SEASONAL MOVEMENTS, SUMMER FOOD HABITS, AND SUMMER PREDATION RATES OF WOLVES IN NORTHWEST ALASKA

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SEASONAL MOVEMENTS, SUMMER FOOD HABITS, AND SUMMER PREDATION RATES OF WOLVES IN NORTHWEST ALASKA

A

THESIS

Presented to the Faculty of the University of Alaska in Partial Fulfillment of the Requirements for the Degree of

MASTER OF SCIENCE

by

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Seasonal movements and summer food habits of 2 wolf (Canis lupus) packs, and summer predation rates of 1 wolf pack were studied in northwest Alaska in 1977 and 1978. The purpose was to identify potential detrimental effects to the wolf population of impending economic development. The methods used were aerial observation (n=546) of radio-collared wolves and examination of wolf scats (n=920). The packs migrated between summer and winter home ranges in response to caribou migrations. Both packs demonstrated a high degree of fidelity to their home ranges. Caribou constituted an estimated 96% of the ungulate biomass which the packs consumed. Inconclusive evidence suggested the occurrence of disproportionate predation on caribou calves. One pack fed upon 94-178 (95% confidence interval) caribou from 20 April to 13 October, 1978. This indicated a summer predation rate of 1.8-3.3 (95% confidence interval) caribou/wolf/month and the availability of 3.2-6.1 (95% confidence interval) kg caribou/wolf/day.
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INTRODUCTION

In recent years 2 major events have emphasized the need to better understand the ecology of wolves (*Canis lupus*) in northwest Alaska. First, a precipitous decline in the size of the Western Arctic Caribou Herd during the 1970's focused attention on competition between wolves and humans for caribou. Second, economic development, including petroleum exploration, has increased and is potentially detrimental to wolves as well as other wildlife.

Wolves in northwest Alaska have been the subject of relatively few studies. Young and Goldman (1944:252) recounted a few incidents of wolf predation on caribou and reindeer. Kelly (1954) presented data on physical characteristics, reproduction, winter food habits, and winter movements of wolves. R.L. Rausch (1958) and R.L. Rausch and Williamson (1959) discussed diseases of wolves. R.A. Rausch's (1967) discussion of wolf population ecology included considerations of reproduction, productivity, age and sex composition, and pack size. Pederson (1978) considered the taxonomy and evolution of wolves. These studies dealt with northwest Alaska wolves only incidental to considerations of the entire Alaska wolf population. Other sources of information, mainly on distribution and abundance, include biological surveys (Dean and Chesemore
1974, Young 1974, Melchior 1976) and unpublished reports (Alaska Department of Fish and Game, Juneau).

In 1977 several wildlife studies were initiated in northwest and northcentral Alaska. The purpose was to compile baseline ecological information necessary for mitigating the impact of increased petroleum exploration and development in the National Petroleum Reserve in Alaska (NPRA). The wolf study was intended to determine distribution and abundance, seasonal movements, productivity, food habits, and several other aspects of wolf ecology. The results were reported by Stephenson (1979) and Stephenson and James (in press). The study presented here is a more detailed analysis of 3 subject areas which were given general consideration in previous reports. Each of the 3 subject areas is a separate chapter in the thesis.

The purposes of this study were to determine the pattern and extent of wolf movements relative to seasonal migrations of caribou (Chapter 1); to determine the summer food habits of wolves denning on caribou summer range (Chapter 2); and to determine the rate of predation on caribou by wolves during summer (Chapter 3). Management implications of these findings are discussed in Chapter 4.

STUDY AREA

The study area lies between 67°30' and 69° N, and 158°
and 164°W in northwest Alaska (Figure 1). Parts of several different physiographic regions are represented. These include the southern section of the Arctic Foothills province and the De Long Mountains, Noatak Lowlands, and Baird Mountains sections of the Arctic Mountains (Brooks Range) province (Wahrhaftig 1965). The southern Arctic Foothills region varies in elevation from 350-1060 m with local relief up to 760 m, "... and is characterized by irregular buttes, knobs, mesas, east-trending ridges and intervening gently undulating tundra plains ..." (Wahrhaftig 1965:20). The De Long Mountains vary from 900-1500 m with local relief up to 900 m or more, and consist of rugged glaciated ridges in the central region flanked to the east and west by lower even-crested ridges. The Noatak Lowlands vary in height from near sea level to a few hundred meters. Flood plains, tundra flats, thaw lakes, and pingos are common in the western lowlands. Irregular rolling plains with scattered morainal and thaw lakes and uplands predominate in the eastern lowlands. Many summits in the Baird Mountains rise to 760-900 m with peaks up to 1350 m. The Noatak River and its tributaries drain the northern and western portion of the Baird Mountains, the Noatak Lowlands, and the southern side of the De Long Mountains. The northern side of the De Long Mountains and the southern Arctic Foothills give rise to several major drainages including the Wulik, Kokolik, and Utukok rivers. Additional

An arctic climate regime prevails north of the De Long Mountains, while to the south the climate is continental. However, climatic differences between the northern and southern sections of the study area are slight because this area is a transition between the 2 climatic zones. Annual precipitation averages 380–510 mm. Annual snowfall depth varies from 1.0–2.1 m and wind-drifted snow is common, especially north of the De Long Mountains. Temperatures vary from a mean annual maximum of 10–16°C to a mean annual minimum of approximately -26°C. Winds are present 85–95% of the time at an average speed of 18–27 kph (Selkregg, n.d.).

Tundra is the most conspicuous vegetative feature of the study area. Forests are restricted to the lower Noatak valley (Mission Lowland) where extensive areas are covered by closed, open, or woodland conifer forest or mixed conifer and deciduous forest. Shrub tundra occurs mainly on riparian sites throughout the area, but covers much less area than does sedge-grass, herbaceous, tussock, or mat and cushion tundras. Tall and low shrublands occur on many of the riparian sites south of the De Long Mountains, especially in the Mission Lowland, where stands of willow (Salix spp) are commonly 1.5 m or more in height. Viereck
and Dyrness (1980) present detailed explanations of the terminology used above. Spetzman (1959) and Young (1974) provide more detailed vegetative descriptions for areas north and south, respectively, of the De Long Mountains.
Wolves (*Canis lupus*) that inhabit the northern latitudes of North America and Eurasia often depend almost exclusively on caribou (*Rangifer tarandus*) or reindeer for food. Local areas normally experience drastic seasonal fluctuations in numbers of *Rangifer* because of their migratory behavior. Wolves dependent on this food source, therefore, often have to migrate to remain near adequate numbers of prey (Kelsall 1968:244, Mech 1970:161).

Kuyt (1962) was the first researcher to document migrations of marked wolves. His studies in the Northwest Territories demonstrated that ear-tagged wolves migrated as far as 360 km in response to caribou migrations. Subsequent to Kuyt's work and the reviews by Kelsall (1968) and Mech (1970), several authors have reported various aspects of the ecology of wolves on barren-ground caribou range (Clark 1971, Kuyt 1972, Parker 1972:80, 1973, Stephenson and Johnson 1973:18, Miller and Broughton 1974, Miller 1975, Chapman 1976, Ballard et al. 1981), but detailed information on wolf migrations and seasonal home ranges, as
defined by Burt (1943), has not been reported.

The purpose of this portion of the study (Chapter 1) was to document seasonal movements and home ranges of wolves on barren-ground caribou range in northwest Alaska.

METHODS

Aerial survey techniques (Stephenson 1978) were used to locate wolves which were then captured using techniques similar to those described by Baer et al. (1978) and Ballard et al. (1981) (Table I). Two combinations of immobilizing drugs were used. In spring and summer 1977 and spring 1978 wolves were immobilized with a solution of 100 mg phencyclidene hydrochloride (Seal et al. 1970). During summer 1978 wolves were immobilized with a solution of 170 mg xylazine, 20 mg Sernylan, and 1.5 mg atropine sulfate; with doxapram hydrochloride used to shorten recovery time (Philo 1978, pers. comm.). The latter combination of drugs was preferred because it did not cause convulsions. The sex of each wolf was determined and each was classified as a pup, yearling, or adult (Van Ballenberghe et al. 1975:8). Radio-collars attached to wolves were monitored via aerial radio-tracking usually accomplished with a PA-18 supercub equipped with a receiver and 2, 4-element yagi antennas.
Most of the radio-tracking flights were accomplished from May to October (Table 2). The winter schedule was intended to document only major movements and averaged about 1 flight per month, although some months were missed entirely because of poor flying conditions. Each time a radio-collared wolf was located its position was recorded as 1 location. When a location resulted in an actual sighting of 1 or more wolves it was also recorded as 1 observation. Often successive locations occurred at the same geographic site such as at a den-site. Locations were also consolidated and recorded as pack-day locations (PDLs). One PDL was the location of 1 or more radio-collared members of a pack on a given day. A summer PDL often included more than 1 geographic site such as when pack members were temporarily separated by as much as 48 km. Geographic sites at which the study wolves were located on 1 or more occasions were recorded on 1:250,000 topographic maps (summer: Appendices 1 and 2, winter: Figure 1).

The distribution and movements of caribou in the study area were determined from observations recorded during radio-tracking flights and from caribou surveys conducted by other biologists. The caribou in the study area and surrounding region were members of the Western Arctic Caribou Herd.
RESULTS

Wolf Movements

Seventeen wolves were live-captured and radio-collared 21 times, including 4 wolves that were captured twice. The data reported here resulted from locations and observations of the Iligluruk and the Anisak packs which included 14 of the radio-collared wolves; 7 in each pack. The number of functioning radio-collars varied from 1-7 in the Iligluruk pack and from 1-4 in the Anisak pack (Table 1). The number of wolves in the Iligluruk pack varied from as few as 2 in spring 1977 to as many as 11 in fall 1978. In the Anisak pack the number varied from 5-7 in spring 1978 to 12-14 for a brief time in early summer 1978.

Five hundred and forty-six locations, including 484 observations, of the Iligluruk and Anisak wolves were made from 13 May 1977 to 11 July 1979 (Table 2). It required 159 flight hours to locate the Iligluruk pack 116 times (PDLs) during 3 summers and 14 times (PDLs) during 2 winters (Figure 1, Appendix 1). Locations of radio-collared wolves in the Iligluruk pack were distributed during the diel period as follows: 2400-0600h, 4%; 0600-1200h, 37%; 1200-1800h, 34%; and 1800-2400h, 25% (N=449). It took 150 flight hours to locate the Anisak pack on 41 and 14 pack days (PDLs) during the summer and winter seasons, respectively (Figure 2, Appendix 2). The diel distribution of
Anisak pack locations was: 2400-0600h, 11%; 0600-1200h, 26%; 1200-1800h, 52%; 1800-2400h, 11%. The Iligluruk pack's summer home range was probably more accurately determined than that of the Anisak pack because the Iligluruk wolves were located more frequently.

**Iligluruk pack.**—Iligluruk wolves were located 78 times (38 PDLs) in the upper Kokolik and Utukok river drainages (Figure 1) during summer 1977. The first sighting of the Iligluruk pack was the alpha pair (NW6d, NW7q) on 1 June 1977, at their den. Previous to that date, tracks of 2 wolves in snow 4 km from the den suggested that the wolves may have been present by at least 28 April 1977. Six months later, tracks in snow 34 km from the den, and near the apparent northeast edge of the pack's home range, indicated that the pack may have been present on 19 October. The last radio-location for the 1977 summer season, however, was made on 10 October. A radio-tracking flight over this area on 28 November 1977 disclosed that the pack was not present and had apparently abandoned its summer range.

During winter 1977-78 the Iligluruk pack was located 10 times (PDLs) for a total of 27 individual locations from 2 December 1977 to 19 April 1978 in the lower Noatak River drainage (Figure 1). The pack was not located between 3
January and 6 April 1978, although 2 flights were made in March. Mountainous terrain may have prevented the reception of the radio-collar signals.

From 22 April to 14 October 1978, Iligluruk pack members were located 313 times (63 PDLs) in approximately the same summer home range used during 1977 (Appendix 1). A female yearling (NW13) dispersed to the Noatak drainage between 7 and 22 September 1978. She was seen with 2 unidentified wolves on 16 November 1978. She was last observed 5 June 1979 at what appeared to be a den located 85 km south of the den at which she was born in May 1977 (Figure 2).

In the fall, 1978, the Iligluruk pack again migrated south to the Noatak drainage. They were located there 4 times (4 PDLs) from 16 November 1978 to 13 February 1979 for a total of 16 locations of radio-collared wolves.

The pack returned the following spring to the summer range on the upper Kokolik and Utukok Rivers. It was first located 4 May 1979, although tracks in snow were seen 29 April 1979. The pack had been located 15 times (15 PDLs) on its 1979 summer range by 11 July 1979 when the study was terminated.

The movements of adult Iligluruk wolves during summer centered around pups at homesites (den or rendezvous sites). In October 1977 and 1978, after the pups abandoned their homesites, the pack began traveling together. At
this time the pack was located several times outside the area in which it was seen earlier while the pups were relatively immobile. For example, the minimum area (Mohr 1947) of the combined 1977 and 1978 summer season locations was 1854 km$^2$. When the late fall locations were excluded, the area was 1197 km$^2$.

**Anisak pack.**-- The Anisak pack was located 38 times (18 PDLs) from 11 May to 22 September 1977. The pack's 1977 summer range was centered around the Anisak River, a major tributary of the Noatak River (Figure 1). The pack had apparently migrated from the area by the time an unsuccessful attempt was made to locate them 28 November 1977. One of the yearling males (NW1) was killed by a trapper 12 January 1978 on the Alatna River (Figure 2). This location was 170 km to the east of the Anisak den at which NW1$\sigma$ was last seen 14 August 1977. He was apparently alone as no other tracks of wolves were seen at the trap site. Another yearling male (NW2) was killed by a trapper 27 December 1977 (Figure 2) in the Killik River drainage, 213 km east of the Anisak den. He had last been seen with the Anisak pack 22 September 1977. Tracks in snow suggested this wolf may have been associated with other wolves. The movements of NW1$\sigma$ and NW2$\sigma$ may have been dispersals.

The Anisak pack was located on winter range 11 times (PDLs) for 23 individual locations from 2 December 1977 to
20 April 1978, in the lower Noatak and upper Wulik river drainages (Figure 1). The winter locations ranged from 123 to 198 km west of the 1977 den-site. On 1 occasion the Anisak and Iligluruk packs were observed only 4 km apart, with no intervening physiographic barriers. No interactions between the 2 packs were witnessed.

In late April 1978 the Anisak pack returned to the summer range used in 1977. Thirty-two locations (22 PDLs) were made from 22 April to 28 September 1978. A yearling male (NW9) apparently dispersed from the pack during June 1978 and appeared to be alone when killed by a trapper on 29 January 1979 near the Avak River about 224 km northwest of the Anisak den (Figure 2). The alpha female (NW17) died from the stress of live-capture 7 July 1978.

The remaining Anisak wolves apparently did not migrate the following winter. They were located 3 times (3 PDLs), in or near their summer range, 16 November 1978 to 13 February 1979.

An adult male (NW8) and an unidentified wolf were observed 1 June 1979 at the same den-site used in 1977 and 1978. This constituted the only Anisak pack location for summer 1979 because all radio-collars in that pack ceased transmitting.

The minimum area of the combined 1977 and 1978 summer season locations was 2033 km². The Anisak wolves were not located often enough to determine whether or not more ex-
tensive movements occurred during late fall, similar to those of the Iligluruk pack.

Caribou Distribution and Movements

Caribou were far more abundant than other ungulate prey in the study area. Dall sheep (*Ovis dalli*) were present in mountainous habitat surrounding the Noatak River. Moose (*Alces alces*) occurred in and near riparian habitat throughout the study area. Both sheep and moose, however, occurred in relatively low numbers (Chapter 2).

Analysis of scats and aerial observations of wolf-prey interactions (Chapters 2 and 3) verified that both wolf packs were highly dependent on caribou for food during the summers of 1977 and 1978. Moose were preyed upon infrequently and no evidence of predation on Dall sheep was noted. Although winter data were gathered too infrequently to be conclusive, they suggest that caribou were also the most important winter prey, supplemented by occasional predation on moose (Stephenson and James, in press).

Observations made during radio-tracking flights were combined with information from Hemming (1971), Davis and Valkenburg (1979), and J.L. Davis (pers. comm.) to illustrate the annual distribution and movements of the Western Arctic Caribou Herd (Figures 3 and 4). The wolf study area included both winter and summer caribou range as
well as traditional spring and fall caribou migration routes. Caribou were present in the Iligluruk and Anisak summer home ranges beginning with the spring migration in May and ending with the fall migration in October, 1977 and 1978 (Chapter 3). Few, if any, caribou were present in the Iligluruk summer range from mid-October to late April. The Anisak summer range was not surveyed during winter 1977-78, but small scattered bands of caribou were in the area from October 1978 to at least January 1979.

Several hundred to a few thousand caribou traditionally overwinter in the lower Noatak and Wulik River drainages (Lent 1966:481, Skoog 1968, J.L. Davis, pers. comm.). This distribution pattern was apparent during 1977-78 and 1978-79 (Alaska Department of Fish and Game files, Fairbanks). Occasionally, a majority of the herd winters in this area (Kelly 1954). On 25 of 28 winter PDLs the Iligluruk and Anisak packs were associated with live or dead caribou.

DISCUSSION

Migration.-- The migrations of the Iligluruk and Anisak wolf packs were not monitored while in progress, so the routes taken and time spent traveling were not precisely
documented. The distances between summer and winter ranges were less than those described by Kelsall (1968) and Kuyt (1972) in Canada. Theoretically, the distances which the Iligluruk and Anisak wolves migrated could have been covered in 24 hours with suitable snow conditions (Mech 1970:159). The 1978 spring migration of the Iligluruk pack required no more than 3 days. The Anisak pack returned to its summer range in no more than 7 days. The east-west oriented Noatak River valley is the logical, although not the only, migration route which the Anisak wolves could have used. The last winter location, 19 April 1978, and the last summer location, 10 October 1978, of the Iligluruk pack were both in a north-south oriented mountain pass formed by the Kokolik and Kelly River drainages. This pass may have been the migration route between the summer and winter ranges. The propensity of wolves to follow well-defined and easily-traveled paths (Mech 1970:156) enhances the likelihood that wolves use traditional migratory routes. The results of the present study were inconclusive on this point.

The Iligluruk pack arrived on its summer range in April 1978 approximately 3 weeks before the alpha female (NW7) gave birth. Circumstantial evidence suggested that they also arrived during late April in both 1977 and 1979. In all 3 instances the near absence of caribou on the pack's summer range in late April suggested that the pack's
arrival preceded, by a few days, the spring migration of caribou. Similarly, Clark (1971:70) observed tundra wolves in Canada that returned to prospective den-sites in spring approximately 3 weeks before whelping and approximately 2 weeks before caribou arrived. These observations support Kelsall's (1968:249) statement that migratory packs may be motivated by the ensuing whelping season to return directly to den-sites even if it requires moving ahead of the spring caribou migration.

The fall migrations of the Iligluruk and Anisak packs occurred during October and November which was about the same time that caribou migrated out of the summer ranges. One exception occurred during fall 1978 when the Anisak pack failed to leave its summer range. Scattered small groups of caribou were present in this area until at least January 1979. Presence or absence of caribou in the Anisak summer range during winter 1977-78 was not determined. Therefore a comparison of caribou distribution between the two winters was impossible. Another complicating factor in the assessment of Anisak pack movements in fall 1978 was the death of the alpha female (NW17) in July 1978. This may have altered pack migration behavior because alpha female wolves may play an important role in determining pack movements (Peterson 1977:72). I am not able to explain conclusively why the Anisak pack remained in and near its summer range during winter 1978-79.
The wide-ranging fall movements of the Iligluruk pack within its summer range coincided with the pups' increasing ability to travel. Concurrently, the number of caribou in the area was decreasing as a result of their southward migration. The pack roamed more widely probably because of increased pup mobility and because it was necessary to search extensively for caribou that were widely-scattered and decreasing in number. It appeared that the distance traveled by the pack during these wide-ranging fall movements on the summer home range was at least equal to the distance which they later traveled to reach their winter range. This suggests that the pack was reluctant to abandon its summer home range so long as prey were available. The eventual inability to obtain prey probably caused the fall migration of the pack.

Home range fidelity.-- Both the Iligluruk and Anisak packs demonstrated a high degree of fidelity to their respective seasonal home ranges. Fidelity of a migratory wolf pack to its summer and/or winter range is in contrast to the fortuitous circumstance of a pack spending summer or winter in whatever locality it happens to be as a result of following migratory caribou. Kelsall (1968:249) reported that during spring and fall wolves sometimes underwent lengthy migrations along routes not used by caribou. Such movements could have resulted from wolves orienting toward a par-
ticular destination (Mech 1970:151, Peters 1979:130) such as a previously used summer or winter home range. Crisler (1956:339) speculated and Kelsall (1968:248) implied that although tundra wolf packs followed caribou in winter, each pack probably migrated back to its traditional denning area every spring.

Clark (1971:64) noted that active wolf dens in his study area were located near traditional migration routes of caribou. He suggested that if packs attempted to raise pups elsewhere, lowered productivity would result. Kuyt's (1972) data indicated that wolf packs experienced less pup mortality in regions where caribou were most abundant. Kelsall (1968:250) and Parker (1972:81) stated that most migratory wolves den in areas where caribou are most likely to be found or, at least, are most likely to be absent for the shortest amount of time during the denning season. It seems logical to assume that if a den and the surrounding summer home range are optimally located relative to traditional caribou movements, it should be advantageous for a pack to reoccupy the site every year (Kelsall 1968:248). Additionally, wolves apparently depend on and benefit from familiarity with topography and other features of their home range or territory (Peters 1979). A wolf pack, therefore, that migrates back to the same summer range avoids having to familiarize itself with a new area.

The explanation of fidelity to winter home range by
the Iligluruk and Anisak packs remains speculative, in part, because the fall wolf migrations were not monitored while in progress. It is possible that the presence of both packs in the lower Noatak region during winter 1977-78 and the Iligluruk pack's presence there during winter 1978-79 resulted from either searching randomly for prey or following migrating caribou or tracks of migrating caribou. Alternatively, it may be that both packs returned to a familiar geographic area in which they had experienced past hunting success. The presence of caribou as well as moose during winter in the lower Noatak area is a relatively consistent ecological feature which makes the latter explanation plausible. Also, familiarity of wolves with their winter range could be just as important as familiarity with their summer range.

**Territory.**—Wolf packs occupy relatively stable territories in areas where prey is available throughout the year (Mech 1972, 1973, Van Ballenberghe et al. 1975). Whether or not territories exist on migratory wolf range has not been determined. Clark (1971:113), however, witnessed aggressive encounters among tundra wolves near densites which suggested territorial behavior on Baffin Island during summer. Observations of concentrations and movements of wolves during winter (Kuyt 1972, Parker 1973, and others) suggest that territorialism either does not exist
during winter or is highly modified.

Territorial behavior of wolves includes active defense (Mech 1977), scent-marking (Peters and Mech 1975, Peterson 1977:88) howling (Harrington and Mech 1979), and cognitive mapping (Peters 1979). Opportunities to observe territorial behavior during the present study were severely handicapped. First, the probability of Iligluruk or Anisak wolves encountering other wolves or their sign was slight because of the very low density of wolves in the region (Stephenson 1979). Second, logistic constraints on airplane use rarely allowed prolonged aerial observation of wolf activities.

No inter-pack encounters were witnessed during this study. Scent-marking and howling by the Iligluruk and Anisak wolves were not observed in situations that necessarily suggested territory maintenance as a stimulus. It is noteworthy, however, that neither excessive distance nor significantly lower prey densities seemed to explain why the Iligluruk wolves did not use areas adjacent to their summer home range. Possibly, this reflected the presence of adjacent packs, or simply that prey availability near the den precluded the need to wander further. It is also possible that the Iligluruk wolves were reluctant to travel outside of familiar range, which could have been a mechanism of territory maintenance (Peters 1979:141). I conclude that none of the observations were inconsistent
with the existence of territorialism.

**Dispersal.**—The only known dispersal from the Iligluruk pack was that of NW139. It is probable that the long distance movements of Anisak wolves NW1♂, NW2♂, and NW9♂ were also dispersals. The straight-line distance between the respective den-sites and the final locations of these wolves varied from 85 to 224 km. These were well within the dispersal distance of 670 km documented by Van Camp and Gluckie (1979).

The late summer and early fall eastward dispersals of yearling males NW1 and NW2 did not conform to any recognized pattern of caribou migration. But neither of these wolves were observed while dispersing so it was possible that they followed errant bands of caribou. The central Brooks Range area in which the wolves were killed is probably used by both resident and migratory wolf packs (Stephenson and Johnson 1973). Caribou, moose, and Dall sheep inhabit this area (Alaska Department of Fish and Game 1973).

NW9♂, a yearling, dispersed northward in the same general direction as caribou migrating toward their calving grounds. Kuyt (1972) and Miller and Broughton (1974) presented evidence which suggested that most wolves seen with migrating caribou on and near the calving grounds were transient non-breeders as was NW9♂. The dispersal of this
wolf towards the calving grounds, however, was during late June and early July which was after the peak of the caribou calving period in early to mid-June. It is doubtful, therefore, that NW9 was ever closely associated with the main part of the caribou migration. He could have, however, followed and preyed upon remnants of the main movement. A fortuitous coincidence between the direction of dispersal by NW9 and the direction of caribou migration cannot be ruled out.

The dispersal and subsequent behavior of NW13 provided an interesting contrast to the migratory behavior of the Iligluruk pack from which she dispersed. This wolf did not migrate northward in the spring of 1979. Instead, the den at which she was seen during May and June 1979 was near the area used as winter range by the Iligluruk and Anisak packs. Possibly NW13 was attempting to adapt to a resident home range or territory as opposed to a seasonal home range. The outcome of this effort was not determined. This suggests that wolves which disperse from migratory packs do not necessarily continue the pattern of seasonal travels between summer and winter ranges. Wolves that do not disperse, however, may provide the continuity that insures perpetuation of migratory behavior.
SUMMER FOOD HABITS OF TWO WOLF PACKS ON BARREN-GROUND CARIBOU RANGE IN NORTHWEST ALASKA

Wolf packs generally travel more widely in winter than in summer when their activities are centered around pups at homesites (Mech 1970:149, Fuller and Keith 1980). This seasonal dichotomy of movement patterns can be subtle in areas where the constant availability of prey such as white-tail deer (*Odocoileus virginianus*) allows the existence of stable wolf pack territories (Mech 1977). In comparison, relatively long distances may separate the winter and summer ranges of wolf packs that prey on migratory barren-ground caribou. These wolves may migrate up to several hundred kilometers in response to movements of caribou (Banfield 1954:44, Kelly 1954, Kelsall 1968:248, Kuyt 1972, Parker 1973). Non-breeding tundra wolves that do not belong to breeding packs may sometimes follow and prey upon migrating caribou even during summer (Kuyt 1972, Miller and Broughton 1974). Breeding packs, however, cannot travel freely during summer because pups lack the necessary mobility. As a result these packs may become temporarily separated from caribou during summer and may
have to shift their diet from predominately caribou to other foods.

In recognition of the above situation, Banfield (1954:47) implied that small, non-ungulate prey could be critically important in the summer diet of wolf packs denning on barren-ground caribou range. Pimlott (1967), however, felt that caribou would continue to be an obligatory source of food during summer even though small prey may be frequently eaten. Pimlott suggested that wolves may commonly prey upon caribou stragglers as defined by Murie (1944:54) in the absence of large numbers of caribou and that the inability to do so would probably be an important limiting factor on wolf numbers. Implicit in Pimlott's argument was the assumption that other species of ungulate prey were unavailable.

The results of summer food habits studies of wolves on barren-ground caribou range support Pimlott's (1967:276) contention that caribou or other ungulates are the primary source of food for wolves in summer as well as in winter (Banfield 1954:51, Clark 1971, Kuyt 1972, Stephenson 1975, Haber 1977, Ballard et al. 1981). Kuyt's (1972:19) data, for instance, demonstrated a wide variety of small prey remains in wolf scats collected in the Northwest Territories. Caribou remains, however, occurred in 80.4% (n=240) of the scats from a portion of the study area where caribou appeared to be nearly absent. The results of
Tener's (1952) study on Ellesmere Island appeared to be an exception. His analysis of scats suggested that arctic hares (Lepus arcticus) contributed more than muskoxen (Ovibos moschatus) to the diet of wolves. This conclusion probably is not valid in view of the findings of Floyd et al. (1978) which demonstrated that frequency of occurrence data in wolf scats do not accurately represent the importance of prey species that differ significantly in size.

The purpose of this portion of the study was to determine if 2 migratory wolf packs in northwest Alaska depended primarily on caribou for food during the denning and pup-rearing summer season in 1977 and 1978; and to determine to what degree wolves used small non-ungulate prey as an alternate source of food.

METHODS

Food Habits

Wolf scats were collected at abandoned summer homesites of the Iligluruk and Anisak wolf packs in 1977 and 1978. The scats were autoclaved, and the maximum diameter of each was recorded. The contents of the dried scats were separated by hand. The remains of prey items in
scats were identified by comparing them to reference specimens collected from the study area or stored in the University of Alaska Museum. Hairs were prepared for microscopic identification of scale pattern (Williamson 1951, Weingart 1973) and medulla pattern (Hausman 1920, Day 1966). These patterns were compared to photomicrographs published by Adorjan and Kolenosky (1969) and Moore et al. (1974). Photomicrographs (400x) of hair from Dall sheep, arctic marmot (Marmota broweri), and arctic ground squirrel (Spermophilus parryi) were prepared during the present study to supplement the above publications. Hairs from caribou or moose up to 2-3 months of age were distinguishable from the hairs of older animals (Peterson 1955:77, Skoog 1968:65). In this chapter, therefore, the term "adult" refers to caribou or moose older than 2-3 months unless specified otherwise.

Frequency of occurrence (FQ) was the absolute number of scats in which the remains of a prey item occurred. Percent frequency of occurrence was the relative number of scats in which the remains of a prey item occurred. The relative volumetric proportion of prey item remains in each scat was visually estimated to the nearest 0.25. When a prey item occurred in a trace amount (substantially less than 0.25) an arbitrary value of 0.05 was assigned. The total of all estimated proportions of a prey item was called the relative estimated bulk (REB) (Lockie 1959).
Statistical analysis of food habits was based on FQ data. Despite shortcomings, I believe that FQ provides useful information about the feeding patterns of wolves. However, biases of FQ have been well documented by Floyd et al. (1978). The equation which these authors developed was therefore used to estimate the actual proportions of the 3 most important prey species consumed by the Illgluruk and Anisak packs.

Statistical comparisons of food habits were based on FQ of 2 general categories of prey, ungulates and small mammals. Additional statistical comparisons were based on the FQ of selected prey species. Chi square values (DF=1) with Yates correction for continuity were derived from 2x2 contingency tables (Zar 1974:62). Statistical significance was at the 5% level.

Analysis of adult and pup wolf diets was based on the contents of scats with maximum diameters ≥26 mm and 13-19 mm, respectively (Peterson 1974:37, Weaver and Fritts 1979). Analysis of pack diets included all sizes of scats including 20-25mm.

Distribution and Relative Abundance of Prey

Descriptions of distribution and relative abundance of the most important prey in the study area during the summer period of May - October were based on observations made
during radio-tracking flights and during ground work. Prey population surveys were not attempted, but the open and sparsely vegetated terrain made it possible to gain a reasonable subjective impression of general prey abundance. Personnel associated with other wildlife studies that were conducted previous to or concurrent with the present study provided additional information about prey abundance and distribution.

RESULTS

Distribution and Relative Abundance of Prey

The Iligluruk and Anisak wolf pack summer home ranges and the summer range of the Western Arctic Caribou Herd in Alaska are illustrated in Figure 3. The following descriptions of caribou distribution and abundance as well as that of other prey refer to the Iligluruk and Anisak pack's summer home ranges and/or adjacent areas during the 1977 and 1978 summer periods of approximately May – October. Differences between years are noted.

Ungulates in the Iligluruk pack summer range.-- Caribou were abundant in the Iligluruk home range from about 20 May 1977 and early May 1978 until early July. This period
encompassed the northward spring migration, the post-calving migration, and the eastward post-calving shift (Lent 1966, Hemming 1971, Davis and Valkenburg 1979). These movements through the Iligluruk range involved thousands of caribou, although the post-calving movements generally consisted of fewer, larger, and more compact groups than did the spring migration. Periodically throughout the summer, and especially from mid-July to mid-August, caribou were scarce, and the few that were present were widely distributed and often alone. The beginning of the southward fall migration resulted in a gradual increase in numbers of caribou, singles as well as small groups, during the latter half of August. They were moderately abundant as they continued to move through in September. By October caribou were nearly absent.

Very few moose were seen in the Iligluruk summer range. Only about 15 were observed in or near stands of riparian willows along the Utukok and Kokolik rivers (Figure 1) during the summer period, 1977. Only 2 were recorded during an aerial survey of the Utukok River in April 1977 (Coady 1979:4). These observations encompassed the Iligluruk home range and considerably more area as well. Sightings of moose in 1978 suggested similar abundance.

Approximately 500 Dall sheep were present in the De Long Mountains between the headwaters of the Wulik and
Nimiuktuk rivers (Heimer 1979) (Figure 1). Iligluruk wolves were never located in mountainous areas inhabited by sheep except during dispersal or migration.

Ungulates in the Anisak pack summer range.—Caribou were abundant in the Anisak home range during the northward spring migration from about 10 May to mid-June 1977, and from late April to early June 1978. Thousands of caribou moved through, sometimes in single-file columns and at other times in discrete groups. From early or mid-June until September, there were usually fewer caribou in the Anisak home range than were observed in the Iligluruk home range. For instance, 12 caribou were counted on 8 July 1978 during a census of an area of approximately 2500 km² (Davis et al. 1979) which included the eastern two-thirds of the Anisak home range. However, observations made during telemetry flights suggested that caribou abundance during mid-summer was not always this low. Small groups of caribou observed in the De Long Mountains along the northern edge of the Anisak home range in mid-September were the first indication of the 1977 fall migration. On 22 September, trails in snow indicated that thousands of caribou had migrated south; most had passed through the area between the southeastern portion of the Anisak home range and Howard Pass (Figure 1). The timing of the 1978 fall migration was not documented, but observations through
the end of August indicated the beginning of a pattern similar to the year before.

Moose were commonly observed in or near riparian willow habitat in the Anisak home range. For instance, 6 moose were seen within 1 km of the Anisak pack's den in September, 1977. However, the greatest number of moose seen along the upper half of the Anisak River during any one flight was never more than 8. The portion of the Noatak drainage between the Nimiuktuk River and Howard Pass supported 300-400 moose (D.A. Johnson, pers. comm.). Presumably no more than 100-150 moose were present in the entire Anisak drainage because this area included only one fourth to one third of the Noatak area referred to above. Furthermore, an unknown proportion of the moose in the Anisak valley were probably unavailable to the Anisak pack because these wolves did not use the entire drainage. The Anisak wolves occasionally used the Nimiuktuk drainage; 5 radio-locations (1977-78) were obtained from that area. This drainage supported as many as 300-400 additional moose (D.A. Johnson, pers. comm.).

Approximately 150 Dall sheep were present in the De Long Mountains between the headwaters of the Nimiuktuk River and Papik Mountain, near Howard Pass (Heimer 1979). The northern extent of the Anisak home range roughly coincided with these mountains. Anisak wolves were radio-located in sheep range on 4 occasions.
Non-ungulate prey.—Arctic ground squirrels and ptarmigan (Lagopus spp.) were far more conspicuous in the Iligluruk home range than in the Anisak home range. Ground squirrels were abundant in elevated, well-drained sites in the Iligluruk home range, especially on the river bluffs that are common in the area. Ground squirrel activity within a few meters of Iligluruk wolves at homesites was noted several times. Ground squirrels readily took over wolf dens within 1 or 2 days after the dens were abandoned. The Anisak den was situated within 300 m of, but not in, habitat suitable for ground squirrels, hence none were observed at the den. But even in suitable habitat up to 3 km from the den few ground squirrels were observed. Ptarmigan that were observed in the Iligluruk and Anisak home ranges were usually associated with riparian willow habitat. Flocks of well over 100 birds were commonly seen in spring and fall in the Iligluruk home range, but no large flocks were observed in the Anisak home range.

Microtine populations were probably low to moderate judging by the relative inconspicuousness of their sign at all sites examined, including areas around wolf homesites. The only exception noted was a high population of Microtus miurus on the Utukok River in the immediate vicinity of the base camp from which this study was conducted.

Snowshoe hares (Lepus americanus) or signs of their activity were not observed in the Iligluruk range. Hares
were present in the Anisak range in apparently very low numbers. More sighting of hares in 1978 than in 1977 suggested that the hare population was increasing.

Food Habits

The contents of wolf scats collected at Iligluruk and Anisak homesites were assumed to reflect wolf diets from approximately May through August, 1977 and 1978. The chronology of the Iligluruk pack’s use of homesites in 1977 and 1978 was such that the scats collected from these sites reflected early (mid-May to mid-July) and late (mid-July to mid-August) summer diets. The 1977 and 1978 Anisak scat collections were from a single den site and represented the food habits from mid-May to late August (1978) or early September (1977). The early summer 1977 Iligluruk and the 1977 Anisak scat collections probably included scats from at least 1 previous summer because both densites appeared to have been used before. Relatively large numbers of scats and other prey remains were present as was herbaceous vegetation growing on soil excavated from burrows.

Identifiable prey items were detected in 920 of 1023 scats. The 103 scats which contained only unidentified material appeared to consist of residues resulting from the digestion of soft tissues, probably from ungulates (Kuyt 1969:59). These were not included in the analysis. Also not included in the analysis were 2 categories of items
which did not appear to represent food. First, trace amounts of wolf hair in scats were probably the result of grooming activities. Second, numerous occurrences of rough vegetation such as sedges, grasses, and small twigs were probably accidentally ingested. There was no evidence of feeding on berries.

Prey items identified included: caribou, adult and calf; moose, adult and calf; arctic ground squirrel; microtine/shrew (no attempt to separate the 2 orders) which were not identified to species; snowshoe hare and ptarmigan (*Lagopus spp.*). Additional categories which were not identified to species included adult ungulate, carnivore, rodent, bird, fish, arthropod, mollusc, and eggshell.

Shown in Table 3 are the FQ and REB data of the above prey categories. Table 4 shows the estimated proportions of biomass and the estimated number of individuals of the 3 most frequently consumed prey species, calculated according to the method of Floyd et al. (1978).

Analysis of ungulate species in the wolves' diet was difficult because adult ungulate hairs in a majority of scats could not be identified to species. The scats containing unidentified adult ungulate hairs characteristically consisted of fragmented hairs or whole hairs usually less than 2 cm in length dispersed throughout the residues of digested soft tissues. In a majority of these cases, and in other instances as well, the scale and medul-
la patterns of the hairs did not resemble those depicted in the photomicrographs (see Methods). The unidentified hairs may have been from the early summer pelage, or from the winter pelage found on the extremities of the animals. Attempts to distinguish between these 2 categories of hair in known caribou and moose samples in the laboratory were unsuccessful.

Exclusion of the unidentified adult ungulate FQ and REB data from subsequent analyses, however, would have resulted in a substantial underestimation of the importance of adult ungulates in the diet of the study wolves. Therefore, the unidentified adult ungulate category was combined with adult caribou. This seemed justifiable on the basis that moose constituted a very small proportion of the identified remains in scats. This procedure probably resulted in an underestimation of the occurrence of adult moose but I believe this error is relatively small.

A mistake made in the laboratory prevented the differentiation of the proportions of unidentified adult ungulate, adult caribou, and calf caribou in the 1977 Anisak scat collection (N=284). Subsequent analyses of the Anisak pack's food habits data were therefore based on the proportions of adult ungulate, adult caribou, and calf caribou remains in the 1978 scat collection (N=85) which was respectively, 70:12:3 for FQ and 68.4:11.9:3.0 for REB.

Although the above subjective methodology probably in-
roduced error into some of the results, I feel that the estimated ungulate species FQ and REB presented a more realistic picture of Iligluruk and Anisak pack diets than would otherwise have resulted. Furthermore, the above procedures did not affect the analyses based on the 2 general categories of ungulate and small mammal FQ.

**General characteristics of the diet.**-- The data in Tables 3 and 4 demonstrate some general aspects of wolf food habits in the study area. Caribou constituted 97 and 96% of the biomass in the Iligluruk and Anisak diets, respectively. In terms of the number of caribou eaten, calves made up 20% of the Iligluruk diet and 6% of the Anisak diet.

Moose constituted only 1 and 4% of the biomass in the Iligluruk and Anisak diets, respectively. The data also indicate that moose calves occurred 2.5 times more frequently than moose adults in terms of number of individuals in the diets of both packs. No evidence of predation on Dall sheep was detected.

The diet of the Iligluruk pack included 3.8 times more individual arctic ground squirrels than individual adult caribou. Biomass of the former, however, was only 3% of the latter. The Anisak pack ate individual adult caribou 3.4 times more often than they ate individual arctic ground squirrels. The biomass of the arctic ground squirrels was only 0.2% of the biomass of caribou adults.
The contributions of the remaining prey categories to the diets of the Iligluruk and Anisak wolves appear to have been much less than the species mentioned above (Table 3).

**Selectivity.**—The FQ data in Table 3 indicate some differences and similarities between feeding patterns of the Iligluruk and Anisak packs. Caribou FQ was not significantly different ($P > 0.05$) between the 2 packs. Calf caribou FQ was significantly higher ($P < 0.001$) in the Iligluruk diet, and adult caribou FQ was significantly higher ($P < 0.001$) in the Anisak diet. Moose FQ appeared to be greater in the Anisak diet, but statistical verification of this was prevented by small sample size. Arctic ground squirrel FQ was significantly higher ($P < 0.001$) in the Iligluruk scat collection. No significant difference ($P > 0.05$) was apparent between the microtine/shREW FQ in the Iligluruk and Anisak diets. Eight occurrences of ptarmigan remains were found in scats from the Iligluruk pack, whereas no ptarmigan remains were found in Anisak scats.

**Ungulate and small mammal comparison.**—Remains of ungulates (caribou and moose) and/or small mammals (arctic ground squirrel and microtine/shrew) were found in 914 of 920 wolf scats. Individually, ungulate and small mammal remains occurred in 855 and 229 scats, respectively (Table 3). The occurrence of remains from other prey was relatively insignificant. The following comparisons were
therefore based on the 2 general categories of ungulates and small mammals as shown in Table 5.

Iligluruk ungulate FQ was not significantly different (P>0.05) from Anisak ungulate FQ in 1977 or 1978. Small mammal remains occurred more frequently (P<0.001) in Iligluruk scats than in Anisak scats in 1978 but not in 1977.

No significant change (P>0.05) was detected in Iligluruk ungulate or small mammal FQ's from early to late summer in either year of the study. However, comparisons involving the Iligluruk late summer 1977 scat collection were difficult to interpret because of the small sample size (n=21). Ungulate FQ in Iligluruk scats decreased significantly (0.01<P<0.025) from 1977 to 1978 and small mammal remains increased (P<0.001). The significant increase in small mammal FQ was also detected (P<0.001) in a comparison between the early summers of 1977 and 1978. No significant difference (P>0.05) in ungulate or small mammal FQ's were apparent between the late summers of 1977 and 1978. Neither ungulate nor small mammal FQ in the Anisak diet changed significantly (P>0.05) from 1977 to 1978.

In 1977 the Iligluruk adult wolf diet included significantly fewer (P<0.001) small mammals than did the pup diet. This difference was also detected in the early summer portion of the 1977 scat collection (P<0.001). No significant difference (P>0.05) was apparent between
Iligluruk adult and pup diets in early or late summer, 1978, despite a decrease \(0.025<P<0.05\) of small mammal FQ in the pup diet from early to late summer of that year. No significant difference \(P>0.05\) was detected between adult and pup diets in the Anisak pack in 1977 or 1978.

It was stated above that the Iligluruk pack diet included more small mammals in 1978 than in 1977. This was strongly reflected by a significant increase \(P<0.001\) of small mammal FQ in the adult diet from 1977 to 1978. This increase was also detected \(P<0.001\) in a comparison between adult scats from early summer 1977 and 1978, but not \(P>0.05\) in the late summer diets. However, interpretive limitations resulting from the small sample size of the Iligluruk late summer 1977 scat collection were previously mentioned. Ungulate FQ in adult scats was significantly less \(0.025<P<0.05\) in early summer 1978 than in early summer 1977. From 1977 to 1978 there was no significant change \(P>0.05\) in small mammal or ungulate FQ in the pup diet.

DISCUSSION

Selectivity

Species selectivity.-- Availability (prey density) and vul-
nerability (ease of capture) of prey are 2 of the major factors which affect the selectivity of wolf predation on different prey species (Mech 1970:172). Examples of this are presented in studies reviewed by Mech (1970) and Frenzel (1974). More recent studies with findings on this subject were reported by Peterson (1974), Quimby (1974:12), Carbyn (1975), Stephenson (1975), Voigt et al. (1976), Haber (1977), Theberge and Cottrell (1977), and Fuller and Keith (1980). Aspects of wolf predation during summer in areas where caribou, moose, and Dall sheep were present were reported by Murie (1944), Rausch (1969), Quimby (1974:12), Stephenson (1975), Haber (1977), Theberge and Cottrell (1977), and Ballard et al. (1981). These studies indicate that wolves generally select for caribou, when there are sufficient numbers available, probably because moose are usually more difficult to kill and Dall sheep usually inhabit terrain which increases their chances for escape.

The summer diets of the Iiligluruk and Anisak wolves appear to have reflected differences in availability and vulnerability of prey species. The marked differences in calf and adult caribou, moose, arctic ground squirrel, and ptarmigan FQ between the scat collections from both packs corresponded with differences in availability of those prey within the packs' respective home ranges. The similarity of microtine/shrew FQ in the Iiligluruk and Anisak diets
also corresponded with field observations of their relative abundance.

A partial explanation of why there was a higher FQ of adult caribou in Anisak scats than in Iligluruk scats may be that the Iligluruk pack's greater reliance on calf caribou substituted for predation that otherwise would have fallen on adult caribou. This probably resulted from the Iligluruk pack's location which was closer to the caribou calving grounds than was the Anisak pack. Additionally, most of the caribou remained north of the De Long Mountain divide during post-calving movements which further enhanced the opportunity for the Iligluruk wolves to prey on calves.

The amount of moose in the diet of the Anisak wolves apparently was not enough to markedly reduce the pack's dependence on caribou. The assumption that moose were more formidable and therefore less vulnerable than caribou to wolf predation partially explains why the Anisak wolves selected for the relatively few caribou present during summer.

The lack of Dall sheep in the diet of the study wolves was not surprising. The Iligluruk and Anisak wolves were rarely located in areas frequented by Dall sheep. Furthermore, Dall sheep were scarce in the few areas of the mountains where the Iligluruk or Anisak wolves were observed.

The REB data indicate that 20% and 6% of the number of caribou consumed by the Iligluruk and Anisak packs, respec-
tively, were calves. Caribou on or near the calving grounds in early to mid-June, 1977 and 1978, consisted of 39% calves. During late June, 1977 and early July, calves made up 29% of the caribou in post-calving aggregations in or north of the De Long Mountains (Alaska Department of Fish and Game files, Fairbanks, AK). These figures suggest no disproportionate predation on calves.

Disproportionate predation on calves could have gone undetected, however, for several reasons. The actual proportion of calves among groups of caribou that migrated through the Iligluruk and Anisak home ranges, and among the caribou stragglers was not determined and could have differed from the population-wide figures mentioned above. Also, the scat data represented food habits beginning in mid-May which was at least 3 weeks before the peak of calving and perhaps 4 or more weeks before relatively large numbers of new-born calves were available to the Iligluruk and Anisak packs. Another factor could have been Cumming's (1975:487) time-distance effect: the Iligluruk and Anisak wolves were within hunting distance of caribou herds with relatively large numbers of calves only during the few hours or few days that it took the herd to pass beyond the wolves' home ranges. Hence, even if the study wolves preyed disproportionately on calves, the time available to do so was probably limited.
Ungulates and Small Mammals in the Wolf Diet

Ungulates, predominately caribou, were the dietary mainstay of the Iligluruk and Anisak wolf packs during summers 1977 and 1978. This occurred despite apparently very low ungulate densities during much of both summers. This aspect of the study packs' feeding ecology was similar to that previously documented for wolves on barren-ground caribou range (see Introduction). These results provide additional support for Pimlott's (1967) belief that denning wolves are able to subsist on very low densities of caribou.


If changes occurred in ungulate (caribou and moose) or small mammal (arctic ground squirrel and microtine/shrew) abundance in the Iligluruk home range from 1977 to 1978...
they were not apparent. Furthermore, I estimated (Chapter 3) that the Iligluruk pack consumed enough caribou during the 1978 summer period to provide an adequate level of nutrition, even without the addition of small mammals. No estimation of the Iligluruk pack's consumption of caribou in summer 1977 was available for comparison. However, there was no evidence to suggest that it was radically different, on a caribou/wolf basis, from 1978.

It seemed unlikely that the increased use of small mammals in 1978 resulted from an increased difficulty in providing food for pups. In summer, 1977, 2 Iligluruk adult wolves successfully raised 7 pups. In summer, 1978, the same 2 adults were presumably aided by 5 yearlings (Mech 1970:145) in providing food for only 4 pups (Stephen- son and James, in press). The number of pups was first determined during the first week of June in 1977 and 1978. No mortality of pups occurred thereafter during either summer. Fewer pups in 1978, however, does suggest the possibility of nutritional stress prior to the summer period of that year. No information was available to confirm or deny this.

The Iligluruk pack's increased consumption of small mammals in 1978 may have reflected the food habits of some or all of the 5 yearlings. Murie (1944:56) reported prolonged mouse-hunting activity by wolf pups. Haber (1977:398) noted a tendency of young, inexperienced pack
members to chase small prey while older, experienced wolves showed little or no interest. Observations made by Crisler (1956) and Clark (1971:132) suggested that young wolves were less skilled than older wolves at hunting caribou. The above observations suggest a plausible basis for expecting a significant degree of small mammal hunting by yearling wolves. During the present study, however, the Iligluruk yearling wolves, apparently unaided by adult wolves, were successful in capturing caribou (Stephenson and James, in press). This suggests that the yearlings were not forced to prey on small mammals because of the inability to capture larger prey.

If a difference in hunting behavior did exist between the adult and yearling wolves, as hypothesized above, factors other than age and experience could have been involved. Sullivan's (1979) study with captive wolves, and the work of others that he reviewed, indicated that a wide variety of hunting behaviors exist among wolves, and that differences in hunting behavior are not easily explained by any one parameter.

The increased use of small mammals in 1978 may have contributed to the nutritional well-being of the Iligluruk pack. It seems doubtful, however, that small mammals were critical for the pack's survival or the pack's ability to successfully raise pups. Byman (1972:60) felt that the availability of small rodents determined their use by
wolves in Minnesota, and he felt that predation on small rodents probably did not decrease predation on larger mammals. Clark (1971:187) reached a similar conclusion while studying wolves on Baffin Island. A similar situation probably existed for the Iligluruk pack. Arctic ground squirrels were abundant along riparian travel routes which the Iligluruk wolves often used. Any of the pack members with a predilection for small mammals probably could have preyed upon them quickly and efficiently, in a manner which need not have detracted from the hunting of caribou.
A WOLF PACK'S RATE OF PREDATION ON BARREN-GROUND CARIBOU DURING SUMMER

Several authors have estimated predation rates of wolves on barren-ground caribou, largely on the basis of indirect evidence. Clarke (1940:109) suggested a winter predation rate of 1.6 caribou/wolf/month. Kelsall (1957:54, 1960:74, 75, 1968:260) surmised annual rates varying from 0.3-1.2 caribou/wolf/month. He also reported an annual rate of 2.5 caribou/wolf/month, suggested by J.D. Robertson. Burkholder's (1959) data indicated a winter predation rate of approximately 1.1 caribou/wolf/month by a wolf pack that also preyed on moose. Skoog (1968:629) assumed a rate of 1.0 caribou/wolf/month, excluding calves, but including some predation on moose. Kuyt (1972:32) used feeding requirements of captive wolves and field observations to estimate that wild wolves accounted for 1.9 caribou/wolf/month. Parker (1972:84) and Smith (1980) calculated 1.1 and 2.3 caribou/wolf/month, respectively. Holleman and Stephenson (1981) used the fallout radiocesium method to estimate a winter predation rate equal to 2.2-2.5 caribou/wolf/month.
Some researchers assumed that caribou were much less available to denning wolf packs in summer than to nomadic wolf packs in winter because the former were unable to follow migrating caribou (Clarke 1940, Banfield 1954, Kelsall 1968, Kuyt 1972, and Parker 1972). These authors assumed a substantially lower predation rate on caribou by wolves during summer as compared to winter. Kuyt (1972) presented strong evidence, based on analysis of scats, evaluation of productivity, and consideration of other observations, that these assumptions were justified. However, no reported study has documented either the summer or winter rate of predation on caribou by wolves. The purpose of this portion of the study was to estimate the summer predation rate of a denning wolf pack on barren-ground caribou.

METHODS

Members of the Ili'gluruk wolf pack were radio-collared and monitored by means of aerial telemetry during a study of wolves in the National Petroleum Reserve in Alaska (Chapters 1 and 2, Stephenson 1979, Stephenson and James, in press). The Ili'gluruk pack depended mainly on caribou for food (Chapter 2). The pack migrated between summer and winter ranges in response to migration of caribou in
northwest Alaska (Chapter 1). In 1978 this pack occupied its apparent traditional summer home range on the upper Utukok and Kokolik River drainages (Figure 1) from approximately 20 April - 13 October.

Caribou that the Iligluruk wolves killed during 11-21 May, 10-18 August, and 28 September - 4 October, 1978 (27 days total) were located during radio-tracking flights. Caribou were abundant during the first period but scarce during the latter 2 periods. The estimation of kill rate was calculated with data obtained from all 3 periods. The estimation formula was

$$ r = \frac{\sum_{i=1}^{3} (Y_i - 1)}{\sum_{i=1}^{3} X_i} $$

with $r$ = daily predation rate (caribou/day), $Y_i$ = number of caribou killed in the $i$th observation period, and $X_i$ = elapsed time from the first to the last kill in the $i$th observation period. The first kill in each sample period was excluded from the above calculation because the first kill was also the last kill of the preceding, but unselected, sample period; hence $(Y_i - 1)$. The death of the first and last caribou in each sample period was not actually observed except for the first kill in the first period. The times of death, therefore, were estimated on the basis of how much of the caribou carcass had been consumed, the distance of the wolf from its last location, and the elapsed time since the last location. The daily preda-
tion rate was extrapolated to the entire 1978 summer period of 177 days to estimate the total number of caribou that the Iligluruk pack fed upon. The above calculation and calculation of the variance of the estimate followed procedures recommended by Cochran (1977:150) and S.J. Harbo (pers. comm.). Confidence limits were expressed at the 95% level.

Known and probable kills were recorded during the 3 observation periods. Known kills were caribou that appeared to have been recently killed and at which at least 1 Iligluruk wolf was observed. The presence of blood and distinctly red muscle tissue was assumed to indicate a recent kill. Probable kills were inferred from circumstantial evidence such as a wolf with blood on its pelage and carrying in its mouth an identifiable portion of a caribou.

The estimated predation rate was also used to estimate the edible weight of caribou which the Iligluruk wolves ingested. Kills were classified as mature bulls, mature cows, adults (either sex and any age except calves), or calves. Average weights were assigned using data presented by Skoog (1968:18,25). I assumed that 61% of the average weight of a kill was available for consumption by wolves; based on information presented by Luick (1970:24) and Kuyt (1972:32), and based on my observations in the field.
RESULTS

During the 1978 summer period of 20 April - 13 October the Iligluruk pack consisted of 2 adults (NW6♂, NW7♀), 5 yearlings (NW11♂, NW12♂, NW13♀, NW14♂, NW15♂), and 4 pups born between 13-20 May. Radio collars were on the 2 adults and 1 yearling (NW11♂) during the May observation period. NW11♂ was constantly associated with 2 other yearlings during this period so that, in effect, 5 of the pack members were monitored. All 5 yearlings in addition to the 2 adults wore radio-collars during the 2 subsequent observation periods. NW13♀ was no longer a pack member during the last observation period because she had dispersed. It was important to monitor as many pack members as possible because they frequently hunted alone or with only 1 or 2 other pack-mates in areas widely scattered throughout the Iligluruk summer home range (Stephenson 1979, Stephenson and James, in press).

The number of wolves in the Iligluruk pack equated to approximately 1628 wolf-days during the 1978 summer period. This number was derived from the presence of 7 adult and yearling wolves from 20 April - 12 September (146 days); 6 adult and yearling wolves from 13 September - 13 October (31 days); and 4 weaned pups from 1 July - 13 October (105 days).
Forty-two radio-tracking flights totaling approximately 49 hours were conducted during the 27 days of the 3 observation periods. At least 1 flight occurred every day except 17 May 1978. Radio-collared Iligluruk wolves were located 217 times and were actually observed on 204 occasions. The 13 instances of no observation resulted from 8 locations of the alpha female (NW7) in the natal den and 5 locations of wolves apparently sleeping or resting (steady radio-signal) in stands of willow (Salix spp.) approximately 1 m high.

Fourteen known and 3 probable kills were recorded. Excluded from the analysis were 2 additional observations. The first instance was in May when a wolf was seen carrying a lower leg from a caribou but was not recorded as a probable kill because no blood was seen on either the leg or the wolf's pelage. The second instance was in August when a wolf was seen feeding on the remains of a caribou which apparently died before the observation period began.

The estimated number of kills which the Iligluruk pack made during the 1978 summer period was 136 (94-178 C.I.=95%) (Table 6). The estimated summer predation rate on caribou by the Iligluruk wolves was 2.5 (1.8-3.3 C.I.=95%) caribou/wolf/month (Table 7). Table 8 shows the age and sex categories of caribou kills and the assumed average weight of each category. These data were used to determine a weighted average for all kills. The resulting
estimated weight of caribou available for consumption by each Iligluruk wolf was 4.7 (3.2-6.1, C.I.=95%) kg caribou/wolf/day (Table 9).

DISCUSSION

The predation rate estimate was subject to 2 major biases. First, the predation rate might have been underestimated. It was unlikely that all caribou which the Iligluruk wolves fed upon were located because some pack members wore no radio-collars during the first observation period. Also, wolves were observed during all 3 observation periods for only 1-15 minutes for each location. This resulted in a considerable amount of time during which the wolves' activity was undocumented. Furthermore, relatively small prey were perhaps less likely than larger prey to be detected, resulting in calves being under-represented in the sample. As an extreme example, scat analysis indicated that the Iligluruk wolves consumed approximately 3 times more individual arctic ground squirrels than caribou (Chapter 2), yet wolves were never observed feeding on squirrels during 2 summers of study.

The second major bias may have resulted in overestimation of the predation rate because of the inability
to conclusively distinguish between wolf-killed caribou and scavenged caribou that had recently died. Theoretically, 14 of the known and probable kills for which the circumstances of death were not proven could have been scavenged. However, I consider that improbable because general observations suggested that the amount of caribou carrion available in the study area was insufficient to account for the frequency with which Iligluruk wolves were seen at caribou carcasses. Also, if caribou carrion was plentiful, it would be difficult to explain why the Iligluruk wolves were apparently more successful than grizzly bears (Ursus arctos) at scavenging. Grizzly bears were more abundant than wolves in the study area; 1 bear/43 km² (Reynolds 1979:142) as compared to 1 wolf/109 km² (Chapter 1).

During 1978, 17 marked individual or family groups of bears which occupied home ranges in or adjacent to the Iligluruk pack's summer home range were located at caribou carcasses only 9 times out of 268 telemetry locations (H.V. Reynolds, pers. comm.).

The results of the present study demonstrated that a wolf pack denning on barren-ground caribou range is capable of maintaining a relatively high rate of predation on caribou. The Iligluruk pack's summer predation rate of 2.5 caribou/wolf/month is the same as the annual (all seasons) rate that J.D. Robertson (Kelsall 1960:75) attributed to wolves in Canada. Comparable also is the winter rate of
2.2-2.5 caribou/wolf/month that Holleman and Stephenson (1981) reported for wolves in Alaska; and the annual rate of 1.9 and 2.3 caribou/wolf/month that Kuyt (1972:32) and Smith (1980) calculated for wolves in Canada. The preceding estimates appear to differ substantially from the annual rates of 0.3-1.2 caribou/wolf/month that other authors (Clarke 1940:109, Kelsall 1957:54, 1960:74, 1968:260, Skoog 1968:629, Parker 1972:84) have suggested. However, there is no reason to doubt the existence of widely divergent predation rates on caribou by wolves, given the dynamic nature of caribou distribution and abundance and, in some situations, the presence of alternate prey.

Some aspects, however, of the relatively high rate of predation on caribou by the Iligluruk pack during summer are in disagreement with some of the assumptions and conclusions stated in previous studies. For instance, Clarke (1940:109), Banfield (1954), Kelsall (1968:260), Skoog (1968:629), Kuyt (1972), and Parker (1972:83) assumed or presented evidence that predation on caribou during summer would be less intensive than in winter because most caribou migrated beyond and were absent for varying periods of time from the denning areas to which most wolves were confined. These appeared to be the general circumstances with which the Iligluruk pack contended in summer 1978 but its predation rate on caribou remained relatively high.
An important consideration in the present study, however, was the location of the Iligluruk pack's summer home range in the upper Utukok and Kokolik River drainages. This location may have enhanced the pack's ability to maintain a high rate of predation on caribou. Varying portions of the spring migration (May), post-calving migration (June), post-calving shift (July), summer dispersal (August), and fall migration (September) (Hemming 1971, Davis and Valkenburg 1979) passed through or near the Iligluruk pack's range, with intervals of up to 4-6 weeks between each movement (Chapter 3). The number of caribou that became available to these wolves as a result of any 1 of the movements was not determined, but varied anywhere from several thousand to less than 100. However, regardless of the precise number of caribou involved, it appeared that the Iligluruk pack occupied an area where the potential availability of caribou may have been greater than in other areas of the Western Arctic Caribou Herd summer range. The abundance of caribou also may have been greater than in some of the study areas reported by the authors mentioned above.

Nevertheless, I believe it would be simplistic and misleading to conclude that the Iligluruk pack's high rate of predation on caribou was possible because caribou were abundant. Admittedly, there is a theoretical lower limit below which it would be impossible for wolves to maintain
the predation rate estimated in the present study. However, the theoretical limit may be much lower than is intuitively plausible. In the present study, caribou were abundant during the May observation period, but they were scarce during the August and September - October observation periods. Predation rates on caribou during all 3 periods, however, were all relatively high. The apparent ability of the Iligluruk wolves to effectively prey on a few widely-scattered caribou paralleled the situation which Murie (1944:54) reported in McKinley Park, and provided support for Pimlott's (1967:271) suggestion that this situation may commonly occur on barren-ground caribou range.

Logically, the summer predation rate of the Iligluruk wolves was influenced by their summer food requirements. Unfortunately, studies pertinent to this consideration are inconclusive. Mech's (1970:183) review of summer vs. winter food requirements of wolves indicated that little was known about the subject. Kuyt (1972:31) thought that captive wolves required less food in summer than in winter. Lentfer and Sanders (1973:624) reported increased food consumption in summer by captive wolves. During summer, pack members capable of hunting must feed themselves as well as growing pups which require 2-3 times more food per unit body weight than grown wolves (Mech 1970:183). Perhaps the need to feed growing pups was a major factor in determining
the Iligluruk pack's rate of predation on caribou.

Observations suggested that the relatively high rate of predation on caribou by the Iligluruk pack may also have been necessary to compensate for less efficient utilization of caribou carcasses in summer as compared to winter. Often only 1-3 wolves fed on a caribou at a kill-site during summer. During winter the entire pack normally attended each kill (Stephenson and James, in press). Compared to the entire pack, a single wolf would have consumed less of a carcass in a given time and would perhaps have been less capable of guarding it against scavengers. If the wolf returned with food to the den or rendezvous site, significant portions of the carcass could have been left completely unguarded. Even caching behavior might have resulted in substantial losses to scavengers (Murie 1944:60). Kuyt (1972) also reported less utilization of carcasses in summer than in winter for reasons similar to the above.

The estimated amount of food, 3.2-6.1 kg/wolf/day, fell within the range of 1.4-10.0 kg prey/wolf/day reported in previous studies (Mech 1966:77, Mech et al. 1971:30, Kolenosky 1972:364, Kuyt 1972:32, Haber 1977:424, Mech 1977:70, Peterson 1977:62, Fuller and Keith 1980:593, Holleman and Stephenson, 1981). The Iligluruk wolves apparently ate more than the minimum food requirement of 1.6-1.7 kg/wolf/day that has been estimated for wild wolves
(Mech 1970:183, Kuyt 1972:32). The estimated rate of food consumption for the Iligluruk wolves may be conservative because the wolves also consumed small mammals and a very small amount of moose (Chapter 2). However, this may have been compensated for to some degree by the tendency to over-estimate food consumption because of relatively inefficient utilization of caribou carcasses.

A better understanding of the significance of the rate at which the Iligluruk pack was preying on caribou would require a determination of the characteristics of sex, age, and physical condition of both those caribou which were present in the wolves' summer home range and those caribou which the Iligluruk wolves killed. Although the data gathered during the present study were inadequate to make these determinations, the following observations are submitted: Aerial observations of 29 caribou carcasses, from May 1977 to August 1978, suggested that the Iligluruk wolves did not select for one sex over the other. Examination of 8 caribou carcasses, at which Iligluruk wolves were located, suggested that older caribou were more susceptible to wolf predation than were younger caribou, with the possible exception of calves. Most caribou killed by wolves were in good nutritional condition and lacked any obvious infirmities (Stephenson 1979, Stephenson and James in press, unpublished data).

The assumption that predation on barren-ground caribou
by denning wolves is markedly reduced should be reconsidered. Even when caribou abundance appears to be very low, some denning wolf packs may experience much greater hunting success than is apparent to observers that do not actually document the rate of predation. Undoubtedly, a wide variation in predation rates among denning wolf packs does exist, including packs that experience extremely low success. However, wolf predation on barren-ground caribou during summer may be a substantially higher source of natural mortality to caribou than has been previously thought, even in the absence of large numbers of non-breeding wolves on the calving grounds.
A substantial portion of the wolf population on the range of the Western Arctic Caribou Herd is probably migratory. References to "resident" and "caribou" (transient) wolves by local residents (personal observation); written accounts by Kelly (1954), Crisler (1956), and Stephenson and Johnson (1973:19); and the results of the present study justify the above conclusion. It is imperative that management of wolves reflect this knowledge in order to promote noncontradictory policies and programs. For instance, a wolf control program south of the Brooks Range may be incompatible with a wolf protection program north of the Brooks Range, because the same wolves may occupy each area at different times of the year. The caribou in northwest Alaska are managed as a herd, on an area-wide basis. It may be desirable to use a similar approach for wolves.

Conflicts between the reindeer industry and wolves in northwest Alaska have been documented (for example see Kelly 1954). This industry is now growing and conflicts with wolves may increase. Wolf control programs may be
proposed to protect reindeer herds. Again, killing wolves even in a limited geographic area may affect the wolf population from a much larger area. Killing wolves to protect reindeer should be monitored to determine the impact on the wolf population.

Results of winter aerial surveys of wolves in northwest Alaska should be interpreted cautiously. If a substantial portion of the wolf population is migratory, then wolf densities documented in a given area at a given time may represent a seasonal phenomenon. This theoretically should not prevent an estimation of wolf numbers on caribou range, given the proper survey technique and correct interpretation of the results. In order to do this it would be necessary to experimentally assess the results of a routine wolf aerial survey. A telemetry study on winter range to determine daily and seasonal movements of wolves as well as numbers of wolves would make it possible to determine the degree of reliability of aerial surveys.

The welfare of many wolves in northwest Alaska probably depends on the welfare of the caribou, if it is assumed that the results of this study are applicable to a large segment of the wolf population. A permanent decline of wolf numbers in this area might be expected if they had to depend on moose, Dall sheep, and other prey as a result of a substantial decline in the number of caribou. The
continued maintenance of a viable wolf population appears to be dependent upon maintaining adequate numbers of caribou.

It is not possible, on the basis of this study, to quantify summer wolf predation on the Western Arctic Caribou Herd. The results suggest, however, that some wolf packs denning on caribou summer range maintain a relatively high rate of predation on caribou. Other packs on caribou summer range may den in areas where high rates of predation are not possible because fewer caribou are available. The proportion of the wolf population in northwest Alaska that dens in optimum habitat with respect to the availability of caribou is, therefore, of obvious importance in assessing the amount of wolf predation on caribou. When wolf numbers are high, optimal denning habitat is probably saturated. High numbers of wolves could also result in a large number of non-breeding wolves that could follow caribou herds throughout the summer (Kuyt 1972, Miller and Broughton 1974). Under these conditions, summer wolf predation could result in substantial mortality to caribou, perhaps at a rate equal to or greater than the winter loss to wolves. This consideration may help to refine future attempts at modeling the interactions between wolves and caribou in northwest Alaska.
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Skoog, R.O. 1968. Ecology of the caribou (Rangifer tarandus


Young, S.B. (ed.). 1974. The environment of the Noatak

Figure 1. Summer home ranges and winter locations of the Anisak wolf packs. The summer home range boundaries include data from May 1977 to July 1979.
Figure 2. Dispersals of radio-collared wolves from the Iligluruk and Anisak packs.
CARIBOU CALVING GROUNDS

ILULISSAT SUMMER RANGE

ANISAK SUMMER RANGE

ALASKA

10 0 20 km

Noatak River

Kivalina

Noatak

Kolik

Colville River

Pitregeg River

Tukuk River
Figure 3. The summer home ranges of the Iligluruk and Anisak wolf packs, and the summer range of the Western Arctic Caribou Herd. The caribou distribution shown is an approximation only and is a modified version of that presented by Hemming (1971).
Figure 4. The winter range of the Iliquirrel and Anisak wolf packs, and the winter range of the Western Arctic Caribou Herd. The caribou distribution shown is an approximation only and is a modified version of that presented by Hemming (1971).
TABLE 1. Background data on radio-collared wolves of the Iligluruk and Anisak packs, and the time during which each wolf was monitored.

<table>
<thead>
<tr>
<th>Wolf identification number</th>
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<td></td>
<td></td>
<td>Capture date</td>
<td>Last radio-contact</td>
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<td></td>
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<tr>
<td>NW6♂ alpha</td>
<td>Adult</td>
<td>10 Jun 77</td>
<td>16 Nov 78</td>
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<tr>
<td>NW6♂ recapture</td>
<td></td>
<td>1 Jul 79</td>
<td>11 Jul 79</td>
</tr>
<tr>
<td>NW7♀ alpha</td>
<td>Adult</td>
<td>6 Jul 77</td>
<td>28 Jun 78</td>
</tr>
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<td>NW7♀ recapture</td>
<td></td>
<td>28 Jun 78</td>
<td>11 Jul 79</td>
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<td>NW11♂</td>
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<td>11 Apr 78</td>
<td>16 Nov 78</td>
</tr>
<tr>
<td>NW12♀</td>
<td>10 months</td>
<td>11 Apr 78</td>
<td>19 Apr 78</td>
</tr>
<tr>
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<td></td>
<td>2 Jul 78</td>
<td>13 Feb 79</td>
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<tr>
<td>NW13♀</td>
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<tr>
<td>NW17♀</td>
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<td>8 Jul 78</td>
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Table 2. Number of locations, observations, and pack-day locations of radio-collared wolves in the Iligluruk and Anisak packs, May 1977 to July 1979.

<table>
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<th>Observations</th>
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<td></td>
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<td><strong>Iligluruk pack</strong></td>
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<td>NW6(^\sigma)</td>
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</tr>
<tr>
<td><strong>Total</strong></td>
<td>477</td>
<td>69</td>
</tr>
<tr>
<td><strong>Total pack-day locations</strong></td>
<td>157</td>
<td>28</td>
</tr>
</tbody>
</table>

\(^a\)Late April - early October
\(^b\)Late October - early April
Table 3. Frequency of occurrence (FQ) and relative estimated bulk (REB) of prey remains in scats collected at summer homesites of the Iligluruk and Anisak wolf packs, 1977 and 1978.

<table>
<thead>
<tr>
<th>Food item</th>
<th>Iiligluruk pack</th>
<th>Anisak pack</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FQ</td>
<td>REB</td>
</tr>
<tr>
<td><strong>Ungulate</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unidentified adult ungulate(^a)</td>
<td>294</td>
<td>263.1</td>
</tr>
<tr>
<td>Caribou adult</td>
<td>157</td>
<td>141.1</td>
</tr>
<tr>
<td>Caribou calf</td>
<td>70</td>
<td>63.1</td>
</tr>
<tr>
<td>Moose calf</td>
<td>2</td>
<td>2.0</td>
</tr>
<tr>
<td>Moose adult</td>
<td>1</td>
<td>1.0</td>
</tr>
<tr>
<td><strong>Small mammal</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arctic ground squirrel</td>
<td>124</td>
<td>65.3</td>
</tr>
<tr>
<td>Microtine/shrew</td>
<td>57</td>
<td>10.6</td>
</tr>
<tr>
<td>Unidentified rodent</td>
<td>5</td>
<td>0.3</td>
</tr>
<tr>
<td>Snowshoe hare</td>
<td>1</td>
<td>0.1</td>
</tr>
<tr>
<td><strong>Other</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ptarmigan</td>
<td>8</td>
<td>0.6</td>
</tr>
<tr>
<td>Unidentified carnivore</td>
<td>6</td>
<td>0.3</td>
</tr>
<tr>
<td>Unidentified bird</td>
<td>5</td>
<td>0.3</td>
</tr>
<tr>
<td>Arthropod</td>
<td>3</td>
<td>0.2</td>
</tr>
<tr>
<td>Mollusc</td>
<td>1</td>
<td>0.1</td>
</tr>
<tr>
<td>Eggshell</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td>Unidentified fish</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td><strong>Total scats</strong></td>
<td>551</td>
<td></td>
</tr>
</tbody>
</table>

\(^a\) Assumed to be adult caribou.

\(^b\) The 1977 Anisak pack FQ and REB ratios are unknown. The 1978 Anisak pack FQ and REB ratios were 70:13:3 (n=85) and 68.4:11.9:3.0, respectively, for unidentified adult ungulate:caribou adult:caribou calf.
Table 4. Relative weights and relative numbers of 3 key prey species which the Iligluruk and Anisak wolf packs consumed during May-August, 1977 and 1978.

<table>
<thead>
<tr>
<th>Prey type</th>
<th>Assumed weight of prey (kg)</th>
<th>Relative estimated bulk^b</th>
<th>Kg of prey eaten</th>
<th>No. of individual prey eaten</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Iligluruk</td>
<td>Anisak</td>
<td>Iligluruk</td>
</tr>
<tr>
<td>Caribou, adult</td>
<td>104</td>
<td>404.1</td>
<td>327.3^c</td>
<td>994.1</td>
</tr>
<tr>
<td>Caribou, calf</td>
<td>22</td>
<td>63.1</td>
<td>12.2^c</td>
<td>51.7</td>
</tr>
<tr>
<td>Moose, calf</td>
<td>72</td>
<td>2.0</td>
<td>5.9</td>
<td>3.6</td>
</tr>
<tr>
<td>Moose, adult</td>
<td>404</td>
<td>1.0</td>
<td>3.0</td>
<td>8.0</td>
</tr>
<tr>
<td>Arctic ground</td>
<td>0.7</td>
<td>65.3</td>
<td>4.0</td>
<td>25.7</td>
</tr>
<tr>
<td>squirrel</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

^aEstimation technique as described by Floyd et al. (1978).
^bAs described by Lockie (1959). See text for explanation.
^cThe relative proportions of adult and calf caribou in the Anisak pack's diet were estimated; see text.
Table 5. Frequency of occurrence and percent frequency of occurrence of ungulate (caribou, moose) and small mammal (arctic ground squirrel, microtine/shrew) remains in scats collected at summer homesites of the Iligluruk and Anisak wolf packs, 1977 and 1978.

<table>
<thead>
<tr>
<th>Scat collections</th>
<th>Ungulate</th>
<th>Small mammal</th>
<th>Total scats</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Iligluruk pack</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1977</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early b</td>
<td>252(94)</td>
<td>53(20)</td>
<td>268</td>
</tr>
<tr>
<td>Adult</td>
<td>232(94)</td>
<td>50(20)</td>
<td>247</td>
</tr>
<tr>
<td>Pup</td>
<td>107(92)</td>
<td>38(33)</td>
<td>116</td>
</tr>
<tr>
<td>Late c</td>
<td>20</td>
<td>3</td>
<td>21</td>
</tr>
<tr>
<td>Adult</td>
<td>4</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>Pup</td>
<td>4</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>1978</td>
<td>249(88)</td>
<td>124(44)</td>
<td>283</td>
</tr>
<tr>
<td>Early</td>
<td>140(88)</td>
<td>72(45)</td>
<td>159</td>
</tr>
<tr>
<td>Adult</td>
<td>69(87)</td>
<td>33(42)</td>
<td>79</td>
</tr>
<tr>
<td>Pup</td>
<td>20(77)</td>
<td>16(62)</td>
<td>26</td>
</tr>
<tr>
<td>Late</td>
<td>109(88)</td>
<td>52(42)</td>
<td>124</td>
</tr>
<tr>
<td>Adult</td>
<td>33(89)</td>
<td>13(35)</td>
<td>37</td>
</tr>
<tr>
<td>Pup</td>
<td>22</td>
<td>7</td>
<td>25</td>
</tr>
<tr>
<td><strong>Anisak pack</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1977</td>
<td>268(95)</td>
<td>38(14)</td>
<td>281</td>
</tr>
<tr>
<td>Adult</td>
<td>123(96)</td>
<td>16(13)</td>
<td>128</td>
</tr>
<tr>
<td>Pup</td>
<td>81(94)</td>
<td>11(13)</td>
<td>86</td>
</tr>
<tr>
<td>1978</td>
<td>86(98)</td>
<td>14(16)</td>
<td>88</td>
</tr>
<tr>
<td>Adult</td>
<td>36(95)</td>
<td>8(21)</td>
<td>38</td>
</tr>
<tr>
<td>Pup</td>
<td>24</td>
<td>2</td>
<td>24</td>
</tr>
</tbody>
</table>

*Percent frequency of occurrence shown in parenthesis when n>26.

*b*Mid-May to mid-July.

*c*Mid-July to mid-August.
Table 6. The number of caribou which the Iligluruk wolf pack killed during 3 observation periods in 1978, and the resulting estimate of the total number of caribou killed during 20 April - 13 October, 1978 (177 days).

<table>
<thead>
<tr>
<th></th>
<th>11-21 May</th>
<th>10-18 August</th>
<th>28 September-4 October</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of caribou killed</td>
<td>8</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>Estimated hours between first and last kill</td>
<td>235</td>
<td>153</td>
<td>49</td>
</tr>
<tr>
<td>Caribou killed per day(^a)</td>
<td></td>
<td></td>
<td>0.7690</td>
</tr>
<tr>
<td>Estimated total caribou killed (95% C.I.)(^b)</td>
<td></td>
<td></td>
<td>136 (94-178)</td>
</tr>
</tbody>
</table>

\(^a\) Based on a total of 14 caribou. See text for explanation. Confidence limits are approximate and may be underestimated because of small sample size (Cochran 1977:156).
Table 7. Estimated rate of predation on barren-ground caribou by the Iigluruk wolf pack during 20 April - 13 October, 1978.

| Estimated number of caribou killed (95% C.I.) | 136 (94-178) |
| Approximate number of wolf days | 1628 |
| Monthly predation rate, caribou/wolf/month (95% C.I.) | 2.5 (1.8-3.3) |
Table 8. Age and sex composition and estimated average weight of caribou which the Iligluruk wolf pack fed upon during 3 observation periods in 1978.

<table>
<thead>
<tr>
<th>Age and sex category</th>
<th>Number observed</th>
<th>Average weight (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mature bull&lt;sup&gt;a&lt;/sup&gt;</td>
<td>4</td>
<td>155</td>
</tr>
<tr>
<td>(5 years and older)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mature cow&lt;sup&gt;b&lt;/sup&gt;</td>
<td>7</td>
<td>77</td>
</tr>
<tr>
<td>(3 years and older)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult&lt;sup&gt;a&lt;/sup&gt;</td>
<td>5</td>
<td>74</td>
</tr>
<tr>
<td>(1 year and older, sex unknown)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Calf&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1</td>
<td>22</td>
</tr>
<tr>
<td>(1 year, sex unknown)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All ages and sexes</td>
<td>17</td>
<td>91&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a</sup>Determined from aerial observation.
<sup>b</sup>Determined from examination on the ground.
<sup>c</sup>Weighted mean.

<table>
<thead>
<tr>
<th>Description</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average edible weight (kg) of caribou carcass</td>
<td>56</td>
</tr>
<tr>
<td>Estimated total caribou (95% C.I.)</td>
<td>136 (94-178)</td>
</tr>
<tr>
<td>Total edible weight (kg) of caribou (95% C.I.)</td>
<td>7616 (5264-9968)</td>
</tr>
<tr>
<td>Approximate number of wolf-days</td>
<td>1628</td>
</tr>
<tr>
<td>Kg caribou/wolf/day (95% C.I.)</td>
<td>47 (3.2-6.1)</td>
</tr>
</tbody>
</table>
Appendix 1. Summer locations of radio-collared wolves in the Iligluruk pack, June 1977 to July 1979. Boundaries depict minimum home ranges for each year. The 5 locations to the northeast and the 3 locations to the southeast of the boundaries were the result of exploratory movements outside the normal home range. The 2 locations to the southwest of the boundaries were the result of migratory movements.