefore it was unrealistic to attempt to determine precisely the volumes or weights of food items present in the stomach.

The stomach contents were removed at the time of post-mortem examination. They were washed and dried in a manner similar to the scats, but not autoclaved. I made a visual estimate of the percent volume of each component after identification and segregation. Food items were identified and classified as either a major item or not by the same method described for scat analysis.

Post-Mortem Examinations

A total of 22 timber wolf carcasses were collected, seven males and 15 females. Trappers in the Bissett area were paid $10.00 for each carcass they brought to me. Two carcasses were obtained in the winter of 1973-74 from the Bissett-Manigotogan area. In 1974-75, one carcass was collected in Lac du Bonnet, three in Pine Falls, three in the Bissett - Manigotogan area, one in my study area and 12 were donated by the Research Branch, Manitoba Department of Renewable Resources and Transportation Services (R.R.T.S.) from the Porcupine Mountains and the north end of Lake Winnipegosis. The carcass which I picked up in my study area (Cat. No. 44) had been shot illegally by aircraft hunters. Because of scavenging by ravens (Corvus corax), this specimen was unfit for post-mortem examination and only the stomach contents were examined. These specimens were weighed and standard measurements were taken where possible.

Dr. L. E. Lillie, of the Veterinary Services Branch, Manitoba Department of Agriculture, performed the post-mortem examination of the carcasses. As part of the examination, the general nutritional condition, reproductive status, presence of parasites, and any gross pathologic abnormalities were noted. The advanced state of autolysis of many of the carcasses, caused by repeated freezing and thawing, prevented a more detailed examination of the specimens. Dr. T. Dick of the Zoology Department examined the diaphragms of these wolves for *Trichinella sp*. I attempted to determine the reproductive state of one male wolf (Cat. No. 38) using sperm smears from the sectioned testes (Heubner, pers. comm.). Following the examination, skeletons were prepared from most carcasses using the enzyme technique (Dubois, pers. comm.). Details of the post-mortem examinations are presented in Appendix I.

Aging

Twenty of the wolf carcasses collected were aged using a technique similar to the one described for coyotes by Linhart and Knowlton (1967). This involved the counting of cementum layers in the sectioned and stained roots of the upper canines. The upper canines were used because they have less lateral curvature than the lower canines resulting in a better section (Johnston, pers. comm.).

The remains of one moose and three white-tailed deer presumably killed by wolves were also examined. Dr. Lillie and I performed a post-mortem examination of a female white-tailed deer killed on Wallace Lake. This deer and the moose found on Bonny Lake were aged using the methods described by Gilbert (1966) and Sergeant and Pimlott (1959) which involved counting cementum layers in the sectioned and stained roots of the first incisor. The fat content of the marrow of these animals was determined using the standard ether extraction method which complies with the official method of the Association of Official Agricultural Chemists (Horwitz, 1965). Both femora were collected from the deer killed on Wallace Lake but only portions of the moose tibiae could be located. The marrow in portions of the tibiae of the two deer found on Wanipigow Lake, approxmately 29 km west of the study area, was analyzed.

Questionnaires

Tourist Questionnaire

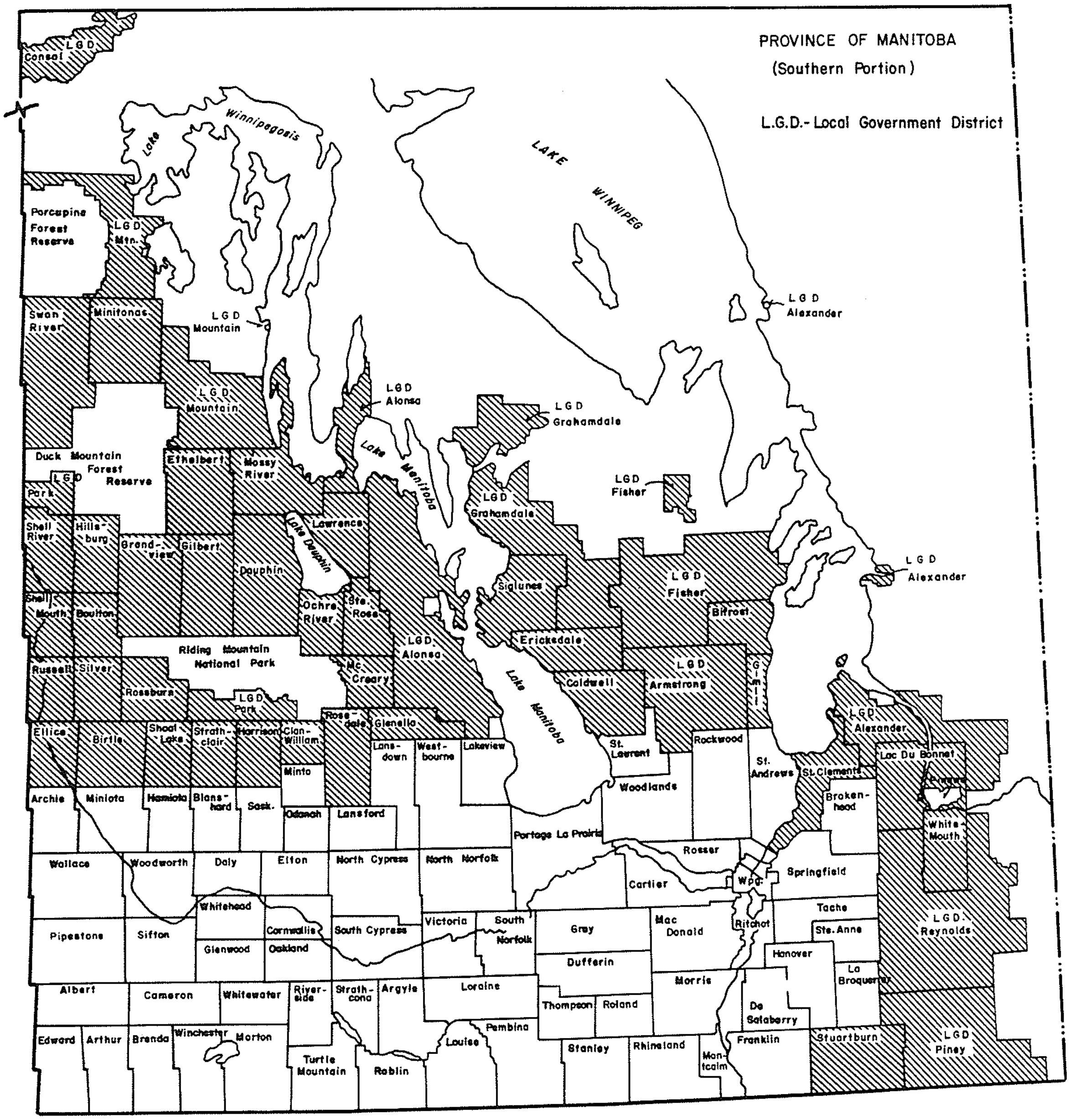
I used two questionnaires in the study. One questionnaire was designed to examine the attitudes of tourists at Wallace Lake toward timber wolves (see Appendix II). This was a fairly short questionnaire, consisting of 15 questions, which was completed by personal interview with the form being filled in by the interviewer. Both transient campers and cottage users were sampled. In order to get as large a sample as possible, the interviewing was done on weekends in July and August, 1974 when the campground was most crowded.

Farmer-Rancher Questionnaire

The second questionnaire was designed to examine the extent of timber wolf predation on livestock, particularly cattle, in Manitoba (see Appendix II). The Statistics and Sociology Departments of the University of Manitoba and the Manitoba Department of R.R.T.S. assisted in designing this questionnaire. The Provincial Department of Agriculture provided a list of cattle owners in Manitoba. The Statistical Program for the Social Sciences (S.P.S.S.) was used in an I.B.M. 168 computer to analyze the data.

For sampling purposes, the province was divided into three regions. These were: Eastern (east of Lake Winnipeg), Interlake and Western (west of Lakes Manitoba and Winnipegosis). I selected those municipalities and Local Government Districts within these regions where timber wolves might present a problem (Fig.3). The following municipalities and Local Government Districts were sampled: Eastern Region: Alexander, St. Clements, Lac du Bonnet, Whitemouth, Reynolds, Piney and Stuartburn; Interlake Region: Grahamdale, Siglunes, Eriksdale, Coldwell, Fisher, Bifrost, Armstrong and Gimli; Western Region: Consol, Mountain, Swan River, Park, Shell River, Hillsburg, Shellmouth, Boulton, Russel, Silver Creek, Rossburn, Ellice, Birtle, Shoal Lake, Strathclair, Harrison, Clanwilliam, Rosedale, Glenella, McCreary, Alonsa, Ste. Rose, Ochre River, Lawrence, Dauphin, Mossey River, Gilbert Plains, Grandview, Ethelbert and Minitonas.

Figure 3. Map of southern Manitoba showing area sampled by Farmer-Rancher Questionnaire.


PROVINCE OF MANITOBA
(Southern Portion)
L.G.D.- Local Government District
LGD Consol
Lake Winnipegosis
LAKE WINNIPEG
Porcupine Forest Reserve
LGD Mtn.
Swan River
Minitonas
LGD Mountain
LGD Alexander
LGD Alonsa
LGD Grahamdale
LGD Fisher
Duck Mountain Forest Reserve
LGD Park
Ethelbert
Mossy River
Lake Manitoba
Lake Dauphin
Lawrence
Shell River
Hillsburg
Grandview
Gilbert
Dauphin
Siglunes
Bifrost
Shell Mouth
Boulton
Ochre River
Ste. Rose
Riding Mountain National Park
Erickedale
Armstrong
Russell
Silver
Rossburn
McCreary
Coldwell
Ellice
Birtle
Shoal Lake
Strathclair
Harrison
Clanwilliam
Rosedale
Glenella
Lansdown
Westbourne
Lakeview
St. Laurent
Rockwood
St. Andrews
St. Clements
Loc Du Bonnet
Minto
Archie
Miniota
Hamiota
Blanshard
Sask.
Odanah
Lansford
Woodlands
Brokenhead
Portage La Prairie
Rosser
Whitemouth
Wallace
Woodworth
Daly
Elton
North Cypress
North Norfolk
Cartier
Wpg.
Springfield
Whitehead
Tache
Pipestone
Sifton
Cornwallis
South Cypress
Victoria
South Norfolk
Grey
Mac Donald
Ritchot
Ste. Anne
LGD Reynolds
Glenwood
Oakland
Hanover
Dufferin
La Broquerie
Albert
Cameron
Whitewater
Riverside
Strathcona
Argyle
Loraine
Morris
Thompson
Roland
De Salaberry
Pembina
Edward
Arthur
Brenda
Winchester
Morton
Louise
Franklin
Stuartburn
LGD Piney
Stanley
Rhineland
Montcalm
Turtle Mountain
Roblin

A 10% systematic random sample of cattle owners in the municipalties and Local Government Districts noted above was selected from a list of cattle owners in the provincial tuberculosis-brucellosis testing program. The starting name was chosen using a random numbers table and then every tenth name was selected. A total of 1059 questionnaires were mailed. The sample sizes were as follows: Eastern Region n = 161, Interlake n = 222, Western region n = 676. Three successive mailings were used to ensure as high a return as possible. The questionnaires were mailed in February, March and April, 1974.

After the third mailing, a small systematic random sample of the non-respondents was selected and contacted in person and interviewed to determine if or how they differed from those who had returned a questionnaire. The starting point among the non-respondents was chosen using a random numbers table and then every tenth one was selected. Contacting non-respondents was limited by time and finances. However, with the assistance of the Research Branch (R.R.T.S.) I was able to obtain completed questionnaires from 14 non-respondents.

RESULTS

WOLF POPULATIONS

The locations and numbers of wolves sighted and the locations of suspected wolf-kills are shown in Fig. 4. Wolves were observed in the study area during three of the six survey flights in 1973-74 and during two of the six flights in 1975. A single wolf was observed 7.2 km east of Bissett on 13 May, 1973 feeding on a road-killed moose, and a pack of three wolves was observed feeding on a deer carcass on Wanipigow Lake approximately 29 km west of the study area on 17 December, 1973.

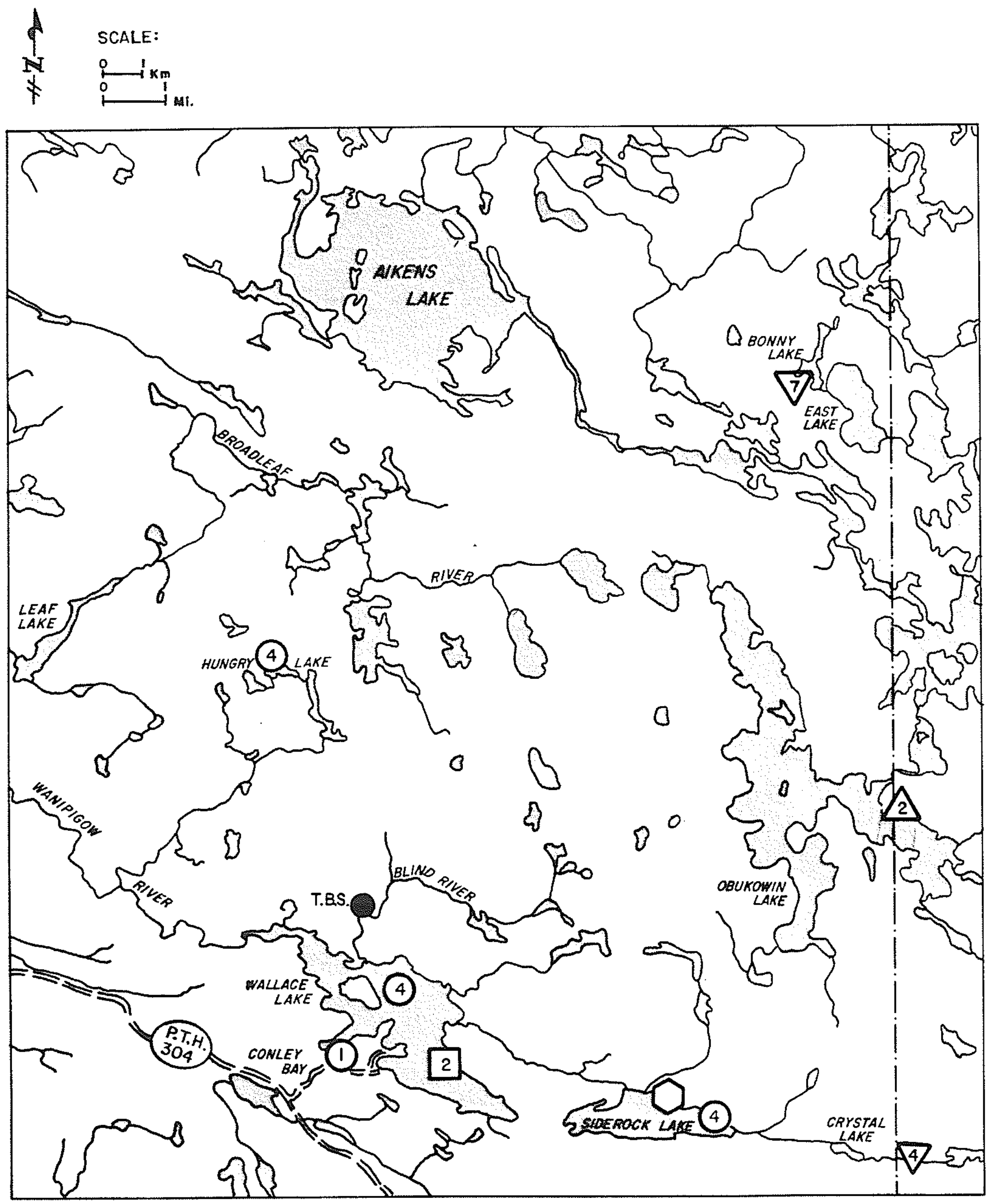
Five packs were observed during the two years of observation and the maximum wolf population in the study area was approximately 20. The estimates of pack composition and range were based on aerial and ground observations of wolves and tracks. The Hungry Lake pack was seen on Hungry Lake on 18 December, 1973. It consisted of four wolves: one black wolf, one very light tan (almost white) wolf and two brown wolves with black backs. No wolves were seen in the Hungry Lake area during the 1975 flights but tracks on neighboring lakes indicated that a pack was still in the area. The Obukowin Lake pack, which consisted of two brown wolves with black backs, was observed at a moose carcass on Obukowin Lake on 13 February, 1974. This pack was observed once more on 14 February, 1974 again feeding on the moose carcass. Tracks on the lake indicated that these wolves had attacked

Figure 4. Map of study area showing sightings of timber wolves and suspected wolf kills.

Number of wolves sighted indicated by number inside symbol.

Sightings:

○	Wolves
△	Moose carcass and wolves winter of 1973-74
▽	Moose carcasses and wolves winter of 1974-75
□	Deer carcass and wolves winter of 1974-75
⬡	Moose carcass



SCALE:
0 1 Km
0 1 Mi.
N
AIKENS LAKE
BONNY LAKE
7
EAST LAKE
BROADLEAF
RIVER
LEAF LAKE
HUNGRY 4 LAKE
WANIPIGOW
RIVER
BLIND RIVER
T.B.S.
OBUKOWIN LAKE
2
WALLACE LAKE
4
P.T.H. 304
CONLEY BAY
1
2
SIDEROCK LAKE
4
CRYSTAL LAKE
4

and killed the moose they were eating. The Siderock Lake pack was observed on Siderock Lake on 14 February, 1974. Two of these wolves were black, one was light tan and one was brown with a black back. This last wolf may have been a pup since it had a gangling appearance and its movements were not as smooth as the others in the pack. This is probably the pack which I observed on Wallace Lake on 3 February 1974 although I was unable to distinguish their colours on that occasion. The Siderock Lake pack consisted of five wolves in the winter of 1974-75. On 6 December, 1974 a group of hunters reported hearing howling and saw the tracks of five wolves at the east end of Siderock Lake. Five days later, I just missed seeing a pack of five wolves at the east end of Wallace Lake near the portage to Siderock Lake. Subsequent following of tracks showed that these wolves had travelled along the Wanipigow River from Siderock to Wallace and then returned to Siderock via the portage trail.

The Siderock pack may have been observed again on 26 February 1975 feeding on a moose carcass approximately one km east of Crystal Lake. However, these wolves appeared to be gray-brown in colour and only four were seen. It is possible that another wolf was in the bush nearby but was not observed.

The Bonny Lake pack was observed feeding on a moose carcass on 24 February, 1975. It consisted of seven wolves, all a typical gray-brown (Mech, 1970) in colour. Two wolves which occasionally travelled as a pack also utilized the

Wallace Lake area.

Bill Conley, a resident trapper, saw one gray-brown wolf near his garage at Conley Bay on Wallace Lake on 3 October, 1974. Drillers working for the Midwest Drilling Company saw two wolves which had killed a white-tailed deer near their drill site on Wallace Lake on 15 February, 1975. The tracks of these two wolves were frequently seen on Wallace Lake and in the surrounding bush.

I had very limited success using howling to locate wolves. On 16 May, 1973, three or four wolves responded when I howled near the moose carcass 7.2 km east of Bissett. Two or three responded on 21 May, 1973 at the same location. I heard wolves howling on two occasions near the Taiga Biological Station. On 6 October 1974 three wolves were heard howling within two km of the Station from a north-westerly direction. When I howled back they seemed to respond. On 28 October, 1974 I heard four or five wolves howling within one km of the Station. This time the howling came from the north-east. On both occasions there was little or no wind and the howling occurred between 0500 and 0900 hours.

I was unable to locate any wolf dens in the study area.

UNGULATE POPULATIONS

During the aerial surveys I paid particular attention to frozen bodies of water and open areas where timber wolves were most visible. This is not an effective technique to use when searching for large ungulates. Therefore, the numbers of moose and woodland caribou which I observed cannot be used to estimate their populations accurately.

I observed approximately 17 different moose, including two calves, during the winter of 1973-74. Eight to 12 moose were observed in the winter of 1974-75, but no calves were seen.

I did not observe any white-tailed deer during the survey flights over the study area. Pilots picking up water on Wallace Lake for fire fighting reported seeing six deer approximately one km south-west of the Taiga Biological Station on 3 July, 1974. This figure may be exaggerated but it does confirm the presence of deer in this area. Deer tracks were observed infrequently.

The locations of the bands of woodland caribou which I observed are shown in Figure 5. In 1973-74 three bands were seen. In 1975 caribou, including a group of 30-35, were observed on four separate flights. All the caribou sightings were within the area described by Stardom (1977) as the winter range of the Aikens group of woodland caribou. Although wolf and caribou tracks were frequently sighted in the same area, I saw no evidence of interaction between the two species.

The remains of one white-tailed deer and four moose which had been fed on by wolves were found in the study area

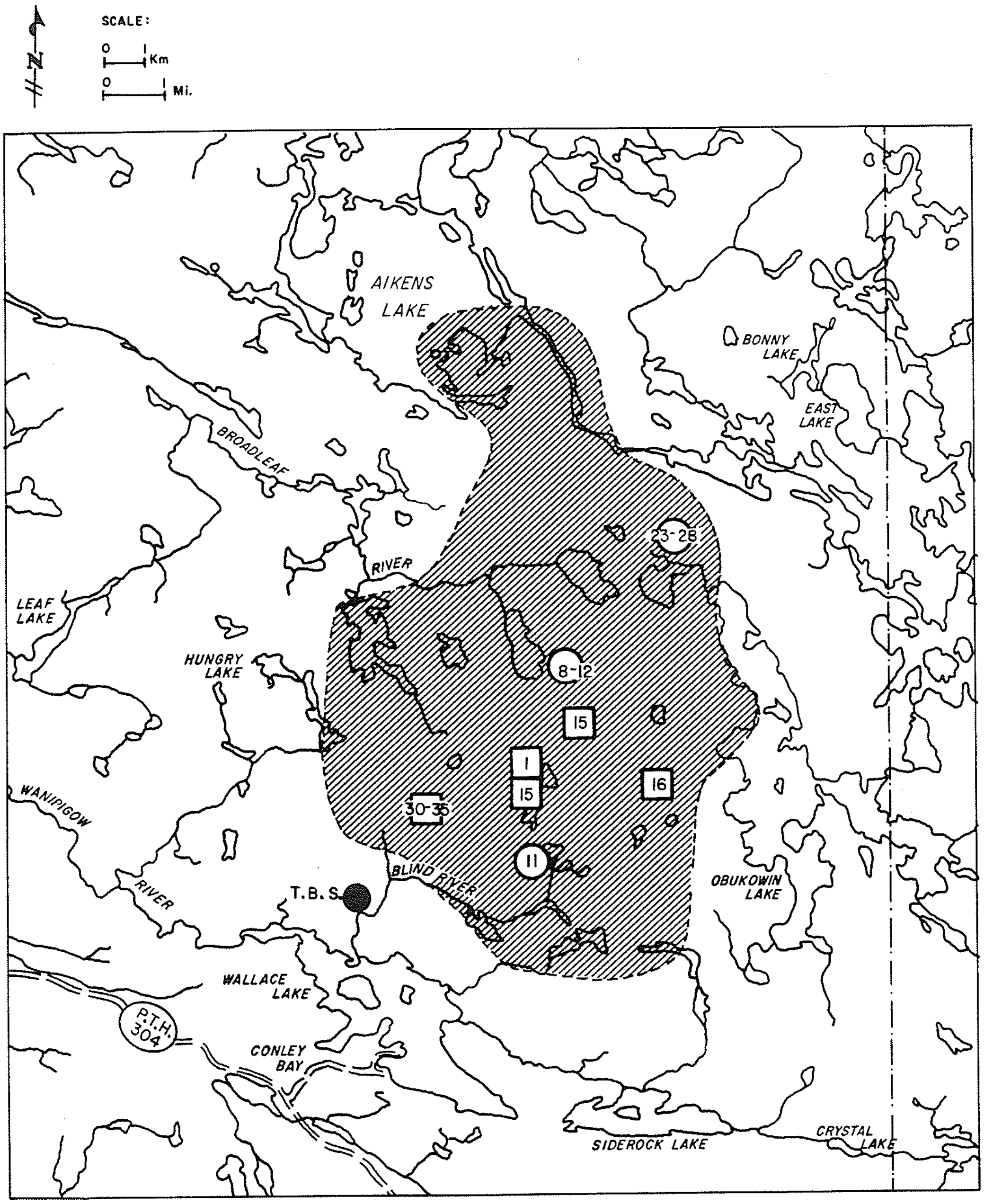
Figure 5. Map of study area showing woodland caribou sightings.

Numbers indicate number of animals sighted.

○ Woodland caribou sightings in winter of 1973-74

□ Woodland caribou sightings in winter of 1974-75

------ Winter range of Aikens group of woodland caribou (Stardom, 1977)


SCALE:
0 1 Km
0 1 Mi.
N
AIKENS LAKE
BONNY LAKE
EAST LAKE
BROADLEAF
RIVER
LEAF LAKE
HUNGRY LAKE
WANIPIGOW
RIVER
23-28
8-12
15
1
15
16
30-35
11
BLIND RIVER
T.B.S.
OBUKOWIN LAKE
WALLACE LAKE
P.T.H. 304
CONLEY BAY
SIDEROCK LAKE
CRYSTAL LAKE

(Fig.4). The remains of two white-tailed deer consumed by wolves were found on Wanipigow Lake. With the exception of the deer on Wallace Lake, the carcasses were consumed except for rumen contents and bone fragments.

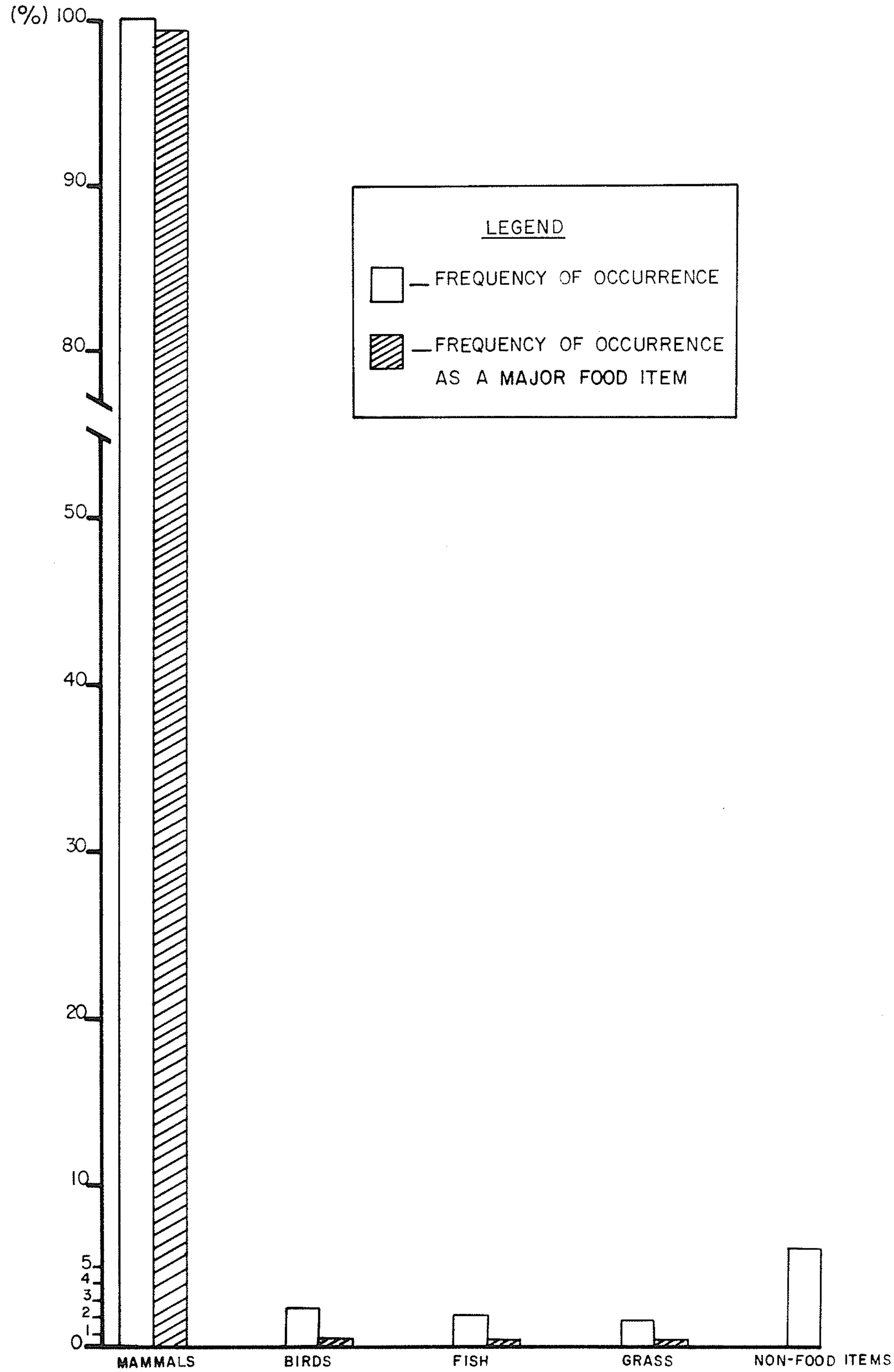
SCAT ANALYSIS

General Food Habits

Mammals comprised the major part of the wolves' diet throughout the study, occurring in 100% of the scats (99.4% M.I.). Birds occurred in only 2.5% (0.2% M.I.) of the scats and fish in 2.0% (0.2% M.I.). The only invertebrates found in the scats were three ticks (Dermacentor variablis). Traces of vegetation, probably either ingested accidentally or collected with the scat, were found in nearly all scats examined. However, I found vegetation, grasses, in larger than trace amounts in 1.0% (0.2% M.I.) of the scats. Debris or non-food items were found in 6% of the scats but never as a major item. I found no trace of cold-blooded terrestrial vertebrate animals.

Figure 6 shows the general food habits of the wolves in my study area in terms of major food groups - mammals, birds, fish and vegetation. The general food habits of wolves did not vary significantly over the two years of the study with respect to these major groups.

Figure 6. Percent Frequency of occurrence and percent frequency of occurrence (M.I.) of the major food groups in 203 scats collected between April, 1973 and June, 1975.


(%) 100
90
80
50
40
30
20
10
5
4
3
2
1
0
LEGEND
— FREQUENCY OF OCCURRENCE
— FREQUENCY OF OCCURRENCE AS A MAJOR FOOD ITEM
MAMMALS
BIRDS
FISH
GRASS
NON-FOOD ITEMS

Specific Food Habits

The contribution of the species which constituted the wolves' diet during the study period is presented in Table I. Moose, white-tailed deer and beaver comprised 89.5% (M.I.) of the diet of wolves in the study area as indicated by scat analysis. Figure 7 illustrates the seasonal importance of these species over the two years of the study. Beaver were the principal prey during the ice-free season while deer and moose were most important during the winter. A chi-square test indicated that there was no significant different in the proportions of beaver, moose and deer between years (χ^2 = 5.4042). Also, the proportions of deer and moose found in the scats in 1973-74 and in 1974-75 were not significantly different (χ^2 = 0.5641).

STAPLE FOOD ITEMS

Alces alces

Moose were an important item in the wolves' diet in both summer and winter. In the summer of 1973 they comprised 12.8% (M.I.) of the diet and 25.0% (M.I.) in the summer of 1974 (Table I). In the winter of 1973-74 they comprised 56.7% (M.I.) of the diet and 35.3% (M.I.) in the winter of 1973-74

Moose calf hair was present in scats in both summers. Calves comprised 15.8% of the moose remains found in summer scats.

Table 1: Percent frequency of occurrence and percent frequency of occurrence as a major item (M.I.) of specific food items found in 203 scats collected from April, 1973 to June, 1975.

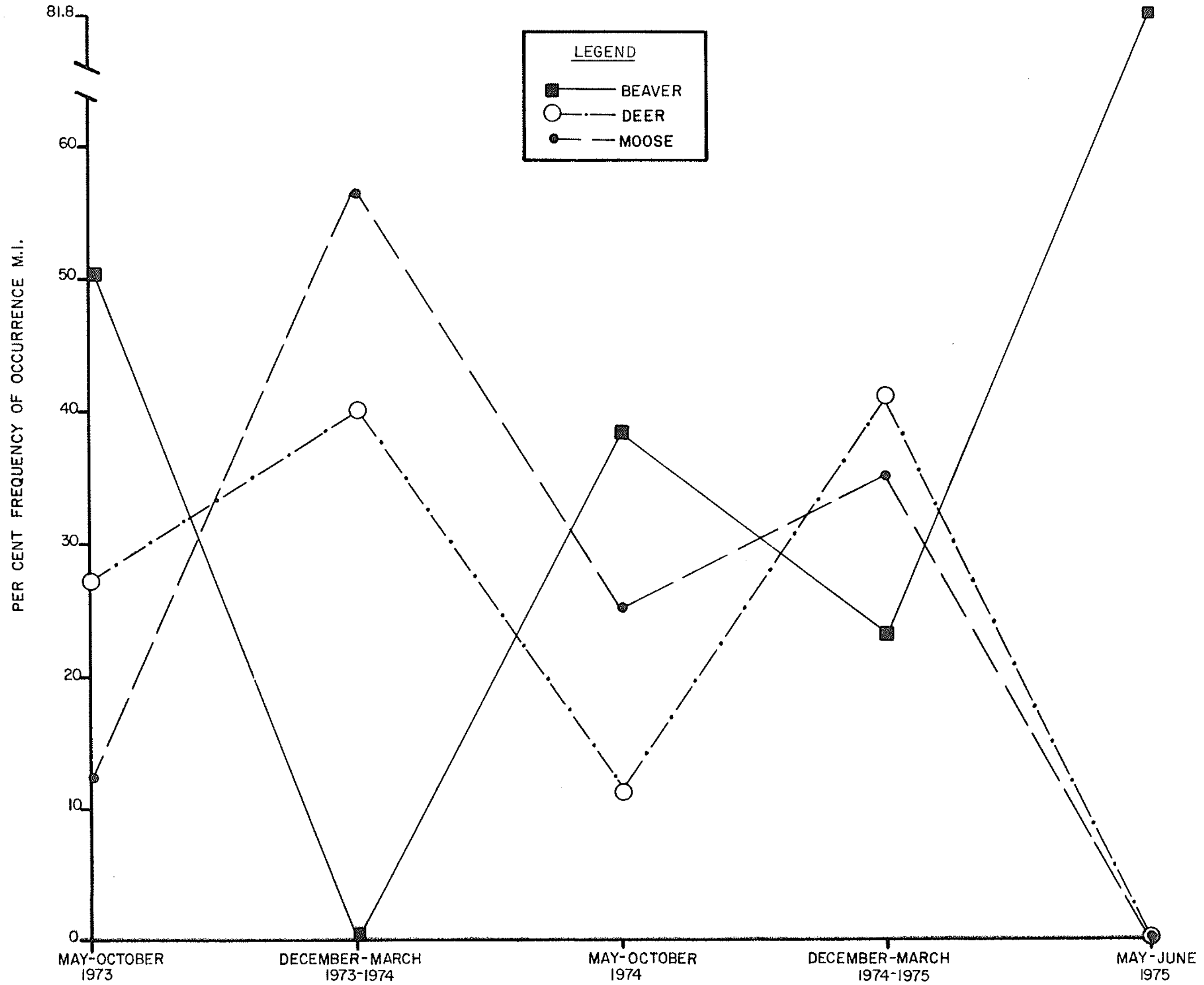
* M.I. seasonal percents are calculated using the number of scats at the top of the column rather than the total sample of 203.

Percent Frequency of occurrence of food items in scats	1973 - 1974					1974 - 1975					1975			GRAND TOTAL
	Apr.	May-Oct.	Nov.	Dec-Mar.	Total	Apr.	May-Oct.	Nov.	Dec-Mar.	Total	Apr.	May-June	Total	
Number of scats collected	16	86	2	30	134	7	26	0	17	50	8	11	19	203
MAMMALIA														
Artiodactyla														
<u>Alces alces</u>														
Total sample	1.5	5.4		8.4	15.3	3.4	3.9		3.5	10.8	2.0		2.0	28.1
M.I. Total sample	1.5	5.4		8.4	15.3	3.4	3.2		3.0	9.6	2.0		2.0	26.9
M.I. Seasonal*	18.8	12.8		56.7		100.0	25.0		35.3		50.0			
<u>Odocoileus virginianus</u>														
Total sample	1.5	14.8	1.0	5.9	23.2		1.5		3.4	4.9	1.0		1.0	29.1
M.I. Total sample	1.5	11.6	1.0	5.9	20.0		1.5		3.4	4.9	0.5		0.5	25.4
M.I. Seasonal	18.8	27.3	100.0	40.0			11.5		41.2		12.5			
<u>Rangifer tarandus caribou</u>														
Total sample				0.5	0.5		1.0			1.0				1.5
M.I. Total sample				0.5	0.5		1.0			1.0				1.5
M.I. Seasonal				3.3			7.7							
RODENTIA														
<u>Castor canadensis</u>														
Total sample	3.9	23.2			27.1		4.9		2.0	6.9	1.0	4.4	5.4	39.4
M.I. Total sample	3.5	21.4			24.9		4.9		2.0	6.9	1.0	4.4	5.4	37.2
M.I. Seasonal	43.8	50.6					38.5		23.5		25.0	81.8		
<u>Ondatra zibethicus</u>														
Total sample		1.0	0.5		1.5		0.5			0.5		0.5	0.5	2.5
M.I. Total sample		1.0			1.0		0.2			0.2		0.5	0.5	1.7
M.I. Seasonal		2.3					1.9					9.1		

	1973-1974					1974-1975					1975			
	Apr.	May-Oct.	Nov.	Dec-Mar.	Total	Apr.	May-Oct.	Nov.	Dec-Mar.	Total	Apr.	May-June	Total	GRAND TOTAL
Tamiasciurus hudsonicus														
Total sample				0.5	0.5									0.5
M.I. Total sample														
M.I. Seasonal														
Marmota monax														
Total sample		1.0			1.0									1.0
M.I. Total sample		1.0			1.0									1.0
M.I. Seasonal		2.3												
LAGOMORPHA														
Lepus americanus														
Total sample	1.5	1.0			2.5		1.0			1.0	0.5		0.5	4.0
M.I. Total sample	1.5	1.0			2.5		0.7			0.7	0.5		0.5	3.7
M.I. Seasonal	18.8	2.3					5.8				12.5			
CARNIVORA														
Ursus americanus														
Total sample							1.0			1.0		0.5	0.5	1.5
M.I. Total sample							1.0			1.0		0.5	0.5	1.5
M.I. Seasonal							7.7					9.1		
Canis familiaris														
Total sample		0.5			0.5									0.5
M.I. Total sample		0.5			0.5									0.5
M.I. Seasonal		1.2												
UNIDENTIFIED LARGE MAMMAL														
Total sample												0.5	0.5	0.5
M.I. Total sample														
M.I. Seasonal														

	1973-1974					1974-1975					1975			
	Apr.	May-Oct.	Nov.	Dec-Mar.	Total	Apr.	May-Oct.	Nov.	Dec-Mar.	Total	Apr.	May-June	Total	GRAND TOTAL
AVES														
Anseriformes														
Anas platyrhynchos														
Total sample							1.0			1.0				1.0
M.I. Total sample							0.2			0.2				0.2
M.I. Seasonal							1.9							
UNIDENTIFIED BIRD														
Total sample	0.5	1.0			1.5									1.5
M.I. Total sample														
M.I. Seasonal														
OSTEICHTHYES														
Total sample		2.0			2.0									2.0
M.I. Total sample		0.2			0.2									0.2
M.I. Seasonal		0.6												
INVERTEBRATA														
Dermacentor variabilis														
Total sample	0.5	0.5			1.0									1.0
M.I. Total sample														
M.I. Seasonal														
VEGETATION														
Grass sp.														
Total sample		1:0			1.0									1.0
M.I. Total sample		0.2			0.2									0.2
M.I. Seasonal		0.6												
NON-FOOD ITEMS														
Total sample														6.0
M.I. Total sample														
M.I. Seasonal														

Figure 7. Seasonal and annual percent frequency of occurrence (M.I.) of beaver, moose and white-tailed deer.



PER CENT FREQUENCY OF OCCURRENCE M.I.
81.8
60
50
40
30
20
10
0
LEGEND
BEAVER
DEER
MOOSE
MAY-OCTOBER 1973
DECEMBER-MARCH 1973-1974
MAY-OCTOBER 1974
DECEMBER-MARCH 1974-1975
MAY-JUNE 1975

I was able to examine the remains of only one presumably wolf-killed moose. It was approximately 21 months old. The fat content of its tibial marrow was 73.5%.

Odocoileus virginianus

The remains of white-tailed deer were found in both summer and winter scats. As shown in Table I, deer comprised 27.3% (M.I.) of the scats found in the summer of 1973 and 11.5% (M.I.) of those found in the summer of 1974. During the winters of 1973-74 and 1974-75, they comprised 40.0% and 41.2% (M.I.) respectively of the scats found.

Fawn remains comprised 16.7% (M.I.) of the scats which contained deer hair in the summer of 1973. No fawn remains were found in scats collected in the summer of 1974.

Although actual predation was not observed, I located the remains of two deer which were probably killed by wolves and one which definitely was. A post-mortem examination of the female white-tailed deer killed by wolves on Wallace Lake during the night of 14 - 15 February, 1975 revealed that it weighed 43 kg and had adequate fat deposits in its body. The fat content of the femur marrow was 86.7%.

I did not find any parasites in the nervous system, heart or lungs. The abdominal organs had been consumed by the wolves. This deer was 5 3/4 years old. The fat content of the tibial marrow of the two deer found on Wanipigow Lake was also high 87.8% and 81.2%.

Castor canadensis

Beaver were an important summer food item for wolves over the entire study period (Table 1). Beaver remains were frequently found in summer scats, but seldom occurred in winter scats.

Incidental Food Items

The remaining species listed in Table I were found infrequently in scats and did not constitute a major part of the wolves' diet during the study. They were probably captured opportunistically or consumed as carrion.

Non-Food Items

Various materials, including undigestible human refuse, acorn shells and pieces of wood were found occasionally in scats throughout the study. They contributed very little to the volumes of the samples.

STOMACH ANALYSIS

The results of stomach analyses are presented in Table 2. These results are presented separately from the scat analyses because of the small number of stomachs which contained food remains and also because most of the carcasses were obtained outside the study area. Few of the stomachs were full and

TABLE 2.

Percent frequency of occurrence and percent frequency of occurrence as a major item (M.I.) of food items found in 13 stomachs.

Food Item	Percent frequency of occurrence	Percent frequency of occurrence as a Major Item
MAMMALIA		
Artiodactyla		
Odocoileus virginianus	38.5	30.7
Alces alces	7.7	7.7
Domestic Animals		
Bos taurus	7.7	7.7
Equus caballus	7.7	7.7
RODENTIA		
Microtus pennsylvanicus	7.7	0.0
CARNIVORA		
Canis lupus (trap debris resulting from self mutilation)	30.8	15.4
Canis familiaris	7.7	7.7
Unidentified Large Mammal	15.4	0.0
Fish	23.1	15.4
Vegetation (trace)	76.9	0.0
Non-food Items		
Rope	7.7	0.0
Paper	15.4	0.0
Parka	7.7	7.7
Matchstick	7.7	0.0
Tinfoil	7.7	0.0

most were less than one-quarter full. Therefore, the importance of such items as the traces of wolf fur and claws which were the result of self-mutilation while in the trap were exaggerated.

Mammal remains constituted most of the food items (76.9% M.I.) found in the stomachs. White-tailed deer remains occurred in four stomachs. One meadow vole (*Microtus pennsylvanicus*) was found in a stomach. Remains of domestic cattle, horses and dogs occurred in the stomach of one individual in each case. The stomach of the wolf collected on East Lake contained moose hair. Fish remains were found in three stomachs. The traces of vegetation were probably ingested while the wolves were trapped.

POST-MORTEM EXAMINATIONS

The median age of the wolves examined was between eight and nine months. If the two oldest animals (a male 9 3/4 years and a female 8 2/3 years) are excluded, the average age was 9.3 months. The average age of the six males was 7.5 months and that of 12 females was 11 months. I assumed that the pups were born in May (Mech, 1970).

The males were heavier (average weight 26.9 kg) than the females (average weight 22.2 kg). Of the 21 animals examined, 20 were in a nutritionally satisfactory condition with adequate body fat deposits and one male (No.26) was emaciated.

According to Rausch (1967), female timber wolves first breed at approximately 22 months. Only three of the females I examined were this age or older. Animal No.41 (8 2/3 years old) had previously been pregnant, but was not at the time of examination. The reproductive tracts of the other females appeared to be quiescent and in a virginal condition.

Smears prepared from the testes of a male wolf (No. 38) did not reveal the presence of any sperm cells. This was expected as male wolves do not usually become sexually mature until they are 22 months old (Rausch, 1967; Rabb *et al*. 1967) and No. 38 was only six months old.

The parasite load of these animals was light and few pathologic abnormalities were found. Animal No. 32 had irregular hemorrhagic mucosal ulcers in the stomach. Unidentified cestode segments were found in the small intestines of animals No's 26 and 32. Several *Toxocara* eggs were present in the faeces of animal No. 33. Organisms resembling *Isopora bigemina* were found in the faeces of animal No. 46. One giant kidney worm (*Dioctophyma renale*) was found in each of animals No. 39 and No. 46. The worm in No. 39 was found within the capsule of the right kidney and had destroyed all the parenchymatous tissue of that kidney. A mature kidney worm (104 cm in length) was found free in the peritoneal cavity of No. 46. Dr. Dick did not find any evidence of *Trichinella sp*. in the diaphragms. There was no evidence of *Echinococcus granulosus* infection in any of the wolves. The level of parasitic infection in the examined wolves (27%) was low compared with that found by Holmes and Podesta (1968) in Alberta. They found that 98% of 98 wolves examined harbored one or more species of helminths with a mean of 2.6 species perwolf.

Three of the wolves (Nos. 40, 41 and 42) had evidence of trauma. Nielsen (1977) reported evidence of traumatic injury in 50.9% of 110 Alaskan wolves examined. These injuries were probably associated with hunting large ungulate prey, intraspecific fighting and trapping.

QUESTIONNAIRES

Tourist Questionnaire

The campground at Wallace Lake contained 69 permanent cottages and 60 unserviced camping sites. In the summers of 1973 and 1974, 757 and 639 camping permits were issued respectively. The owners or users of 38 cottages were interviewed along with 88 "transient" campers for a total sample of 126.

Three quarters of the people who visited Wallace Lake (74.6%) were from Winnipeg. Most of the campers (80.7%) visited Wallace during the summer while many cottage owners used the area on a year-round basis. Cottage owners spent more time at the lake annually and also spent more time away from the campground than campers.

The three most popular outdoor activities of the two groups were fishing, swimming and powerboating. The groups were approximately equal in the amount of travelling done to see wildlife. Cottage owners had seen much more wildlife in the Wallace Lake area than the campers. When asked what wildlife they would like to see, campers expressed more interest in moose and "big game" than cottage users. Both groups wanted to see white-tailed deer.

Twenty-nine percent of the cottage users had heard wolves howling in the Wallace area while only 14.8% of the campers had. Similarly 21.1% of the cottage users had seen a wolf while only 6.8% of the campers had. While a large majority of both groups said they would like to hear and/or see a wild timber wolf, a larger percentage of the campers expressed this desire than the cottage users. A majority of both groups said they would be willing to make an effort to hear timber wolves howl.

To test the hypothesis that the campers and cottage users were homogeneous in their interest in wolves, 2 x 2 contingency tables were prepared for questions 12, 13 and 15. Chi-square tests indicated that campers were significantly more interested in hearing and seeing wild wolves than cottage users ($\chi^2 = 4.3905$ and $\chi^2 = 6.1358$ respectively). However, there was no significant difference ($\chi^2 = 2.0136$) in the effort the two groups would make to attend an organized "wolf-howl".

Questionnaire respondents were also grouped according to sex or type of family group encountered in order to determine whether they was any sex-related reaction to timber wolves. The groups tested were male, female, husband and wife and "other". Because of the small sample size, the responses from families, children and the non-recorded group were grouped together to form an "other" category. Questions 12, 13 and 15 were correlated with these groups.

To test whether these groups were homogeneous in their responses, 2 x 4 contingency tables were prepared for questions 12, 13 and 15. Chi-square tests indicated that these groups were homogeneous in their desire to see wolves (χ^2 = 4.8771) and the effort they would make to attend an organized "wolf-howl" (χ^2 = 4.3367). Women, however, were significantly less interested in hearing wolves howl (χ^2 = 9.7871) than the other groups tested.

Farmer-Rancher Questionnaire

The questionnaire used to examine the extent of timber wolf predation on domestic livestock was sent only to cattle owners because very few operators in Manitoba raise sheep as a primary source of income. Because of this sampling bias, the incidental data collected regarding losses of sheep, swine, and poulty were not examined in detail.

Of the 1059 questionnaires mailed out, 455 were completed and returned. A further 66 were returned unanswered or unusable since the farmers had retired, moved, died or mutilated the form so that their region could not be identified. This gave a total return of 521 or 49.2% of the number mailed originally.

A large majority of the respondents did not have any predator problems. Eighty-one percent had not lost any livestock to predators within the last five years and 76.1% did not think there was a predator problem in their area. One hundred respondents (23.9%) said there was a problem in their area and 84 (19.0%) had lost livestock to predators over the last five years. These losses included poultry, swine, sheep and cattle.

Three hundred and nine respondents had free ranging cattle, while 211 used a feed lot system. Approximately 65 farmers used both systems, putting their cattle out to pasture in the spring. Fifty-eight percent of those with free ranging cattle had 25 - 100 head. Fifteen respondents with free ranging cattle stated they had wolf problems while only seven feed lot operators did so. Twenty-seven of the respondents kept sheep as well as cattle. Ten of these kept their sheep in a feed lot while 17 allowed them to pasture away from their buildings.

Reported losses of cattle and sheep during the five year period between 1969 and 1973 are presented in Table 3. The total number of farmers who suffered losses during that period is exaggerated in Table 3 as some lost both calves and

TABLE 3.

Reported livestock losses to predators between 1969 and 1973.

Region	Calves	Cattle	Lambs	Sheep
Eastern	39 (12)*	10 (3)	0	0
Interlake	14 (11)	4 (2)	18 (3)	3 (2)
Western	213 (65)	64 (18)	115 (13)	27 (5)
Total	266 (88)	78 (23)	133 (16)	30 (7)

* Number in parentheses indicates number of farmers who reported losses.

cattle or both sheep and lambs to predators. Seventy-four respondents (16.3%) lost 266 calves and 78 cattle and nine respondents (2.9%) lost 133 lambs and 30 sheep. The actual losses may have been higher since 15 respondents (3.3%) stated they had suffered losses but did not quantify them. The annual losses of livestock were fairly constant over that period and averaged 52.3 calves and 15.8 cattle per year. The respondents who reported losses to predators lost an average of 4.7 cattle each. The average loss per farmer reporting losses was highest in the Eastern region at 5.4 cattle each. The Western region was second with 5.0 cattle each and the Interlake region was lowest with 1.9 cattle each. The number of respondents reporting losses was highest in the first mailing (47) and declined in the second (28) and third (8) mailings. Most losses occurred during the summer according to 40.6% of 288 respondents followed by spring (30.9%), fall (25.4%) and winter (3.1%).

Losses to predators within the 12 month period prior to receiving the questionnaire (approximately 31 March 1973 to 31 March 1974) are presented in Table 4. Assuming average values of $150.00 for calves, $325.00 for cattle and $30.00 for lambs and sheep, these losses totalled $25,000.00. These losses were incurred by 67 respondents (14.7%). Of the 68 respondents who indicated how certain they were of predators actually killing livestock rather than scavenging on carcasses 58.8% were positive, 20.6% were fairly certain, and 20.6% were not certain.

TABLE 4.

Livestock losses to predators between 31 March 1973 and 31 March 1974.

	Calves	Cattle	Lambs	Sheep
Coyotes	47	12	32	4
Black Bear	34	4	5	3
Timber Wolf	19			1
Domestic Dog	11			
Magpie	2			
Unknown	10			
Total	123	16	37	8

Eight respondents (1.8%) lost livestock valued at $2,880.00 to wolves within that 12 month period. Four lost one calf each, one lost two calves, one lost four calves, one lost nine calves and one lost one sheep. Seven of these respondents had free-ranging cattle while the farmer who lost nine calves had a feed lot operation. All were very certain that wolves caused these losses. Five of these farmers were in the Western region, two in the Interlake and one in the Eastern region. Two men (Western region) lost stock only to wolves while the others had also lost stock to bears and/or coyotes. All the farmers with losses to wolves indicated that both wolves and coyotes were present in their areas and four had losses to coyotes which exceeded their losses to wolves. Losses to wolves occurred in the spring, summer and fall.

Canids were blamed for most of the predator problems. Twenty-one respondents (4.6%) stated that dogs did kill livestock in their areas while 326 (71.6%) said there was no problem with them. Seventy-six and one half percent of the respondents stated that coyotes were present in their area. When asked about timber wolves, 148 (32.5%) respondents replied that they were present, 97 (21.3%) said they were not and 210 (46.2%) did not reply. The large proportion of non-respondents to this question may indicate that wolves were not present in many areas or that some respondents had difficulty in identifying them. Ninety-six farmers reported seeing lone wolves, while 51 reported seeing packs. The majority of wolf packs seen (55.6%) consisted of two or three animals. Packs of four to six animals were reported by 25.9% of the respondents and packs of seven or more were seen by 11.1% while 7.4% of these men were unable to say how large the packs were. Six respondents reported that single wolves killed calves and four stated that packs were responsible for stock losses.

I also asked which predator caused most of the problems in their area. Coyotes were the worst offenders according to 26.6% of the farmers sampled. They were followed by red fox (*Vulpes vulpes*) (16.3%), black bear (15.4%), domestic dog (7.0%), timber wolf (6.2%) and lynx (*Lynx lynx*) (2.2%). Other predators mentioned were skunks (*Mephitis mephitis*) (3.7%), raccoon (*Procyon lotor*) (1.5%), magpie (*Pica pica*) (1.1%), grey foxes (*Urocyon cinereoargenteus*) (0.2%), badgers (*Taxidea taxus*) (0.2%) and mink (*Mustela vison*) (0.2%). Problems caused by species other than bears, wolves, coyotes and magpies were related to livestock other than cattle and sheep.

Eighty-six farmers replied to a question asking what action they took when losses occurred. The results were as follows: shooting predators (29.1%), nothing (24.4%), asked for a control program by conservation officers (20.9%), trapping (9.3%), different handling of stock (8.1%) and "Other" (8.1%). "Different handling of stock" included keeping calves in the farm yard, checking stock more often, putting stock out to pasture later in the summer, and moving stock to a different area. "Other" included selling sheep and buying cattle, informing police, skidoo and aircraft hunting, and informing the local council of the problem.

I also asked the farmers what, in their opinion, is the best way to deal with a predator problem. This elicited 403 replies. A bounty system was suggested by 28.3% of the respondents. Other responses were: hunting (22.1%), trapping (21.6%), removal of individual problem animals by specialists (13.1%), an annual government poison bait control program (9.2%), modification of livestock handling methods (2.2%) and "other" (3.5%). "Other" included aircraft and skidoo hunting, loss compensation and shooting predators "on the spot."

The only non-respondent I contacted in the Eastern region had sold all his cattle and therefore had not responded to the questionnaire. Twelve non-respondents were contacted in the Interlake. Two of these completed questionnaires. Only one mentioned that he had suffered a loss, possibly one calf to a black bear, but he was not certain that the bear had actually killed the calf. Of the remaining non-respondents, two had died, one had moved, four had sold their cattle, and three had no predator problems. Twelve non-respondents were contacted in the Western region and completed questionnaires. Of these, ten had no problems with predators, one had sold his livestock, and one had lost a calf to coyotes within the last twelve months.

The following data were taken from the questionnaires completed by the 14 non-respondents from all areas. Four of these farmers kept cattle in a feed lot and 12 allowed them to free-range (at least in the summer). None of them kept sheep.

Two of them thought there was a predator problem in their area while eleven did not. Two had lost one calf each within the last five years. Coyotes and a black bear were blamed for the losses, but only in the case of the coyotes was the farmer very certain of the cause of death. The loss of the calves occurred in the summer. One farmer reported there was a problem with dogs killing sheep in his area.

Eleven stated there were coyotes in their area while two said there were none. Seven farmers said wolves were present while six said they were not present. Coyotes were seen more frequently than timber wolves. Of the men who said wolves were present in their areas two said they were usually alone while three said they were in packs of two or three animals. When asked which predators cause most of the problems in their area, two replied black bears and coyotes, one said red foxes, and three said skunks. The foxes and skunks caused poultry losses.

Neither of the farmers who suffered losses from predators took any action. However, all the farmers contacted had opinions on how to deal with a predator problem. Their suggestions were: a bounty system (50%), hunting (21.4%), an annual poison bait program (14.3%), the removal of problem animals by specialists (14.3%) and trapping (7.1%).

DISCUSSION

POPULATIONS

Aerial surveys and ground track observations in the study area suggested that it was utilized by eleven wolves - the Hungry Lake pack, the Siderock Lake pack and a pair which frequented Wallace Lake. The ranges of these packs included portions of the study area but were not wholly encompassed by it. This yields a density of one wolf per 51 km^2 (1/19.7 sq. miles).

During the winter of 1976-77, after I had ceased field studies, I received reports of a pack of ten to 20 wolves in the study area (Conley and Darby, pers. comm.). If Rausch's (1967) hypothesis that the frequency of larger packs is higher in populations of higher density is correct, then the large pack may indicate an increasing population in the study area.

A number of authors, Pimlott (1967a) Pimlott *et al*. (1969), Mech (1970), Van Ballenberghe *et al*. (1975), and Stephenson (1975a) have reviewed the literature on wolf population densities. They found a wide variation in densities across North America. The highest recorded density was on Isle Royale in 1975 (Peterson and Allen, 1974) with one wolf per 13.3 km^2. Kuyt (1972) found one wolf per 17.9 km^2 near Abitau Lake in the Northwest Territories in an area of caribou concentration. Parker (1973) also reported very high densities of wolves (up to one wolf per 20.2 km^2) in wintering areas of barren-ground caribou in Manitoba and Saskatchewan. Very low densities have also been reported. Pimlott (1967a) stated that in 25,900 km^2 of moose range in Ontario, the wolf density was between one wolf per 259 km^2 and 518 km^2. Riewe (1975) observed 12 wolves in the area of approximately 22,000 km^2 in the Jones Sound region of the eastern High Arctic. This would be a density of less than one wolf per 1800 km^2.

As Pimlott (1967a) pointed out, obtaining accurate data on wolf and prey densities has proven to be the major problem in understanding the influence of wolves on prey populations. Cowan (1947) estimated that the summer density of wolves in Jasper National Park was between 225 and 287 km^2 per wolf. In the winter, because of range compression into lower altitudes the density increased to approximately one wolf per 26 km^2. This density remained constant over a five year period. Cowan's population figures are based on reports received from park wardens while Pimlott's figures were based on extensive aerial surveys.

More recent work has been carried out in Ontario and Minnesota using radio-collared wolves. Kolenosky (1972) found that a pack of eight wolves in Ontario utilized a winter range of 224 km^2 (a density of one wolf per 28 km^2). Van Ballenberghe _et al_. (1975) studied five packs in Minnesota and estimated their density at one wolf per 24 km^2.

The exact number of large ungulates in the study area was unknown. It was estimated that there were approximately 66 moose and 37 woodland caribou (Stardom, 1977). White-tailed deer were very scarce and were probably concentrated along the north shores of Wallace and Siderock Lakes. The population estimates for deer and moose are probably low.

GENERAL FOOD HABITS

On the basis of their frequency of occurrence in scats (Table 1), deer, moose and beaver can be considered staple items in the diet of wolves in the study area. The importance of these three species is in agreement with the findings of other studies although the relative importance of these species varies between studies (Mech, 1970).

I did not find a dramatic shift to moose calves or deer fawns in the summer as other authors have reported (Mech, 1966; Pimlott _et al_. 1969; Van Ballenberghe _et al_. 1975). I had difficulty distinguishing between adult and juvenile hair in some cases and this may have resulted in a slight under-estimation of the importance of young ungulates in the summer diet of the wolves.

There is some disagreement as to how accurately remains found in scats reflect the proportion of adult and juvenile deer and moose consumed by wolves. Mech (1970) contended that juveniles are over represented in scat collections because the ratio of surface area to body mass is greater in juveniles and more hair may be consumed because the skin can be more readily torn apart and ingested. Also juveniles may be consumed more quickly allowing the wolves to move on leaving a higher proportion of scats containing juvenile remains scattered along trails where they are collected rather than concentrated in one area. Pimlott et al. (1969) assumed that the proportion of juveniles and adults indicated by scat analysis approaches the proportion that are killed. I followed Pimlott's assumption but omitted three groups of scats, each found in a small area associated with a kill.

As Knowlton (1964) observed, scat analysis is a crude tool for determining the food habits of carnivores, but it does allow the collection of relatively large samples from discrete areas without endangering future collections. Also scats can be accurately dated when collections are made regularly.

Pimlott (1967a) discussed some problems associated with determining food habits by scat analysis. The material found in scats does not provide any information concerning the physical condition of the prey which made it susceptible to predation. Furthermore, one cannot distinguish between food items obtained by predation and scavenging. These problems also apply to the analysis of stomach contents. Because of selective predation, a prey species can show higher importance as a food item without occurring in higher densities in the area (Frenzel, 1974). It is also often difficult to determine the cause of death of a carcass upon which wolves have fed. Unless one has actually observed the act of predation, the cause of death is usually an assumption.

STAPLE FOOD ITEMS

Moose were the most abundant large ungulates found in the study area. Stardom (1977) estimated the population to be 66; a density of one moose per 8.5 km^2. They were concentrated in suitable habitat along the lake and river systems on the periphery of the study area and were seldom seen in the central area. Low productivity was indicated by the fact that I saw only one calf and later found the tracks of another. The low occurrence of calf remains in scats may also indicate relatively low productivity. The population and productivity estimates were probably conservative as no intensive surveys for moose were conducted.

There was a hunting season for moose in the study area during the two years of the study. Native hunters also took an unknown number of moose along Highway 304 during both winters. Traces of hunter-killed moose undoubtedly occurred in scats I collected because wolves fed on gut piles and wounded animals which escaped the hunters.

A number of authors, Peterson (1955), Pimlott et al. (1969) and Mech (1970), have observed that the importance of