SUMMER SCAVENGING ACTIVITY IN NORTHEASTERN ALASKA

A MASTER OF SCIENCE THESIS

BY AUDREY J. MAGOUN

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Biology and Resource Management Project
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Cover design: Wolverine tracks, Igloo Creek, Mount McKinley National Park. Posterized from Kodachrome photo by F. Dean.

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A

THESIS

Presented to the Faculty of the

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By

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ABSTRACT

The scavenging behavior of animals on the North Slope of the eastern Brooks Range was investigated during the summers of 1972 and 1973. Grizzly bears (*Ursus arctos horribilis* Rausch), wolves (*Canis lupus tundrarum* Miller), and ravens (*Corvus corax* Linnaeus) each scavenged at over 50 percent of 15 large mammal carcasses. The major activities of feeding, moving, and resting were accompanied by minor activities such as caching, scraping, and inter- and intraspecific interactions. Behavior at the carcasses varied considerably, being influenced particularly by the dominance hierarchy of the scavengers present. The raven appeared to rely on scavenging more than the other species. Once a large mammal carcass was found by wolves or bears, it was disposed of within 2 to 10 days; avian scavengers required more than 10 days. The remains of a carcass may indicate which scavengers had visited the carcass.

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INTRODUCTION

Most biologists recognize that many species of animals, from lemmings (Mullen and Pitelka 1972) to lions (Schaller 1972), are scavengers to some degree; yet, there has been relatively little scientific study of the scavenger role and of the conditions which govern scavenging activities. Most literature available on scavenging is in the form of short notes in scientific journals (e.g. Field 1970, Smith 1974) or of peripheral comments made in scientific papers or popular arcticles by biologists whose interests do not include a detailed discussion of scavenging.

With few exceptions (Matyushkin 1974, Alvarez 1975), the most comprehensive studies on the role and the behavior of scavengers have been done in Africa where large predators and their prey are most abundant and diverse and where possibly the only vertebrate, "pure" scavengers are extant (e.g. griffon vultures: Houston 1974). Kruuk has studied the spotted hyaena (1970, 1972a) as well as several species of vultures (1967) in Tanzania, East Africa. Houston (1973) has added to the knowledge of the scavenging activities of vultures in Africa. Estes (1967) discussed at length the dual role of predator-scavengers in the Ngorongoro Crater.

The sporadic nature of scavenging activity and unpredictable sources of carrion in the Arctic reduce the chances for observing scavengers in this ecosystem; yet, the eastern Alaskan Arctic is one of the few areas in North America where natural predator-prey and predator-scavenger relationships still exist undistorted by intensive human activity and by "artificial" food supplies available to scavengers in recent human settlements.

It is the purpose of this study to describe scavenging activity at large mammal carcasses in the eastern Alaskan Arctic and to discuss factors which affect an animal's role as a scavenger and influence its activity patterns.

STUDY AREA

Physiography and Vegetation

The study was conducted during the summers of 1972 and 1973 in two adjacent areas essentially encompassing the upper Canning River drainage (Fig. 1). This river is located on the Arctic Slope about 126 mi (201.6 km) west of the U.S.-Canadian border and flows north 100 mi (161.0 km) to the Arctic Ocean.

The northern portion of the study area includes Cache Creek and Eagle Creek valleys, a small section of the upper Sadlerochit River, and that section of the Canning River from the mouth of Eagle Creek south for a distance of about 8 mi (12.8 km). This area includes approximately 50 mi (80.0 km) of major drainage lines. It is near the northern limit of the Brooks Range Province and is bounded on the east and west by the Arctic Foothills Province (Payne et al. 1951). The valleys are from 1 to 3 mi (1.6 to 4.8 km) wide, and the mountains rarely exceed 4,500 ft (1,350 m) in elevation.

In 1973 a continuation of the study was conducted along 30 mi (48.0 km) of the Marsh Fork, beginning approximately 7 mi (11.2 km) south of the 1972 area. The valley averages less than 1 mile (1.7 km) in width and the mountains rise steeply to elevations over 5,000 ft (1,500 m).

The habitat of the study area is typical of the northern foothills and mountains of the Arctic Slope. The major plant forms along the stream bottoms are trees and shrubs from 3 to 20 ft (0.9 to 6.1 m) in height

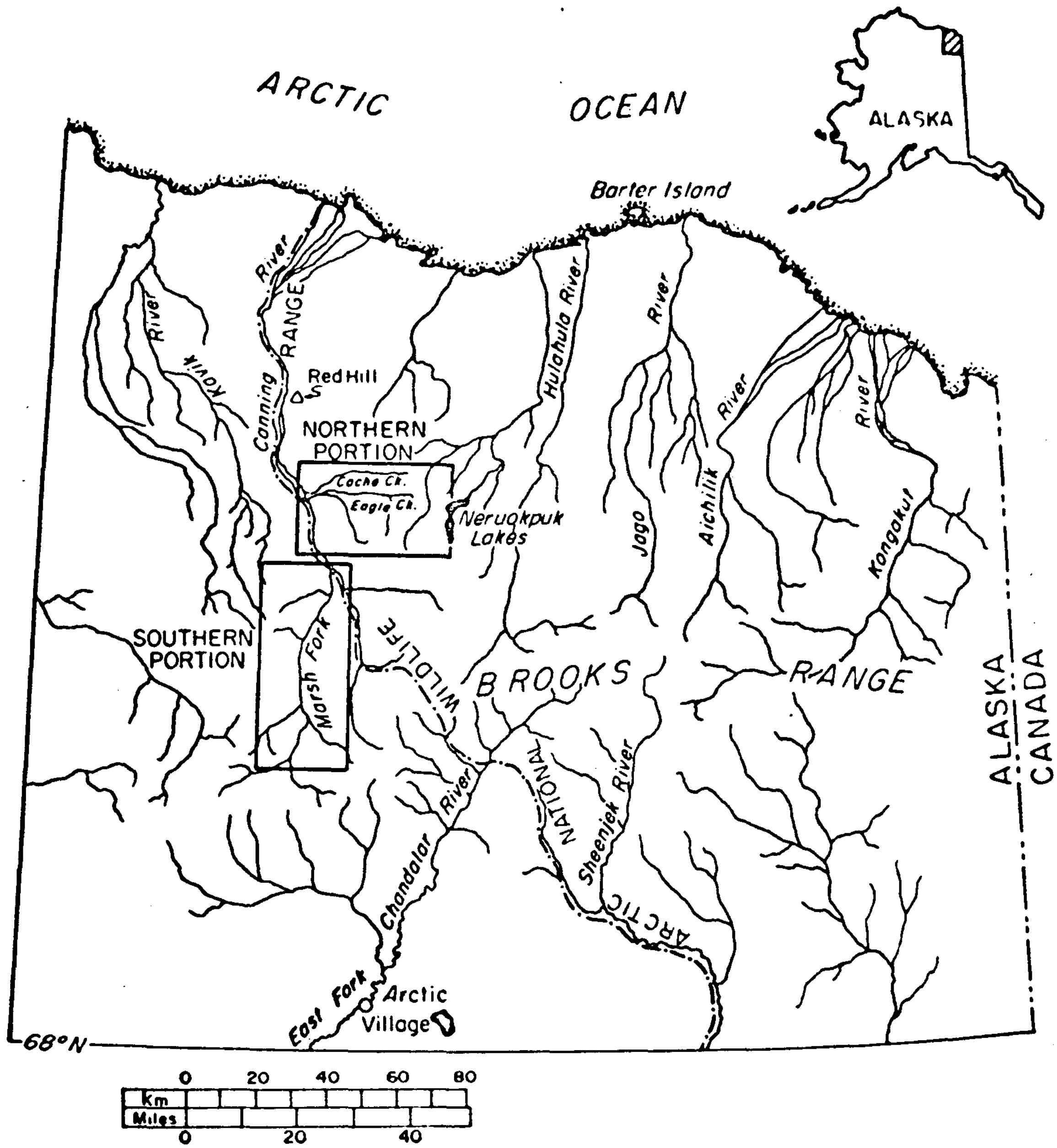


Figure 1. Map of the study area.

among which _Salix_ spp. predominates (see Photo 1). The active floodplain supports very little vegetation and is wide enough along many stretches of the river to inhibit any significant plant growth, even along the margins of the braided streambed. Detailed descriptions of floodplain, terrace, and cutbank communities can be found in Spetzman (1959) and Bliss and Cantlon (1957).

As the land slopes upward from the floodplain, there occurs a mosaic of generally homogeneous vegetation types usually less than 2 ft (0.6 m) in height (see Photo 2). Dwarf shrub heath, frost scar collective, and _Salix_ types described by Churchill (1955) and wet sedge meadow, dry upland meadow, and outcrop and talus vegetation types described by Spetzman (1959) are the predominant forms. The occurrence and extent of these vegetation types are dependent upon many biotic and physical features among which the most important are drainage, angle and aspect of slope, depth of snow, protection from wind, parent rock, and development of the soil.

The steep mountain slopes at lower elevations are covered with moist moss/lichen growth, generally on north-facing slopes (see Photo 3) and with mat-forming species mixed with _Dryas_ spp. on drier slopes and at higher elevations (see Photo 4).

Climate

In the foothills and mountains on the north side of the Brooks Range where this study was conducted, the predominating influence is continental except during summer months when marine influences are

Photo 1. The Marsh Fork Valley showing extensive stands of willow along the active streambed.

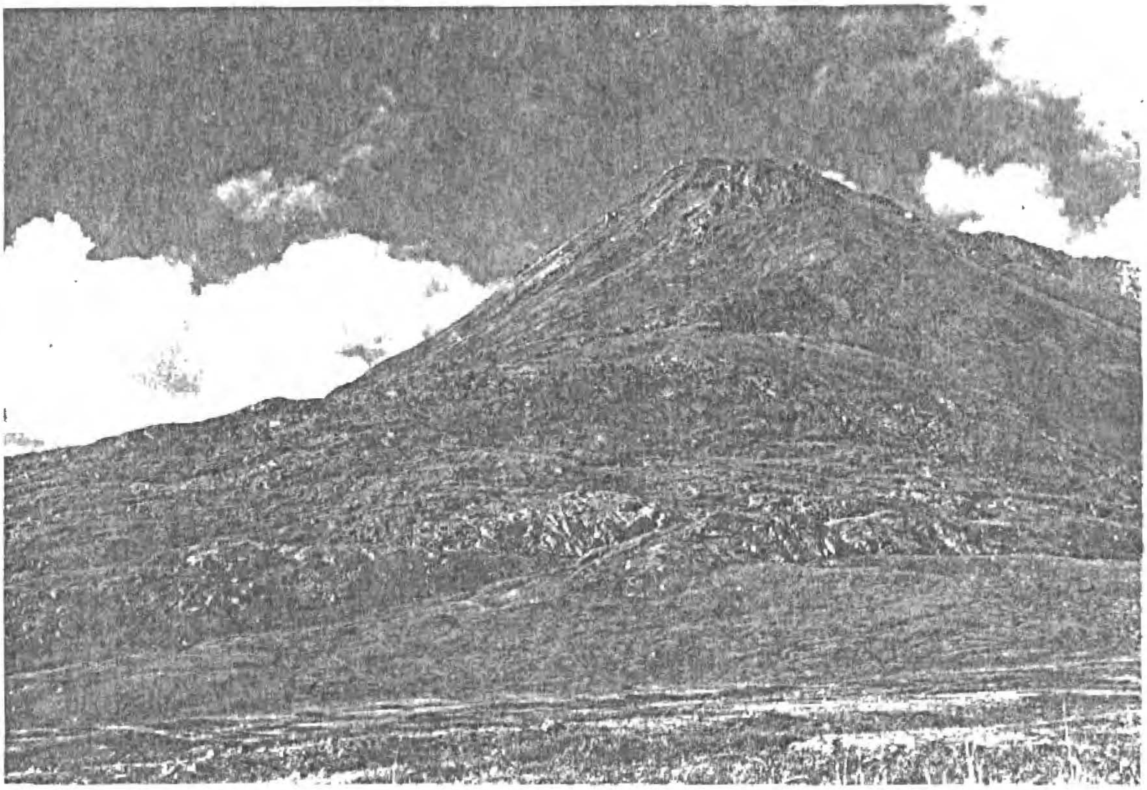


Photo 2. A mosaic of vegetation types occur as the land slopes upward from the streambed.

Photo 3. Steep mountain valleys often support thick moss/lichen growth on north-facing slopes, as seen in the lower left corner of this photograph.

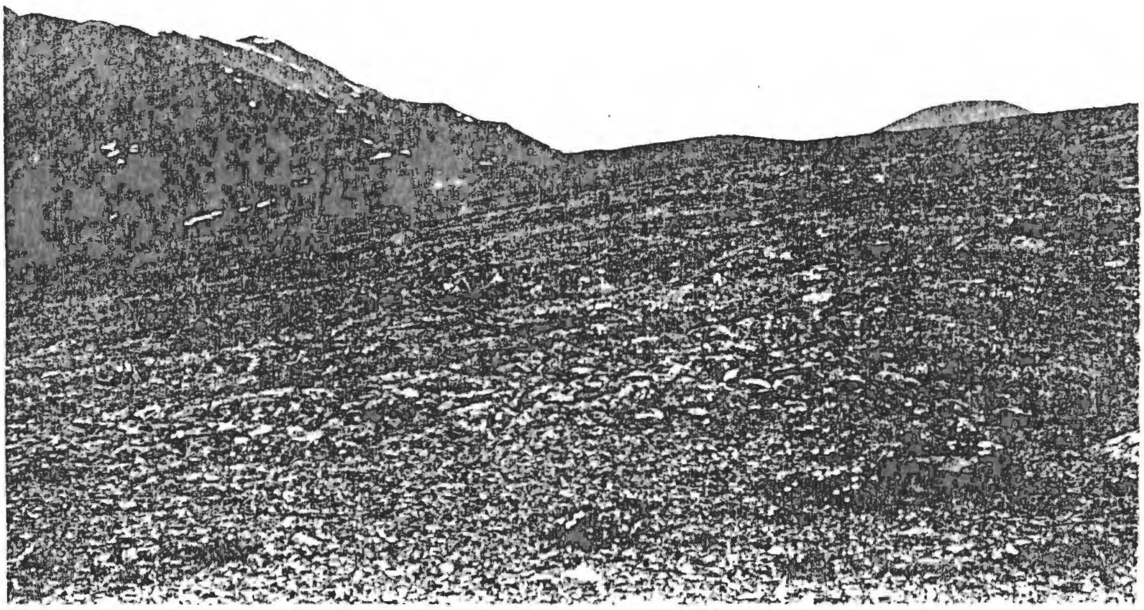


Photo 4. At higher elevations, the dry slopes are covered with mat-forming vegetation types.

important (Searby and Hunter 1971). Temperatures may range from -60°F (-51°C) in the winter to over 90°F (32°C) in the summer. I did not record temperatures while conducting the study but both freezing temperatures and hot weather were experienced during June, July, and August. Temperatures were generally between 50°F (10°C) to 70°F (21°C) during the summer. The highest temperature recorded by Renewable Resources Consulting Services, Ltd. (RRCS) biologists, who were also in the study area in 1973, was 73°F (23°C) on 23 July (Jakimchuk 1974). During 1972 the temperatures seemed to be somewhat higher.

Precipitation is relatively light in the study area, most of it falling as rain during the summer months. Snow may fall in any month but winter snows usually begin in September and last through May, often into June.

Winds are generally moderate in the study area.

Wildlife

The results of a study on scavenging behavior are, in part, dependent upon the complex of animals present in the study area. Lists of the mammals and birds observed in the area are given in Appendices A and B respectively; however, comments on the relative abundance of some of these species are necessary. The following figures were obtained mainly through my personal observations and data collected by RRCS biologists in approximately 500 hrs of flying (fixed-wing and rotary-wing aircraft) in the Canning River drainage in 1972 and 1973.

Moose (*Alces alces gigas* Miller) were most often observed along the main Canning River drainage. Lenarz et al. (1974) stated that "fall surveys revealed a minimum population of 69 moose in the Canning River Drainage proper" in 1973. They presented evidence that there is some movement of moose between the Canning River and the Kavik River to the west. Their estimate of the moose population in these two drainages combined was 96 animals. The highest numbers they recorded in the Canning River drainage were in mid-October, in March, and in April; only 26 moose were seen in mid-May. They made no comprehensive surveys during summer months since

> heavy foliage along the rivers obscured all but a few moose. Miscellaneous sightings suggest that the bulk of the population remains in an area bounded by (1) Red Hill on the north (approximately 69°37'N); (2) Kavik River on the west; (3) the confluence of the Main and Marsh Forks on the south; and (4) the headwaters of Cache and Eagle Creeks on the east.

A few moose do drift north onto the coastal plain (Roseneau and Stern 1974).

The study area is within the range of the Porcupine caribou herd (Hemming 1971) which numbers around 100,000 animals. The caribou (Rangifer tarandus stonei Rausch) calve anywhere from the Babbage River in Canada west to the Canning River (LeResche 1972). In 1972 most calving occurred east of the Hulahula River about 9 mi (14.4 km) from the study area, although a few hundred caribou calved in the Kavik-Prudhoe Bay area (LeResche 1972). Movement of the herd after calving is generally away from the area of my study. I saw only two cows with calves in the two summers combined. Bulls, cows without calves, and yearling caribou passed through the study area, usually traveling alone or in small groups; occasionally a herd of 50 to several hundred animals appeared in the study area for a short period of time. Caribou occurred much more frequently in the northern portion of the study area. In 1972 caribou were seen on 50 percent of the days spent in the study area; 8 of 47 groups (15%) had 10 or more animals. In a report by RRCS, Ltd. (1973), only eight groups of caribou were recorded in the northern portion of the study area in 1972, seven groups with 10 or fewer animals and one group with 400 animals. In 1973 I saw caribou on only 8 percent of the days spent in the study area; 2 of 10 groups (20%) had 10 or more animals; a group of 700 animals passed through the Marsh Fork valley in July. Though 2,000 caribou wintered near the head of the Marsh Fork in 1972-73, the Marsh Fork was devoid of caribou by the end of June.

The Marsh Fork supports several hundred Dall sheep (*Ovis dalli dalli* Nelson) particularly along the southern half of the drainage. Movements of these sheep are restricted to that area, and the adult population in winter and summer is relatively stable. I saw no sheep in the northern part of the study area though a few have been sighted by other biologists (Quimby, pers. comm.).

Quimby (1974a) stated that "there were two and possibly four distinct wolf packs which utilized the mountains and foothills of the Canning River drainage" in 1972 and 1973. Two of the dens were within the study area while two were in nearby drainages. Quimby's observations of wolves (*Canis lupus tundrarum* Miller) agree closely with those that I made during the study. As many as 7 to 10 adult wolves may have been present in the study area at any one time. Three to eight may have frequented the northern portion of the study area and four to six the southern portion.

Red foxes (Vulpes vulpes alascensis Rausch) are common on the North Slope in the mountains and southern foothills. RRCS biologists made 18 observations of red foxes in the Canning River drainage in 1972 (Quimby and Snarski 1974) and 25 observations in 1973 (Quimby 1974a). They found four active dens in the Canning River drainage in 1973 and a fifth den that had been active in 1972 (Quimby 1974a). Three of the dens active in 1973 were located in the Marsh Fork; the fourth on the west bank of the Canning River. From my observations of foxes in 1972, I suspect there were at least three additional dens in the northern portion of my study area and one in the southern portion. The minimum number of adult red foxes in the study area was between 8 and 16 but the actual number was undoubtedly higher.

Arctic foxes (Alopex lagopus innuitus Merriam) rarely occur in the study area.

During 1973 and 1974, biologists working for RRCS and the Alaska Department of Fish and Game conducted a tagging and radiotelemetry program on grizzly bears (Ursus arctos horribilis Rausch) in the Canning River drainage. In 1973, 15 bears were tagged in the study area (H. Reynolds, pers. comm.); in 1974, 11 of these bears were recaptured in the study area (Curatolo, pers. comm.). Two more bears that had been tagged in an adjacent area in 1973 were recaptured in the study area. Eight new bears were tagged, giving a total of 21 bears. Eight sightings of untagged bears in the study area were also made in 1974 (Curatolo, pers. comm.). Curatolo stated that at least 80 percent of the adult bears in the study area had probably been tagged. This would mean that at least 26 bears, not including cubs, were in the Canning River drainage. In 1973 two of the tagged sows had two cubs each, bringing the total number of bears to 30. This total does not include areas totally within the Arctic National Wildlife Range since tagging was not permitted inside the Range. During 1972 I observed a sow and cub and a single bear in the upper part of Cache Creek and a single bear along the Sadlerochit River, all of which may not have been sighted in the tagging study. If these four bears are added to the total, then at least 34 bears may have used the study area. This agrees with the estimate of 35 provided by Reynolds (pers. comm.) for 1973 and with the estimate made by Quimby (1974b).

Six of the radiotagged bears spent all or most of their time within the study area, three in the northern portion, two in the southern portion, and one in parts of both portions. Another bear frequented the upper Marsh Fork. In addition, eight of the recaptured bears were in the study area during both years that they were captured, suggesting that at least 15 adult bears were consistent in their use of the study area in 1973 and 1974.

Wolverine (*Gulo gulo luscus* Rausch) are not common in the study area. I made one possible sighting of a wolverine during 1972 in the Eagle Creek area. RRCS biologists made only nine sightings (four in 1972; five in 1973) in the Canning River drainage in two years of intensive survey of the area (Quimby 1974a). Several of their sightings were made in the Marsh Fork and may have involved the same wolverine.

Arctic ground squirrels (Spermophilus undulatus kennicottii Ross) were common and microtines were abundant during the study. Snowshoe hares (Lepus americanus dalli Merriam) are always scarce, probably only occurring in the study area when hare populations in interior Alaska are high.

The avian species which should be mentioned are the raven (Corvus corax Linnaeus), golden eagle (Aquila chrysaetos Linnaeus), glaucous gull (Larus hyperboreus Gunnerus), and long-tailed, parasitic, and pomarine jaegers (Stercorarius longicaudus Vieillot, S. parasiticus Linnaeus, and S. pomarinus Temminck respectively). In every part of the study area, at least one pair each of ravens and golden eagles were seen. Because individuals of these species are difficult to identify, it is not possible to say how many pairs were in the area. No active raven nests have been located in the study area; three active eagle nests were located in the Canning River drainage in 1973 (Roseneau, pers. comm.). No more than two ravens were seen together until after the young began to accompany the adults, when as many as six ravens could be seen together. Whenever three eagles were seen together, one could always be identified as an immature. Glaucous gulls were common along the Canning River but were only occasionally present in the Marsh Fork. Long-tailed and parasitic jaegers were not common in the study area except during the spring migration. There probably were less than eight nesting pairs of the two species combined. Pomarine jaegers were only seen during the spring migration.

Annotated lists of all wildlife which I observed in the study area during 1972 and 1973 can be found in Valkenburg et al. (1972a and 1972b) and Magoun and Valkenburg (1973).

METHODS AND MATERIALS

Data Collection

During the summers of 1972 and 1973, 15 large mammal carcasses were used for making observations of scavenging activity. Eleven of the animals were shot under special permit provisions made by the Alaska Department of Fish and Game and the U.S. Fish and Wildlife Service. An attempt was made to space these carcasses in time and distance to simulate a natural situation. Three additional carcasses were of animals that had died of natural causes; another was shot by a hunter. The locations of the carcasses are shown in Figure 2. Descriptions of the carcasses and the observation sites are presented in Table 1.

Two attempts were made to simulate raven and wolf caches using parts of carcass no. 8 and fish remains. The meat was cut into portions of approximately the same size as that which these scavengers were seen to cache and was placed in areas and in a manner similar to that used by the scavengers. An attempt was made to eliminate, as much as possible, human scent from the meat and the caching sites. Unfortunately, because of time limitations, only a few simulated caches were made, and they were checked only once or twice shortly after their disposition.

Whenever a carcass was located, a green 4-man tent was set up at the most suitable vantage point for observation. The tent was placed in a position that would allow a maximum in observation ability for a minimum of potential disturbance. A variable power Redfield scope (15x

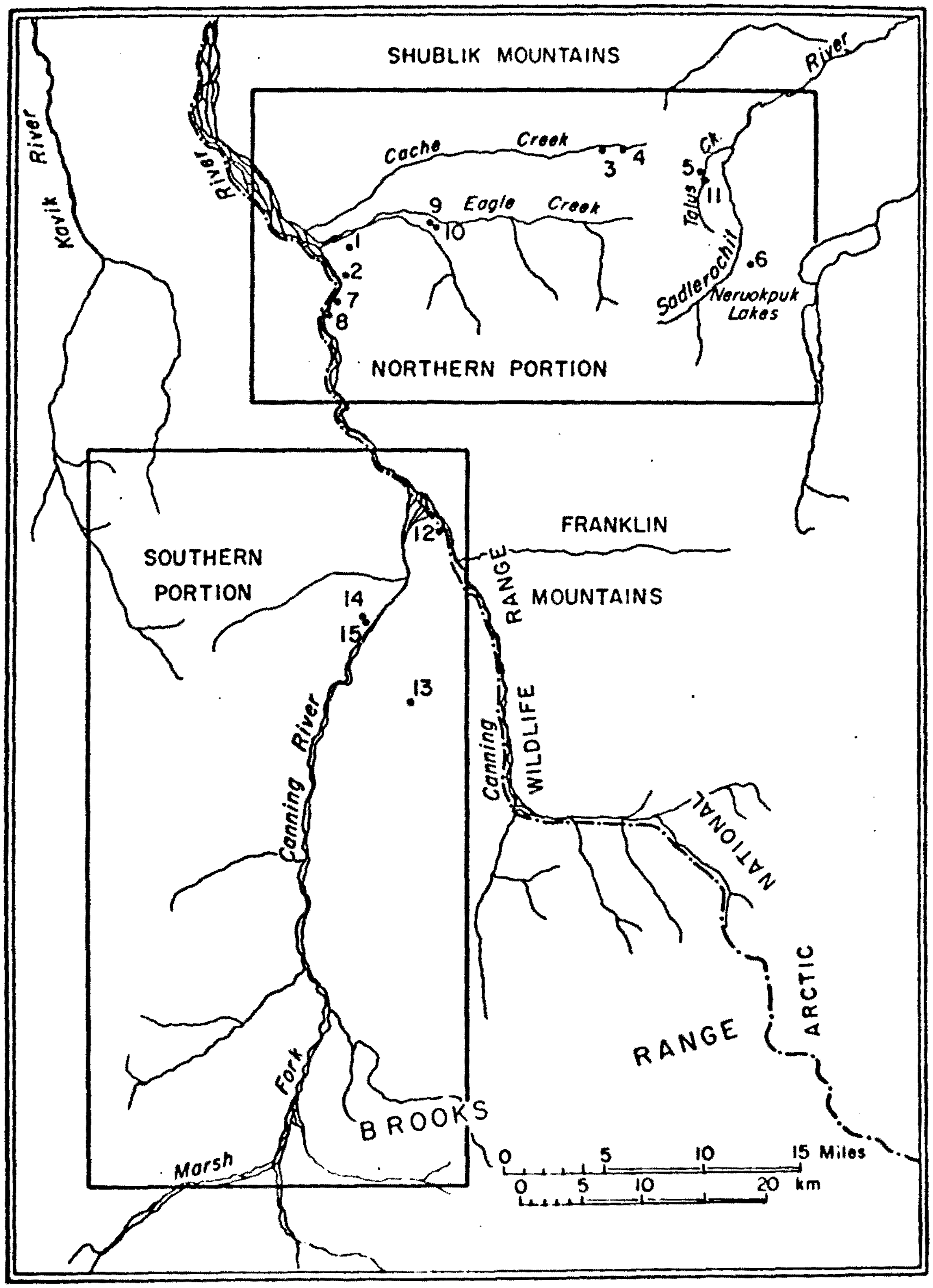


Figure 2. Location of the carcasses.

Table 1. Description of the carcasses and the observation sites.

Carcass	Date obtained	Species	Description of the carcass	Description of the carcass site	Description of the observation site	Comments
1	27-V-72	Moose	Bull; wt ≈ 800 lb (363 kg); bullet wound in spinal cord.	Mouth of Eagle Creek; elev 1,000 ft (305 m); large willow stand; willows 6 to 15 ft (2 to 5 m) high, interspersed with open spaces.	About 2 mi (3 km) E of carcass; elev 2,500 ft (762 m).	Carcass not handled; extended observations.
2	10-VI-72	Caribou	Cow; wt ≈ 200 lb (91 kg); bullet wound in shoulder; throat cut.	About 2 mi (3 km) S of mouth of Eagle Creek or E side of Canning River; elev 1,600 ft (488 m); open sedge meadow.	About 1 mi (2 km) NE of carcass; elev 2,200 ft (691 m).	Carcass was transported by helicopter; extended observations.
3	1-VII-72	Caribou	Bull; wt ≈ 300 lb (136 kg); bullet wound in head; several small holes in part of lower neck.	Upper Cache Creek on S bank; elev 2,600 ft (733 m); dry tundra.	About 1 mi (2 km) NE of carcass on opposite side of Cache Creek; elev 3,000 ft (915 m).	Available at the same time as carcass no. 4; carcass was transported by helicopter; extended observations.
4	1-VII-72	Caribou	Bull; wt ≈ 200 lb (91 kg); large bullet wound in shoulder and back.	Same as that of carcass no. 3, one half mile E.	Same as that for carcass no. 3.	Same as that for carcass no. 3.
5	7-VII-72	Caribou	Sex undetermined; wt ≈ 150 lb (68 kg); several bullet wounds.	Upper Talus Creek on W side; elev 3,600 ft (1,098 m); slope with dry tundra vegetation.	No observation site.	Carcass not handled; few observations made.
6	8-VII-72	Caribou	Bull; wt ≈ 250 lb (114 kg); bullet wound in head and left shoulder.	E side of Upper Sadlerochit River; elev 3,000 ft (915 m); open sedge meadow.	About one half mile (1 km) E of carcass; elev 3,600 ft (1,098 m).	Carcass dragged by observers 300 ft (92 m); extended observations.
7	25-VII-72	Caribou	Bull; wt ≈ 150 lb (68 kg); bullet wound in head and shoulder.	About 4 mi (6 km) S of mouth of Eagle Creek on E side of Canning River; elev 1,000 ft (305 m); gravel riverbed.	About 300 ft (92 m) E of carcass; elev 1,100 ft (335 m).	Carcass not handled; observers remained inside tent almost entirely hidden behind a knoll; extended observations.
8	4-VIII-72	Caribou	Bull; wt ≈ 150 lb (68 kg); parts of carcass removed for cache simulation: foreleg, hindleg, heart, some meat from back and other hindleg; body cavity opened.	Same as that of carcass no. 7, 1 mile (2 km) S.	About one half mile (1 km) SE of carcass; elev 1,400 ft (427 m).	Carcass handled and some meat removed by the observers; extended observations.

Table 1, continued.

Carcass	Date obtained	Species	Description of the carcass	Description of the carcass site	Description of the observation site	Comments
9	16-IX-72	Caribou	Bull; wt α 300 lb (136 kg); bullet wound in undetermined area.	Lower Eagle Creek on S side; elev 2,300 ft (700 m); dense shrub growth 2 to 5 ft (1 to 2 m) high.	About 2 mi (3 km) W of carcass; elev 2,600 ft (794 m).	Carcass not handled; extended observations.
10	21-IX-72	Caribou	Bull; wt α 250 lb (114 kg); bullet wound in chest.	Same as that of carcass no. 9, 900 ft (274 m) W.	Same as that for carcass no. 9.	Carcass obtained a day after termination of carcass no. 9; extended observations.
11	18-VII-72	Caribou	Bull; probably remains of recent wolf kill; only head, neck, thoracic vertebrae, and rib cage remaining with little meat.	Upper Talus Creek; elev 2,600 ft (793 m); open dry tundra.	No observation site.	No observations.
12	5-VI-72	Caribou	Sex undetermined; wt undetermined; fresh wolf kill; wounds undetermined.	About 1 mi (2 km) S of confluence of Marsh Fork with main Canning River; elev 1,400 ft (427 m); gravel riverbed; scattered willows.	Hillside on W side of Canning River about 1 mi (2 km) from carcass; elev 2,000 ft (610 m).	Carcass found shortly after a wolf made the kill; carcass not handled; extended observations.
13	1-VII-73	Dall Sheep	Ewe; wt α 100 lb (45 kg); bullet wound in hindlegs, lower abdomen, and chest.	Small tributary stream of Marsh Fork; elev 4,000 ft (1,220 m); steep north-facing slope covered with thick moss/lichen growth with scattered boulders and talus.	On south-facing slope of the stream about 1,200 ft (366 m) from carcass; elev 4,300 ft (1,310 m).	On 7-V-73 carcass examined and rolled 400 ft (122 m) to bed of the stream; extended observations.
14	24-V-73	Moose	Bull; wt α 700 lb; cause of death unknown; no wounds on carcass when it was found.	Marsh Fork about 7 mi (12 km) S of confluence with main Canning River; elev 1,800 ft (549 m) willows 6 to 15 ft (2 to 5 m) high.	About 900 ft (274 m) W of carcass; elev 2,100 ft (640 m).	Apparently died during late winter or early spring; observations include those of RRCS biologists; limited observations.
15	9-VI-73	Grizzly Bear	Sex undetermined; wt undetermined; shot by hunters and head and hide removed.	Same as that of carcass no. 14.	Same as that for carcass no. 14.	Limited observations.

to 60x) and 10x40 Leitz binoculars were used to watch the carcass for the longest period of time possible. Detailed notes of all that occurred at the carcass or in the surrounding area were kept in field notebooks. The exact time of day was recorded before each entry in the notebook. Three observers were sometimes available but only two observers were used most of the time. Mainly because of physical limitations and weather conditions, it was not possible to obtain a constant watch of the carcasses at all times. When the carcasses were not being watched continually, an attempt was made to check activity at the carcass at regular intervals. These intervals usually ranged from a few minutes to an hour.

Whenever possible, individuals of the same species at a carcass were identified in the notes and given a specific code number for data analysis.

At some carcasses, a Vivitar Super 8 mm camera that had been modified to take a single frame exposure every 3 minutes was set up to record the presence of scavengers. Because of mechanical defects, the cameras were not dependable but some useful data were obtained.

If the observation distance from the carcass was short enough, it was possible to determine the order in which scavengers disposed of carcass parts and the percent of the carcass which remained. Before leaving a carcass site, the area was checked for any remaining parts of the carcass.

Data Analysis

All scavengers and their activity patterns were coded (Table 2) and punched on computer cards in 5-minute sections of observation time for each day of each carcass. More detailed explanations of the activites are given in Appendix C. For each 5-minute period, there is a record of all scavengers present with their respective activities in the vicinity of the carcass. The number of times certain activities occurred is recorded; another number indicates which activities occurred simultaneously in a 5-minute period. For example, a card which reads

1890207 1805 B1FCC 1 R1FCP 1 R1CA 3 1 B1FCC 2 R2RP 2

would represent the following information:

189 Day of the year

02 Carcass no. 2

07 The seventh day of the carcass

1805 Time of day, between 1800 and 1805

B1FCC 1 Bear no. 1 was feeding constantly at the carcass at the same time that R1FCP 1 and R1CA 3 1 were occurring

R1FCP 1 Raven no. 1 was feeding on carcass parts at the same time that B1FCC 1 and R1FCP 1 were occurring

R1CA 3 1 Raven no. 1 made three caches away from the carcass at the same time that B1FCC 1 was occurring

B1FCC 2 Bear no. 1 was feeding on the carcass constantly at the same time that R2RP 2 was occurring

R2RP 2 Raven no. 2 was resting in proximity to the carcass at the same time that B1FCC 2 was occurring

Table 2. Abbreviations for scavengers and their activities.

SCAVENGERS*

B - Bear

E - Eagle

F - Fox

G - Gull

J - Jaeger

R - Raven

S - Ground Squirrel

W - Wolf

ACTIVITIES

Major activities:

FCC - Feeding on the carcass continuously

FCI - Feeding on the carcass intermittently

FCP - Feeding on parts of the carcass that have been removed from the main carcass

FC - Feeding on caches

F - Feeding on items other than the carcass

MA - Moving in the area of the carcass

MP - Moving in the proximity of the carcass

RA - Resting in the area of the carcass

RP - Resting in the proximity of the carcass

Table 2, continued.

Minor activities:

AA - Scavenger initiates an aggressive act away from the carcass

AAR - Scavenger is the recipient of an aggressive act away from the carcass

AC - Scavenger initiates an aggressive act at the carcass

ACR - Scavenger is the recipient of an aggressive act at the carcass

CA - Caching in the area of the carcass

CP - Caching in the proximity of the carcass

D - Drinking

G - Grooming

NAA - Non-aggressive interactions

S - Scraping

U - Urinating or defecating

VA - Vocalizing in the area of the carcass

VP - Vocalizing in the proximity of the carcass

*A number following a species code letter indicates the individual of that species at a particular carcass (e.g. B1 indicates the first bear at a particular carcass). Numbering was started over for each carcass.

In the above example, the first (R1) raven did not engage in feeding activity (FCP) for the entire 5-minute period. Most sessions of continuous activity that are presented in the results are in terms of the number of 5-minute periods (observation periods) in which the activity occurred rather than in minutes or other units of time. By multiplying the number of observation periods by five, one would obtain the maximum amount of time (in minutes) that the activity could have occurred.

A number of programs have been written in COBOL that have essentially sorted the data and totaled various amounts of activity times. Appendix D is a description of these programs and a sample of the output.

RESULTS

Extended observations were made at 11 of 15 carcasses listed in Table 1, totaling 11,643 observation periods or approximately 970 hours (total observation time). Attempts to make observations during 999 potential periods were unsuccessful because the carcasses were obscured by rain, fog, snow, heat waves, or darkness. No observations were attempted during 11,752 additional potential observation periods. The observed activity by scavengers occurred during 3,465 observation periods (30% of the total observation time). There was no visible activity during 8,179 observation periods (70% of the total observation time). The majority of inactivity at a carcass occurred during the first days after a carcass became available, before scavengers had begun to feed on it. A breakdown of actual observation time and activity time by carcass is given in Table 3.

There was probably some activity during two-thirds of the time when there was no visibility and during a quarter of the time when no observations were being made. This estimate of "probable activity" was made subjectively but after close scrutiny of the field notes. The estimate of "probable activity" during periods of no visibility was based on the number of times weather obscured the carcass when scavengers were at the carcass. The estimate for "probable activity" during periods of no observations was based on the number of times a carcass was checked after a long period of no observations and either there was a scavenger there when observations were resumed or there was evidence to indicate

Table 3. Summary of observation time and activity time for each carcass.*

Carcass number	Total time of carcass (TTC)	Observation time (OBT)	OBT as % of TTC	No activity (NACT)	NACT as % of OBT	Activity (ACT)	ACT as % of OBT
1	4,763	2,108	44%	669	32%	1,439	68%
2	2,082	1,054	50	850	81	204	19
3	1,602	1,133	71	750	66	383	34
4	1,920	1,280	67	1,124	88	156	12
6	2,586	1,631	63	1,541	94	90	6
7	2,779	1,783	64	1,448	81	335	19
8	2,772	1,499	52	1,003	67	496	33
9	1,154	179	16	143	80	36	20
10	1,159	276	24	214	78	62	22
12	574	284	49	197	69	87	31
13	3,003	416	14	240	58	176	42
	24,394	11,643	48%	8,179	70%	3,464	30%

*Observation time and activity time expressed in number of 5-minute observation periods.

a scavenger had been there when there were no observations being made.

The nine species which scavenged at carcasses included four mammalian species (grizzly bear, wolf, red fox, and arctic ground squirrel) and five avian species (golden eagle, raven, glaucous gull, long-tailed jaeger, and parasitic jaeger). The number of individual animals which visited the carcass vicinities varied from 3 to 12; they are listed for each carcass in Table 4.

Not all of the animals that visited a carcass actually fed on it, and particular individuals spent much more time at the carcass than others. Table 4 lists each individual that visited a carcass, the amount of time it spent at the carcass, and how its time was distributed among the various activities.

Ravens, wolves, and bears each scavenged at over 50 percent of the 11 carcasses that were observed for extended lengths of time (100%, 72%, and 63% respectively). All other species scavenged at less than 30 percent of the carcasses (jaeger and gulls, 27%; foxes and eagles, 18%; and ground squirrels, 9%). Ground squirrels could have been present at other carcasses without being seen, but this probably did not occur often, if at all.

Except for the red fox and the raven, the order of arrival at the carcass sites of each scavenger species was variable. The red fox only visited two carcasses but was one of the first two scavengers to appear at these carcasses; the raven was the first species to arrive at 8 of 11 carcasses (73%) and was one of the first two species to arrive at 100 percent of these 11 carcasses.

An average of 1.25 days passed before a fox arrived at a carcass

Table 4. Number of observation periods each scavenger was in the vicinity of a carcass and the distribution of time among the major activities.*

Carcass number	Scavenger	Activity time (SACT)	SACT as a % of OBT**	SACT as a % of ACT**	Feeding				Moving		Resting		
					FCC	FC1	FCP	FC	MA	MP	RA	RP	RC
C1	B1	1060	39	74	88	54	2		38	86	74	478	223
	B2	116	4	8	19	7			8	13	56	10	2
	B3	99	4	7	12	3			21	18	41	7	
	E1	34	1	2					7	1	28		
	E2	4	0	0					4				
	G1	1	0	0					1				
	R1	276	10	19	10	177			26	33	8	7	23
	R2	121	<1	8	1	93			10	7		1	3
	W1	351	13	24	21	17	22		31	66	109	73	3
	W2	54	2	4	1				9	5	28	13	
	W3	5	0	0					2	4			
	W4	2	0	0					1	2			
C2	B1	63	6	31			29		8	4		6	19
	B2	37	4	18			5		44	9			
	E1	37	4	18	3	2			9		26		1

Column group heading over Feeding, Moving and Resting: Number of observation periods

Table 4, continued.

Carcass number	Scavenger	Activity time (SACT)	SACT as a % of OBT**	SACT as a % of ACT**	Number of observation periods: Feeding				Moving		Resting		
					FCC	FC1	FCP	FC	MA	MP	RA	RP	RC
	E2	34	3	17					10	1	29	2	1
	F1	5	<1	2	4					1			
	R1	10	1	5		3			3	1			1
	R2	2	<1	1					1			1	
	W1	100	10	49	2	12	27		19	30		36	
	W2	67	6	33	2	8	1		17	14		30	
C3	B1	32	3	8					31		5		
	J1	4	<1	1					1	3			
	J2	4	<1	1					1	3			
	R1	166	13	43	14	68	57		8	14	13	15	7
	R2	40	3	10		1	15		9	5	13	3	
	W1	321	25	84	6	6	27	9	43	55	54	182	
C4	B1	41	3	26	6	1	1		28	4	3		
	B2	48	3	31	8	2	3		2	15		18	
	B3	48	3	31	8	2	10		2	12		14	

Table 4, continued.

Carcass number	Scavenger	Activity time (SACT)	SACT as a % of OBT**	SACT as a % of ACT**	Number of observation periods: Feeding				Moving		Resting		
					FCC	FC1	FCP	FC	MA	MP	RA	RP	RC
	J1	35	2	22	10	1	18		4	2			
	J2	20	1	13			18		2				
	R1	19	1	12			2		15	1		1	
	W1	17	1	11			1		5	13		4	
C5	B1	- - - - - - UNKNOWN - - - - - -											
	E1												
C6	B1	40	2	44	9	12			18	6			
	E1	1	<1	1					2				
	J1	13	1	14					9		1		
	J2	6	<1	7					4		1		
	J3	1	<1	1					1				
	J4	1	<1	1					1				
	R1	40	2	44		22	2		4			4	1
	R2	4	<1	4					1	1		1	
	R3	3	<1	3					1	1		1	

Table 4, continued.

Carcass number	Scavenger	Activity time (SACT)	SACT as a % of OBT**	SACT as a % of ACT**	Number of observation periods								
					Feeding				Moving		Resting		
					FCC	FCl	FCP	FC	MA	MP	RA	RP	RC
C7	B1	3	<1	1					3				
	E1	7	<1	2					5		3		
	E2	2	<1	1					2				
	F1	1	<1	<1					1				
	G1	184	10	55	2	13	14		61	48	8	51	
	G2	52	3	15									
	R1	117	6	35		6	4	4	56	4	36	2	
	W1	114	6	34	30	1	3		42	5	47		
	W2	13	1	4	6		7		1	4			
C8	E1	85	6	17	35	32			13	11	22		
	E2	15	1	3			1		1	1		14	
	G1	162	10	33	25	49	14		30	44	35	15	
	G2	22	1	4					15	4	4		
	J1	191	12	39	57	60	7		8	44	9	37	
	J2	1	<1	<1					1				
	R1	232	15	47	34	119	8	2	23	33	28	3	2

Table 4, continued.

Carcass number	Scavenger	Activity time (SACT)	SACT as a % of OBT**	SACT as a % of ACT**	Number of observation periods: Feeding				Moving		Resting		
					FCC	FCl	FCP	FC	MA	MP	RA	RP	RC
	R2	177	11	36	19	81	11	2	19	24	28	8	1
	R3	39	3	8		1	9		7	12	18		
	R4	8	<1	2					1		8		
	W1	4	<1	1		4			4	4			
C9	B1	34	19	94		16						29	
	R1	3	2	8		1							
	R2	3	2	8		1							
C10	B1	4	1	6	2	2				1			
	F1	16	6	26		14							
	R1	22	8	35		16	1			1			
	R2	14	5	23		14				1			
	W1	19	7	31					7	12			
	W2	19	7	31		7			7	8			
C11	- - - - - - UNKNOWN - - - - - -												

Table 4, continued.

Carcass number	Scavenger	Activity time (SACT)	SACT as a % of OBT**	SACT as a % of ACT**	Number of observation periods: Feeding FCC	FCI	FCP	FC	Moving MA	MP	Resting RA	RP	RC
C12	G1	8	3	9					7	5		5	
	R1	21	7	24		2	7		8	10		8	
	R2	8	3	9			5		3	6		1	
	W1***	65	23	75		19	6		21	13	2	53	
	W2	14	5	16	6	3	2		4	3			
C13	E1	15	4	8					11		2		
	E2	5	1	3					5				
	R1	136	32	77		10	7	10	40	29	12		
	R2	115	28	65		5	5	1	30	30	9		
	R3	99	24	56		5	5	1	24	17	17		
	R4	47	11	27		2	4	1	16	10	18		
	R5	25	6	14					9	4	8		
	R6	5	1	3					5				
	S1	5	1	3	2	2				1			
	W1	31	7	18	9	3			13	6	2		
	W2	1	<1	<1					1				

Table 4, continued.

Carcass number	Scavenger	Activity time (SACT)	SACT as a % of OBT**	SACT as a % of ACT**	Number of observation periods: Feeding FCC	FCl	FCP	FC	Moving MA	MP	Resting RA	RP	RC
C14	W1	- - - - - - -	UNKNOWN	- - - - - - -									
	B1												
	R1												
	R2												
C15	W1	- - - - - - -	UNKNOWN	- - - - - - -									
	R1												

*Total of all activities of the scavenger does not add up to activity time (SACT) because more than one of the activities could occur within one observation period.

**See Table 3.

***This wolf killed the caribou and is not considered a scavenger.

(Table 5); for the raven, the average was 2.00 days (0.00-4.50). The average for glaucous gulls was 2.25 days (0.25-4.50), for bears 3.25 days (1.25-6.00), and for jaegers 3.50 days (2.50-4.75). Wolves averaged 3.75 days (0.50-7.50) and golden eagles 4.75 days (4.00-5.50). Ground squirrels visited only one carcass, arriving after 3.50 days.

For the particular species which I observed and at the numbers I observed them, the following hierarchy existed at the carcasses in descending order of dominance: single adult bear, sow with cub, wolf, adult eagle, immature eagle, adult raven, immature raven, glaucous gull, and jaeger. Foxes and ground squirrels were not seen at carcasses with other species.

Major Activities

Three major activities occurred in the vicinity of the carcasses. Before discussing these, it is important here to establish the difference between "in the area" and "in the proximity" so that the following text will be clear to the reader. "In the area" refers to a distance from the carcass within which the scavenger is in the view of the observer and close enough to be able to find the carcass yet not so close as to affect the behavior of the other scavengers at the carcass. "In the proximity" of the carcass refers to a distance from the carcass within which a scavenger may have some effect on other scavengers at the carcass. Since these distances varied from situation to situation and from species to species, no set figures can be given to them. When no distinction between "in the area" and "in the proximity" is intended in the text,

Table 5. Arrival of each scavenger at the carcasses.*

Carcass number	Scavenger	Days passed before arrival
1	B1	1.25
	R1	2.25
	R2	2.75
	W1	2.75
	W2	3.75
	W3	3.75
	W4	3.75
	B2	4.75
	B3	4.75
2	R1	1.50
	F1	1.75
	W1	5.00
	W2	5.00
	E1	5.50
	E2	5.75
	B1	6.00
	B2	6.00
3	R1	0.75
	W1	1.25
	R2	1.50
	J1	2.50
	J2	2.50
4	R1	1.50
	W1	3.00
	B1	3.50
	B2	4.75
	B3	4.75
	J1	4.75
	J2	5.50
6	R1	2.25
	B1	2.50
	R2	7.25
	R3	7.25
7	R1	4.50
	G1	4.50
	W1	5.25
	W2	6.25
8	R1	1.50
	G1	2.25
	G2	2.25
	R2	2.50
	R3	3.50
	J1	3.50
	E1	4.00
	E2	5.25
	W1	7.25
	R3	9.25

Table 5, continued.

Carcass number	Scavenger	Days passed before arrival
9	R1	2.50
	R2	2.50
	B1	3.50
10	F1	0.75
	R1	1.25
	R2	1.25
	W1	1.75
	W2	1.75
	B1	1.75
12	R1	0.00
	R2	0.00
	G1	0.25
	W2	0.50
13	S1	3.50
	R1	3.75
	R2	3.75
	R3	3.75
	R4	3.75
	R5	3.75
	R6	3.75
	W1	7.50
	W2	9.25

*Only the scavengers that arrived in the proximity of the carcasses.

I refer to the "vicinity" of the carcass or the "carcass site."

The first and most important activity was "feeding" for which there are five categories: feeding on the carcass constantly, feeding on the carcass intermittently, feeding on fragments or parts of the carcass, feeding on caches made from the carcass, and feeding on items other than the carcass.

The second major activity is "moving" with two categories recognized: moving in the area of the carcass and moving in the proximity of the carcass.

The third major activity is "resting" with three categories: resting in the area of the carcass, resting in the proximity of the carcass, and resting on the carcass.

Proportion of time spent at each major activity

At most of the carcasses, the feeding behavior of the scavengers as well as the lack of visitations by some species was obviously related to the activity of other scavengers in the area. Though the proportion of time spent feeding by a particular scavenger species might remain nearly the same from one carcass to another regardless of other scavengers, the type of feeding that occurred was variable depending on the presence or absence of more dominant scavengers. The lower position of some species in the dominance hierarchy mentioned above did little to alter their feeding behavior at a carcass since these species simply avoided a carcass site if more dominant scavengers were present (e.g. foxes and eagles); however, other species attempted to feed even though more dominant scavengers were present (e.g. wolves and gulls), and the competition that resulted led to variation in the type of feeding behavior from one carcass to another.

It is difficult to say how the presence of other scavengers affected the amount or the type of moving or resting that occurred at a carcass, but it appeared that those species which tended to spend large proportions of time moving or resting at a carcass site did so despite the presence or absence of more dominant scavengers. For example, wolves spent larger proportions of time resting while waiting for an opportunity to feed on a carcass, but they would also rest long periods after gorging on a carcass. Eagles, on the other hand, spent proportionally smaller amounts of their time resting while at carcass site and most of the resting was done away from the carcass (RA).

Unfortunately, the data is not complete enough to generalize for all the scavenger species, but the following examples will illustrate some specific cases of how particular scavengers divided their time among the three major activities while they were at a carcass site and what factors appeared the most influential in this division.

At carcass no. 1, the grizzly depicted in Figure 3 had undisputed possession of the carcass during its first four days at the carcass. It spent most of its time resting on or near (RC, RP) the carcass with some short trips away from it (MP, MA) to scratch itself on willow bushes or paw at vegetation. Except when chasing off scavenging wolves or ravens or when scraping debris onto the carcass, the bear's feeding was largely uninterrupted (FCC vs FCI).

Figure 3. Proportion of time spent at the major activities by the bear and the wolf at carcass no. 1.

FCC - Feeding on the carcass continuously

FCI - Feeding on the carcass intermittently

FCP - Feeding on carcass parts

MA - Moving in the area

MP - Moving in the proximity of the carcass

RA - Resting in the area

RP - Resting in the proximity of the carcass

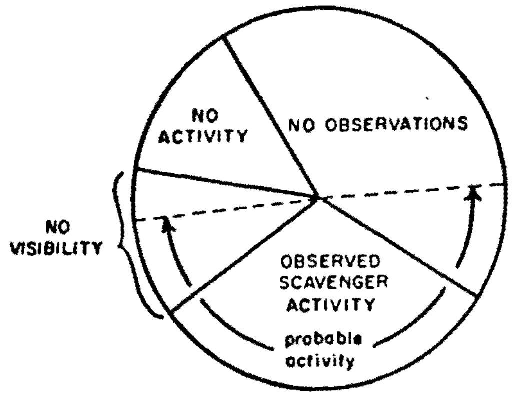
M-R - Combination of moving and resting

M-S - Combination of moving and scraping

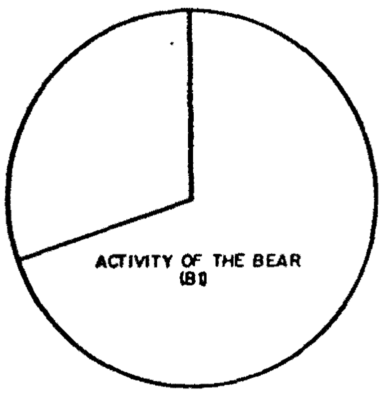
F-M - Combination of feeding and moving

R-F - Combination of resting and feeding

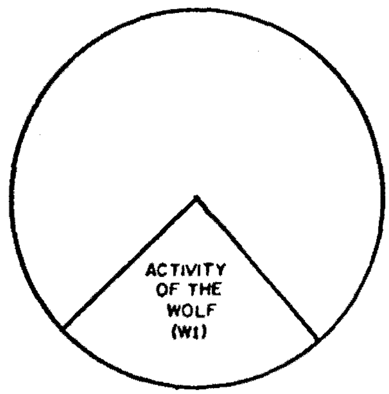
TOTAL TIME OF CARCASS NO. 1



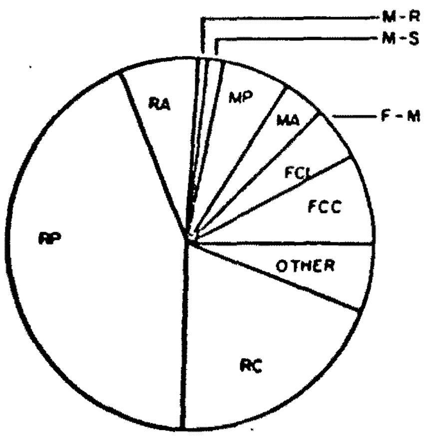
OBSERVED SCAVENGER ACTIVITY



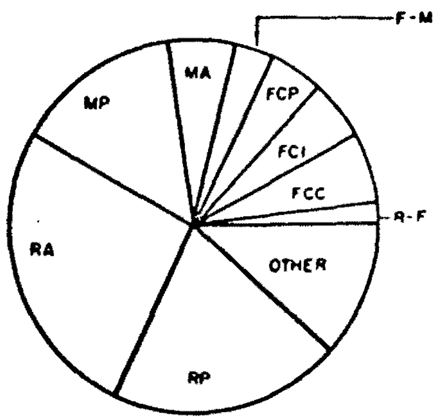
OBSERVED SCAVENGER ACTIVITY



ACTIVITY OF THE BEAR (B1)



ACTIVITY OF THE WOLF (W1)



However, the wolf at carcass no. 1 had to wait nearly 40 hours before it could feed on the carcass because the bear guarded the carcass closely until that time. Nearly 50 percent of this wolf's time at the carcass site was spent lying down waiting for an opportunity to feed. Occasionally the wolf would get up and approach the carcass while the bear was there, circling around and around (MP) while the bear made short lunges at it. Other times, the wolf merely walked about the site (MP, MA) sniffing the ground in various places before lying down again. When it was finally able to feed on the carcass (FCC), most of the meat had been eaten by the bear. The wolf would sometimes interrupt its feeding (FCI) to dig through the debris that the bear had scraped onto the carcass. The wolf also fed on carcass pieces (FCP) that the bear had spread about the site.

The eagle was the most dominant scavenger at carcass no. 8 (Fig. 4). This species did not visit carcasses if more dominant animals were present. Most of this eagle's time was spent feeding, usually without interruption (FCC). Typically, it would rest near the carcass (RP) for a short while after feeding, then fly to a promonotory in the carcass area where it would sometimes rest for long periods (RA).

The jaeger, most subordinant of the scavenger species, spent an even larger proportion of its time feeding than the eagle (Fig. 4). Occasionally it squatted nearby (RP) or moved about (MP) while the other scavengers fed, but usually it would leave the area to return later when no other scavenger was present. At these times, it would begin feeding immediately and without interuption (FCC), then fly or swim away from

Figure 4. Proportion of time spent at the major activities by the eagle and the jaeger at carcass no. 8.

FCC - Feeding on the carcass continuously

FCI - Feeding on the carcass intermittently

FCP - Feeding on carcass parts

MA - Moving in the area of the carcass

MP - Moving in the proximity of the carcass

RA - Resting in the area of the carcass

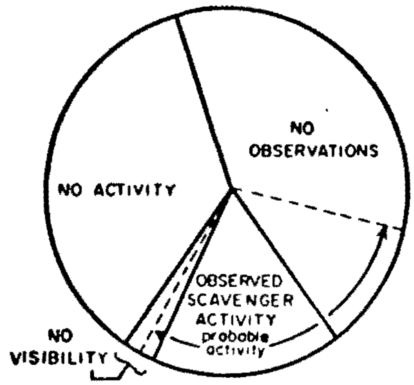
RP - Resting in the proximity of the carcass

M-R - Combination of moving and resting

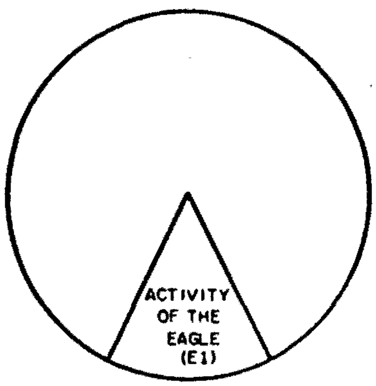
F-M-R Combination of feeding, moving, and resting

F-R - Combination of feeding and resting

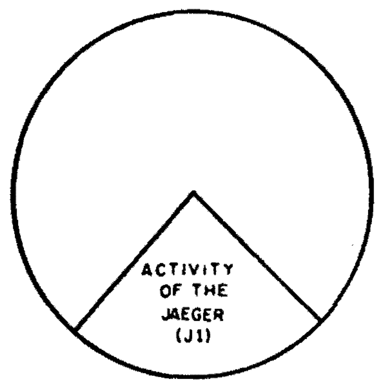
TOTAL TIME OF CARCASS NO. 8



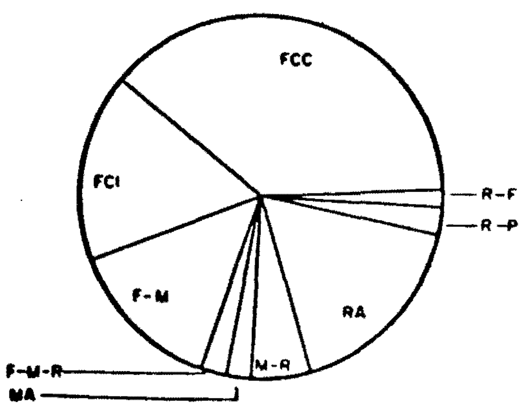
OBSERVED SCAVENGER ACTIVITY



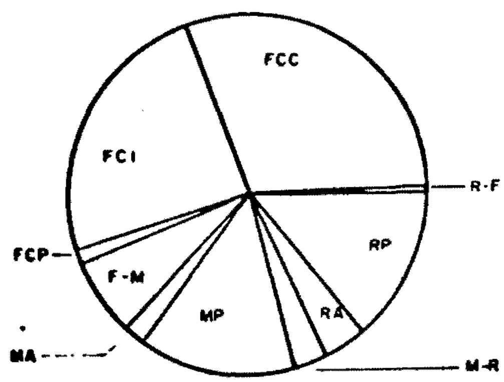
OBSERVED SCAVENGER ACTIVITY



ACTIVITY OF THE EAGLE (E1)



ACTIVITY OF THE JAEGER (J1)



the carcass site. It sometimes made successful attempts to feed at the carcass when a raven or gull was present, but its feeding was constantly interrupted by these more dominant scavengers (FCI).

Human scent may also affect the manner in which scavengers (particularly the mammalian scavengers) proportion their time at a carcass. Because carcass no. 3 (Fig. 5) had been handled by several people, the wolf that found the carcass was afraid to approach it and would not feed on it for over 39 hours. Over 65 percent of the wolf's time at the carcass site was spent lying down (RP). Despite a plague of mosquitoes and a heavy rainstorm, it did not leave the carcass vicinity. Once it move higher up the slope above the carcass where it lay down again (RA). On several occasions it spent short periods investigating the area around the carcass site (MA), sometimes catching mice and occasionally finding raven caches to eat (F-M). Only the awareness of an approaching grizzly, still a mile or more upstream, induced the wolf to start feeding on the carcass. It fed rapidly, almost immediately disconnecting one of the hind legs of the caribou carcass. It alternately fed on the main carcass (FCC, FCI) and on this leg (FCP). With the aid of several caching trips, the wolf was able to remove much of the meat during this first day of feeding. The grizzly had stopped at another carcass farther upstream and never did visit the carcass on which the wolf was feeding.

Neither bears nor human disturbance interfered with the behavior of the wolf at carcass no. 7 (Fig. 5). Though the proportion of its feeding time was nearly the same as that of the wolf at carcass no. 1 (Fig. 3), nearly all of its feeding was without interruption (FCC).

Figure 5. Proportion of time spent at the major activities by the wolf at carcass no. 3 and the wolf at carcass no. 7.

FCC - Feeding on the carcass continuously

FCI - Feeding on the carcass intermittently

FCP - Feeding on carcass parts

MA - Moving in the area of the carcass

MP - Moving in the proximity of the carcass

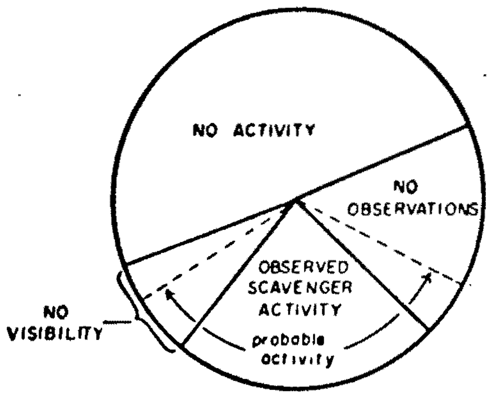
RA - Resting in the area of the carcass

RP - Resting in the proximity of the carcass

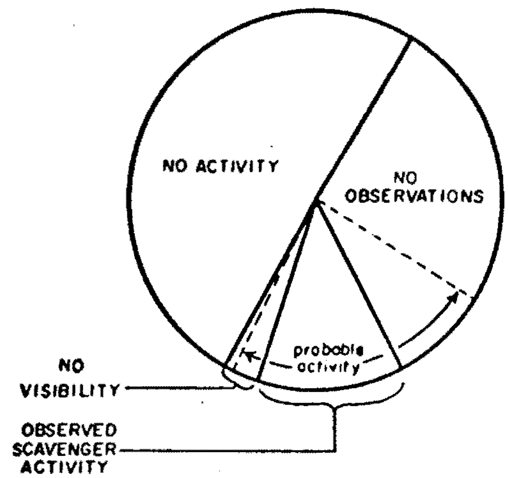
M-R - Combination of moving and resting

F-M - Combination of feeding and moving

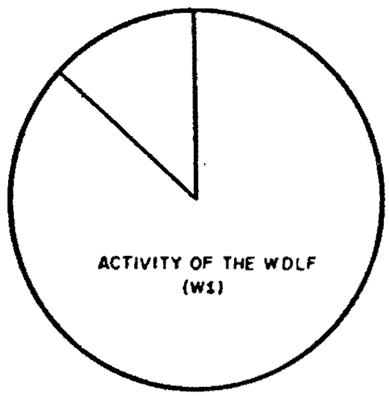
TOTAL TIME OF CARCASS NO. 3



TOTAL TIME OF CARCASS NO. 7



OBSERVED SCAVENGER ACTIVITY



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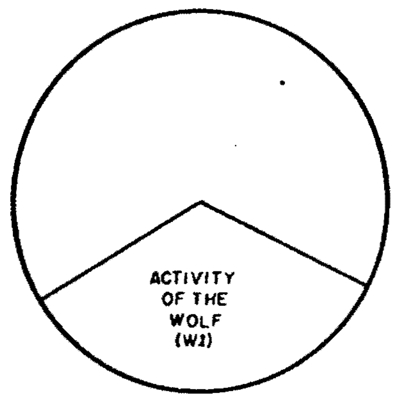
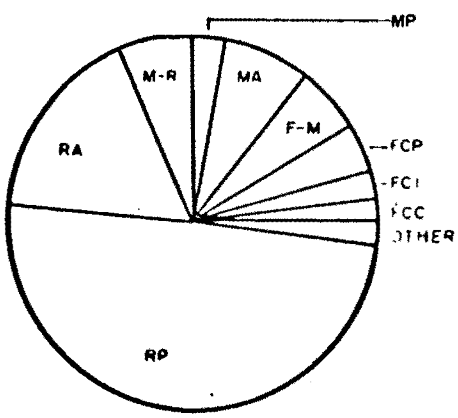
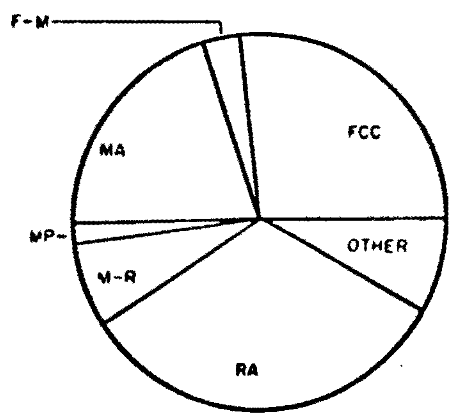


ACTIVITY OF THE WOLF (W1)



ACTIVITY OF THE WOLF (W1)



Feeding sessions were often followed by periods of rest (RA, RP). The wolf did not spend much time moving about (MA, MP) except when caching meat, looking for raven caches, or leaving the carcass to return to a den site.

The same scavenger may react very differently at two different carcasses with no obvious reason for the difference. I believe the gull at carcass no. 7 (Fig. 6) was the same as the one at carcass no. 8. Shortly after wolves finished carcass no. 7, carcass no. 8 became available 1 mile (1.6 km) upstream. When the gull visited carcass no. 7, it appeared to be apprehensive about approaching even when no other scavengers were in the area. The bird spent much of its time moving about the site (MA, MP), picking up scraps of meat and dried blood (FCP, F-M) or drinking water (F-D). About a quarter of its time was spent resting near the carcass (RP). Only on the gull's third visit to the carcass did the bird begin to feed (FCC, FCI) and then only sporadically. Whenever a wolf, the major scavenger at this carcass, was in the carcass vicinity, the gull left the area.

No mammalian scavengers fed on carcass no. 8 during my observations. When the more dominant among the avian scavengers were not present, the gull fed on this carcass without interruption (FCC). It often fed intermittently in the company of ravens and eagles (FCI). After feeding, the gull would rest or move about in the area, sometimes preening or fishing in the river nearby. The apprehension with which the gull approached carcass no. 7 was not seen at carcass no. 8.

Figure 6. Proportion of time spent at the major activities by a gull at carcasses no. 7 and no. 8.

FCC - Feeding on the carcass continuously

FCI - Feeding on the carcass intermittently

FCP - Feeding on carcass parts

MA - Moving in the area of the carcass

MP - Moving in the proximity of the carcass

RA - Resting in the area of the carcass

RP - Resting in the proximity of the carcass

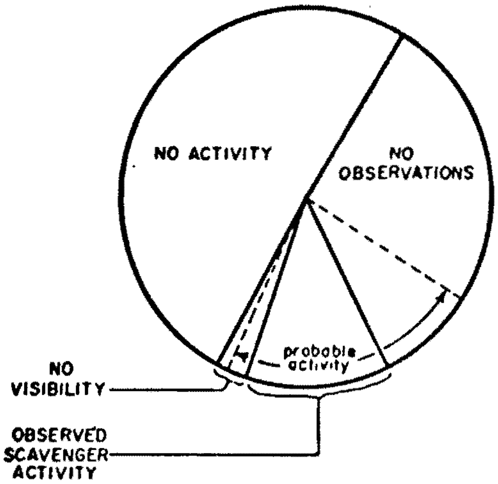
F-D - Combination of feeding and drinking

F-M - Combination of feeding and moving

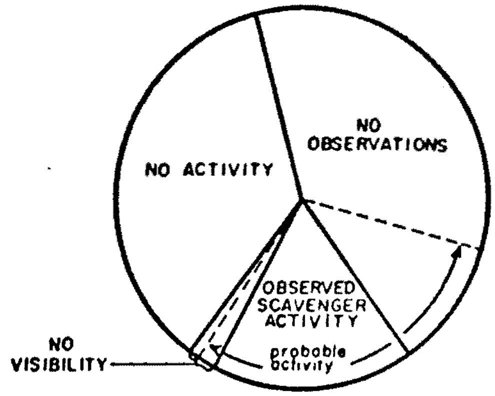
M-R - Combination of moving and resting

R-F - Combination of resting and feeding

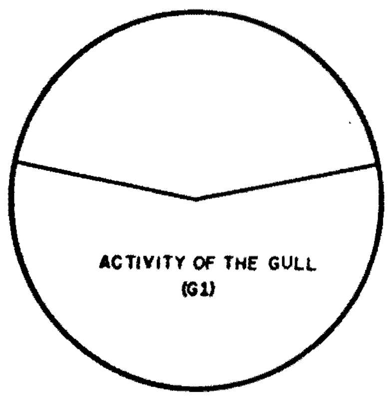
TOTAL TIME OF CARCASS NO. 7



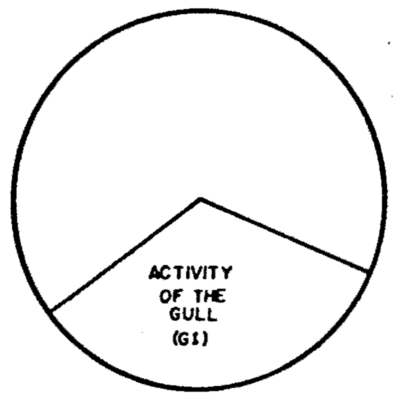
TOTAL TIME OF CARCASS NO. 8



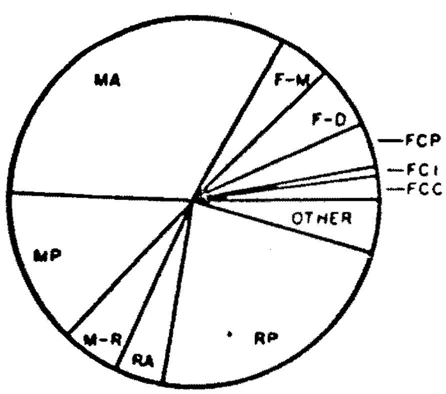
OBSERVED SCAVENGER ACTIVITY



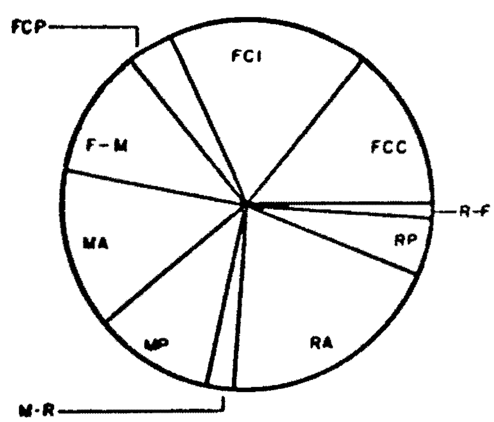
OBSERVED SCAVENGER ACTIVITY



ACTIVITY OF THE GULL (G1)



ACTIVITY OF THE GULL (G1)



Average duration of major activities

Each major activity and its components are graphically displayed in Figures 7, 8, and 9 to show the average duration of that activity for each species of scavenger. The longest session and the total number of sessions of each activity are shown beneath the respective graph. Since the shortest sessions were nearly always of 5-minute duration or less, they are not shown on the graphs. Table 6 gives the frequency of occurrence of each major activity within seven categories of duration for each species to show the variability in duration.

There is no significant difference (x^2=0.602) between each species' average feeding session and the mean session for all the species combined. The difference between the shortest average session (19 minutes for the wolf and the raven) and the longest (24 minutes for the jaeger) is only 5 minutes. However, there is some variation among the species in the way "feeding" is distributed among its component parts. The eagle did not feed on carcass fragments (FCP) as all the other scavengers did. The raven spent longer sessions at intermittent feeding (FCI) than the other scavengers due to the frequent interruption of feeding at short intervals for caching purposes. Sessions of feeding without interruption (FCC, FCP) were proportionally longer than intermittent feeding (FCI) for bears, wolves, and jaegers. Bears and wolves, the animals highest in the scavenging hierarchy, had fewer interruptions from more dominant scavengers; the jaeger often waited until all other scavengers which might interrupt its feeding had left the carcass site before it fed.

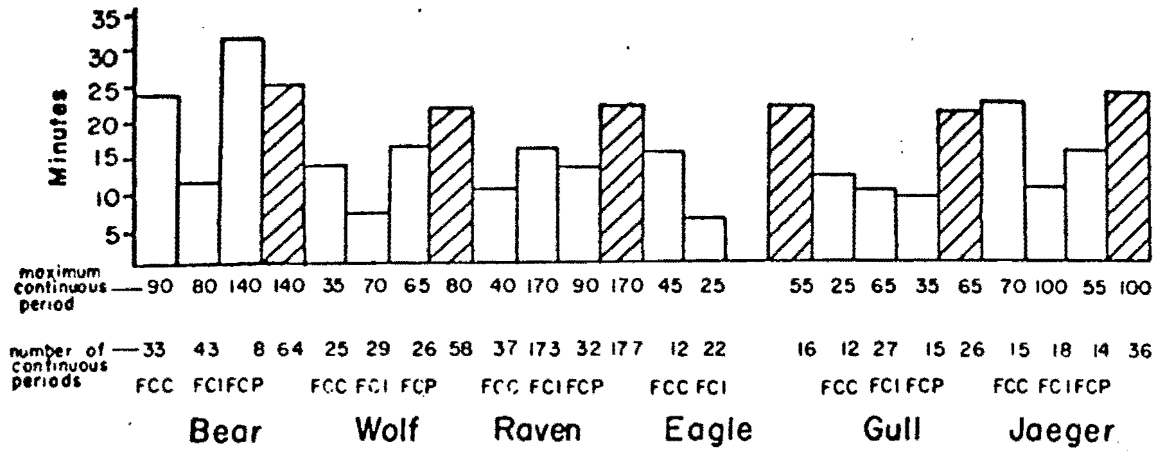
Although there is no significant difference between the average

Figure 7. Average duration of continuous feeding sessions.*

Figure 8. Average duration of continuous moving sessions.

Figure 9. Average duration of continuous resting sessions.

*Shaded bars indicate all components of the major activity combined.


Minutes
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maximum continuous period — 90 80 140 140 35 70 65 80 40 170 90 170 45 25 55 25 65 35 65 70 100 55 100
number of continuous periods — 33 43 8 64 25 29 26 58 37 173 32 177 12 22 16 12 27 15 26 15 18 14 36
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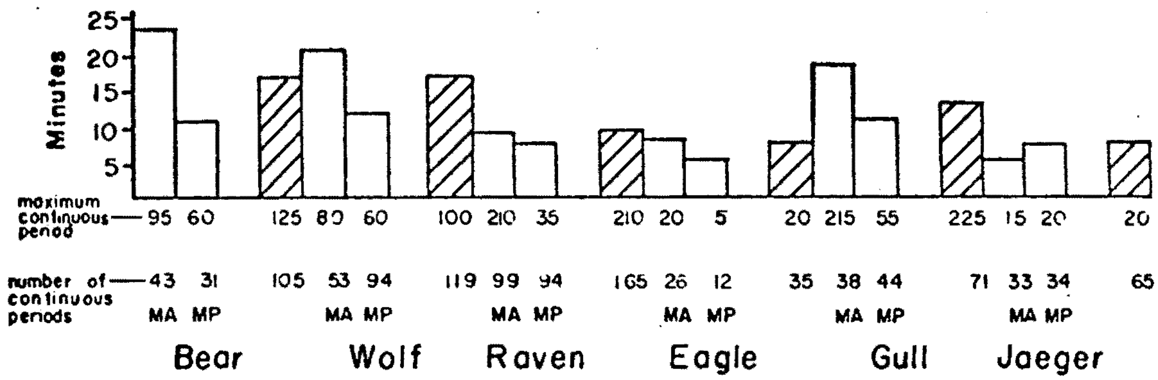
Bear Wolf Raven Eagle Gull Jaeger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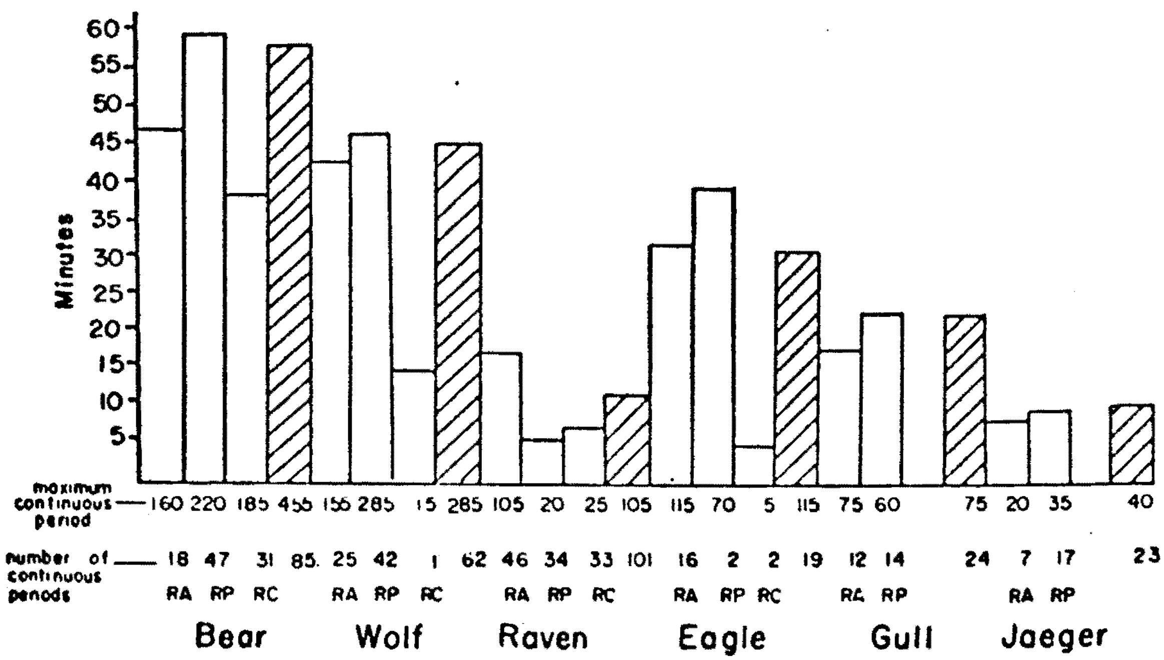
Bear Wolf Raven Eagle Gull Jaeger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number of continuous periods — 18 47 31 85 25 42 1 62 46 34 33 101 16 2 2 19 12 14 24 7 17 23
RA RP RC RA RP RC RA RP RC RA RP RC RA RP RA RP
Bear Wolf Raven Eagle Gull Jaeger

Table 6. Variation in the duration of the activity sessions (% of the activity sessions that occurred in seven categories of duration).

	Minutes						
	-5	10-30	35-55	60-80	85-105	110-130	135-155
FEEDING							
Bear	32	44	17	3	2	0	2
Wolf	38	43	14	5	0	0	0
Raven	31	53	11	3	1	0	0
Eagle	19	62	19	0	0	0	0
Gull	27	50	19	4	0	0	0
Jaeger	39	33	22	3	3	0	0
MOVING							
Bear	43	47	7	1	1	1	0
Wolf	38	53	5	2	2	0	0
Raven	67	32	0	1	0	0	0
Eagle	71	29	0	0	0	0	0
Gull	65	24	6	3	0	0	0
Jaeger	78	22	0	0	0	0	0
RESTING							
Bear	28	22	16	11	7	6	1
Wolf	35	18	18	14	2	2	6
Raven	62	31	5	1	1	0	0
Eagle	26	37	16	16	0	5	0
Gull	33	33	21	13	0	0	0
Jaeger	61	35	4	0	0	0	0

session of "moving" (x^2=6.320) for each species and the mean session of "moving" of all the scavengers, it is obvious that bears, wolves, and gulls on the average have longer sessions of "moving". Although about 40 percent of the movement sessions for bears and wolves were less than 5 minutes long (see Table 6), they undertook some lengthy movements while searching for fragments of the carcass or other food items. Confrontations between bears and wolves and among conspecifics of these two species at a carcass site sometimes involved long sessions of movement. The gull's relatively lengthy average movement session was in response to its tendency to remain in the carcass area, even after feeding, and to spend long sessions preening and attempting to catch fish in the river nearby. The difference between the shortest average session of "moving" (7 minutes for the jaeger) and the longest (17 minutes for the gull) is 10 minutes.

There is a significant difference at the .001 level between the average session of "resting" for each species and the mean for the average rest session of all the species. The difference between the shortest average session (10 minutes for the jaeger) and the longest (60 minutes for the bear) is 50 minutes. Length of average rest sessions, in general, declined with the position of the species in the dominance hierarchy. The raven is the only species that is misplaced in this scheme. Ravens rarely rested in the area of the carcass.

Activity in relation to time of day

Tables 7, 8, and 9 are the total feeding, moving, and resting

Table 7. Feeding in relation to four quarters* of the day.

Species	Quarter	Total feeding time (no. of 5-minute periods)	Expected value**	No. of days feeding observed in this quarter	Expected value
Wolf	First	50	77	9	77
	Second	98	79	12	12
	Third	79	76	13	12
	Fourth	75	69	12	12
Bear	First	92	78	9	10
	Second	38	78	5	10
	Third	75	78	11	10
	Fourth	99	69	16	10
Eagle	First	10	18	2	2
	Second	49	22	7	2
	Third	12	18	3	2
	Fourth	3	15	2	2
Raven	First	67	184	9	22
	Second	305	200	29	22
	Third	328	205	37	22
	Fourth	87	197	14	22
Gull	First	9	26	2	4
	Second	34	30	7	4
	Third	40	30	5	4
	Fourth	34	31	4	4
Jaeger	First	1	41	1	6
	Second	22	43	7	6
	Third	85	41	9	6
	Fourth	63	46	8	6

*First quarter 0005-0600; Second quarter 0605-1200; Third quarter 1205-1800; Fourth quarter 1805-2400.

**Random distribution of the activity assumed and the values adjusted according to the amount of observation time in each quarter.

Table 9. Resting in relation to four quarters* of the day.

Species	Quarter	Total feeding time (no. of 5-minute periods)	Expected value**	No. of days feeding observed in this quarter	Expected value
Wolf	First	142	166	11	9
	Second	152	172	5	9
	Third	253	165	13	9
	Fourth	107	151	7	9
Bear	First	162	255	7	9
	Second	181	255	8	9
	Third	324	254	11	9
	Fourth	323	224	10	9
Eagle	First	3	32	2	4
	Second	22	38	4	4
	Third	73	31	4	4
	Fourth	30	27	4	4
Raven	First	6	86	4	21
	Second	214	93	36	21
	Third	110	96	35	21
	Fourth	37	92	9	21
Gull	First	4	26	1	4
	Second	35	30	7	4
	Third	35	30	5	4
	Fourth	44	31	4	4
Jaeger	First	0	11	0	3
	Second	16	12	2	3
	Third	21	12	5	3
	Fourth	11	13	4	3

*First quarter 0005-0600; Second quarter 0605-1200; Third quarter 1205-1800; Fourth quarter 1805-2400.

**Random distribution of the activity assumed and the values adjusted according to the amount of observation time in each quarter.

times, respectively, of each species of scavenger for four quarters of the day. For each species, times were calculated for the total amount of feeding, moving, and resting by all individuals of that species for each of the four quarters. A value was also calculated for the time a species would be expected to feed, move, or rest in each quarter if the activity was randomly distributed among all quarters. A chi-square value was then obtained to test whether the actual times spent in each activity for each quarter was significantly different from the expected values. The same test was run to determine whether the number of days a species was observed at the activity for each of the four quarters was significantly different from the expected values.

There were significant differences between the expected values and the actual amounts of time that bears (0.001 level), wolves (0.1 level), gulls (0.01 level), and jaegers (0.001 level) spent feeding in the four quarters of the day. There was no significant differences between the expected values and the numbers of days they fed in the different quarters. For eagles and ravens, the difference was significant for both the amounts of time (0.001 level for both) and the numbers of days (0.05 level and 0.001 level, respectively).

There were significant differences between the expected values and the actual amounts of time that bears (0.02 level) and wolves (0.001 level) moved in each of the four quarters, but no significant differences in the numbers of days they moved in the respective quarters. The differences were significant in both the amounts of time and the numbers of days for the eagle (0.01 level; 0.02 level), the raven (0.001

level; 0.001 level), the gull (0.001 level; 0.05 level), and the jaeger (0.001 level).

Lastly, all the species show a high significant difference (0.001 level) between the expected values and the amounts of time they spent resting in the four quarters. The differences between the expected values and the numbers of days were significant for the wolf (0.035 level), the raven (0.001 level), the gull (0.035 level), and the jaeger (0.05 level) but were not significant for the bear and the eagle.

Change in the amount of feeding over the days of the carcass

The situation from one carcass to another varied so much with the number and kind of scavengers, with the size and condition of the carcasses, and with weather, human interference, and other factors that a generalization about the change in feeding time of the scavengers as the carcass was utilized is not possible at this time. Therefore, I have presented some of the changes that occurred from day to day, to point out various influencing factors that effected these changes.

Figure 10 illustrates the feeding times of three scavengers at carcass no. 1, a moose carcass. There was a gradual decline in the bear's feeding time and a gradual increase in the wolf's while the raven showed an abrupt increase followed by a rapid decline.

The gradual decrease in the feeding time of the bear was most probably due to the satiation of the bear's post-denning hunger; the bear found the carcass on 28 May when the ground was still snow-covered. The bear's feeding time was not affected by other scavengers until the

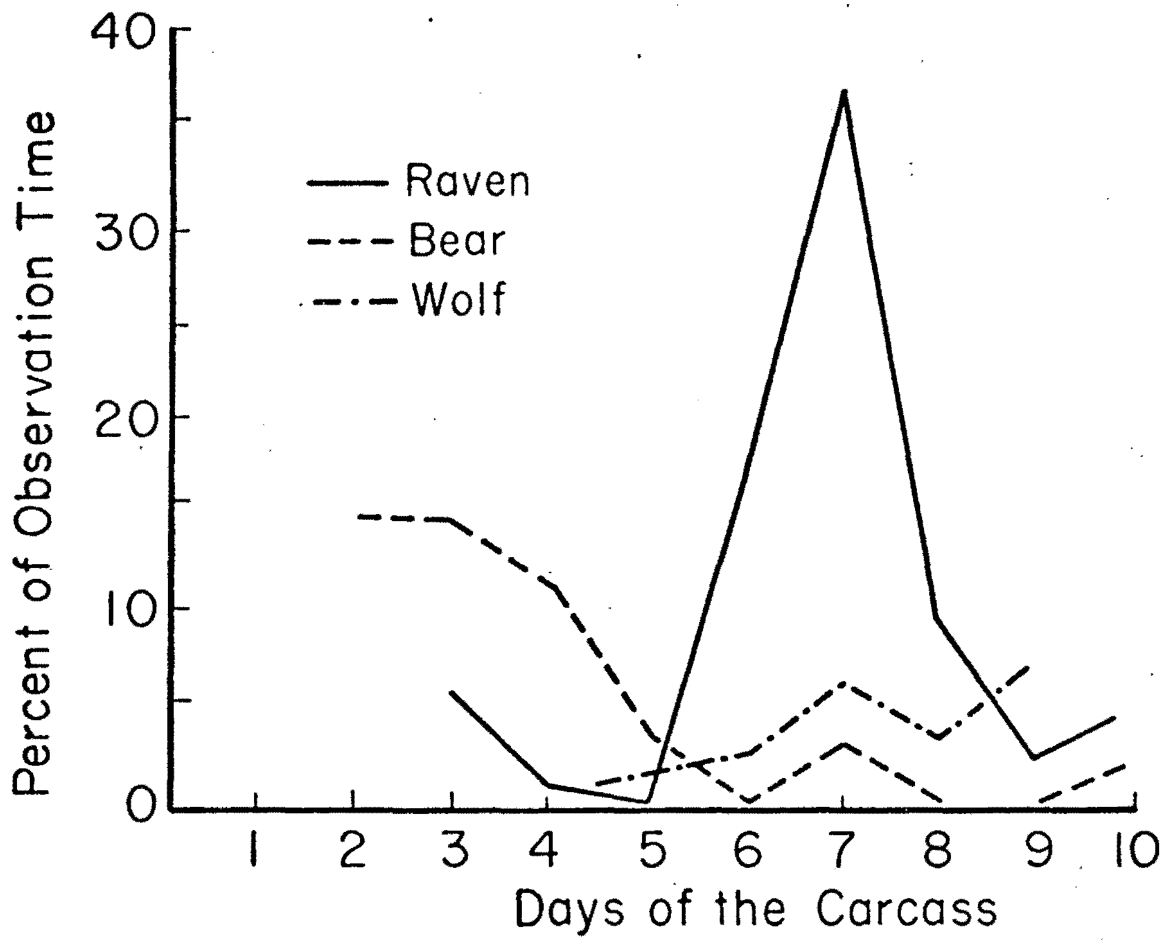

Figure 10. Feeding time of three scavengers at carcass no. 1.

Day 1 - Carcass became available at 0400

Day 2 - Bear (B1) arrived at 0931

Day 3 - Raven (R1) arrived at 0852 and B1 began scraping; wolf (W1) arrived at 1830

Day 5 - Two more bears (B2 and B3) arrived at 2330 and uncovered the carcass

Day 6 - No bears present from 0500 to 2000

Day 7 - No bears until B1 returned at 1700

Day 8 - No bears present; carcass nearly gone arrival of a more dominant boar late on the fifth day. By that time, however, the bear depicted in the graph had already decreased its feeding to a level which it sustained throughout the remaining days even when no other bears were present.

The wolf's feeding time was influenced by the presence of the bear. Though the wolf arrived late on the third day, its feeding did not begin to increase until late on the fifth day when the carcass lay unguarded during a confrontation between two bears at the carcass site. Since the bears were gone on the sixth and most of the seventh day, the wolf was able to increase its feeding time on those days. However, by the seventh day, most of the meat from the carcass had been eaten, and the wolf spent some of its time gnawing on bones and even tried to catch mice in the carcass area. Its feeding time never reached the level observed for the bear and the raven.

The raven's feeding time was directly related to the activity of the other scavengers. It arrived on the third day and managed to feed on the carcass during a small percentage of the observation time despite 20 attempts by the bear to chase it away. However, the raven's time decreased on the fourth and fifth days despite a decrease in the bear's feeding time and an increase in its resting time. The reduction in the raven's feeding activity occurred because the bear had begun scraping litter onto the carcass when the raven arrived; it continued scraping material onto the carcass on the fourth and fifth days. I believe the scrapings prevented ravens from feeding on the carcass. Late on the fifth day, two more bears arrived and uncovered the carcass to feed.

A wolf also arrived and removed some of the litter. The next two days, raven activity increased markedly with minimal disturbance. Wolf activity was sporadic during those two days, and no bears were present until 1700 on the seventh day.

Carcass no. 3 (Fig. 11) and no. 7 (Fig. 12) were both caribou carcasses at which the wolf was the dominant scavenger. Carcass no. 3 had been handled by the observers; carcass no. 7 had not been. When a wolf arrived at carcass no. 3, it was very apprehensive and moved cautiously around in the carcass vicinity; it would lie down for short periods and then move around the area again. It did not feed on the carcass at all on this day, but it did check some locations of caches made by ravens and may have eaten one of these caches. There was a small amount of meat exposed at the site of a bullet wound. Though ravens had landed at the carcass at 1530 on the second day, they did not begin to feed until the wolf's arrival at 1900. Raven feeding and caching continued for three hours late into the evening.

On the third day, the wolf was not in sight from 0020 to 0530; for the remainder of the day, it rested and moved around in the vicinity of the carcass, feeding on raven caches or catching microtines. It approached the carcass to within 20 ft (6.1 m) but remained timid and would not feed on the carcass. The increase in the wolf's feeding time shown on the graph for the third day is entirely due to the wolf's feeding on raven caches. The raven continued to feed around the wound during most of the day but the feeding activity was less intense. Most caches were made near the carcass even though the wolf was finding and

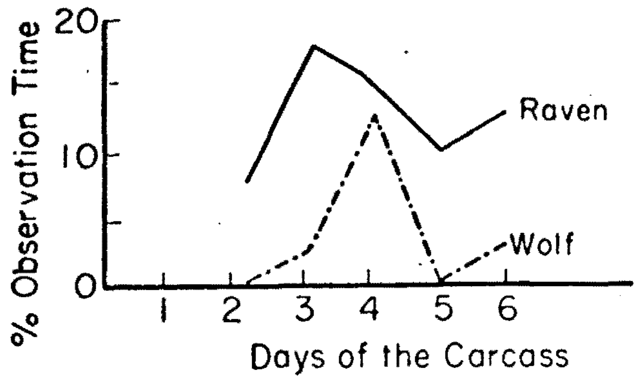

Figure 11. Feeding time of a wolf and a raven at carcass no. 3.

Day 1 - carcass became available at 1800

Day 2 - Wolf (W1) arrived at 1900; two ravens (R1 and R2) arrived at 1530

Day 3 - W1 fed on raven caches only

Day 4 - W1 detected grizzly in the area at 0948 and began feeding on the carcass at 1010

Day 5 - Carcass nearly gone

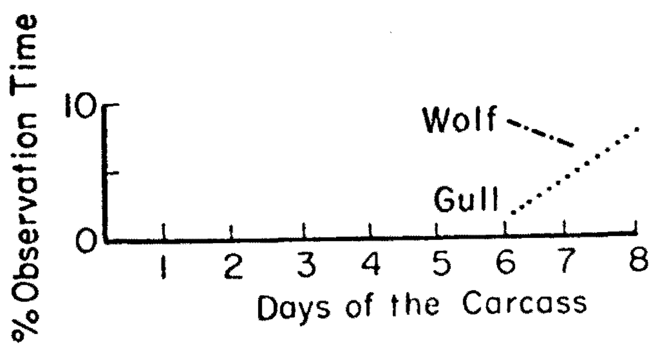

Figure 12. Feeding time of a wolf and a gull at carcass no. 7.

Day 1 - Carcass became available at 1730

Day 5 - A gull (G1) seen near the carcass at 1415

Day 6 - A wolf (W1) arrived at 0715; G1 arrived at 1000

Day 7 - W1 returned at 0120; another wolf (W2) arrived at 0622; both wolves gone by 2015

Day 8 - Carcass nearly gone

eating many of them. Later in the day, raven feeding activity became very sporadic.

The wolf had still not fed on the carcass by the morning of the fourth day. When the raven landed at the carcass, it pecked for 20 minutes on the carcass then left the carcass site without caching. On the fourth day at 1445, the wolf approached to within 10 ft (3.0 m) of the carcass but suddenly jumped backward as if frightened. It moved away and disappeared into the creekbed nearby. At 0947 I saw a bear about 1 mi (1.6 km) upstream moving down the valley toward the carcass. The wolf came out of the willows near the bear and moved hurriedly toward the carcass. The wolf began feeding on the carcass at 1010 without hesitation. Twelve minutes after the wolf began feeding, the raven returned to feed and cache for the next 2 hours. By 1024 the wolf had skinned the entire visible portion of the carcass and had removed much of the meat from one of the hind quarters. It would still jump away from the carcass on occasion but continued feeding until 1036 when it moved to the bank of the creek and cached some meat. It returned at 1038, fed until 1047 then disappeared until 1122 when it returned to feed again until 1145. It continued its feeding and caching activity until 1355 when it began a period of rest. Then it left the carcass area and was not seen again until the sixth day. There was not much of the carcass remaining by then. In less than two days after the feeding began, a single wolf had removed most of the meat from the caribou carcass.

Although the wolf at carcass no. 7 may have been aware of humans in the area, I feel that its behavior closely typified that of wolves at carcasses where there is no interference from bears or humans. The wolf located the carcass six days after the carcass became available. Until then no other scavenger had fed on the carcass except a raven which removed the eye shortly before the wolf arrived. From 0715 on the sixth day to 0235 on the seventh day, the wolf fed six times, ranging in duration from 10 minutes to 35 minutes. The feeding sessions were separated by intervals of 21 minutes to 7 hours and 42 minutes. During these intervals, the wolf cached meat, rested, or was gone from the carcass vicinity. At 1622 on the sixth day, the wolf returned accompanied by a second wolf. They fed together for 25 minutes before the first wolf left. The second wolf continued to feed and returned to feed one more time that day, but not much of the carcass remained by then. Two wolves, in less than 3 hours of feeding in two days (67% by the first wolf), disposed of almost an entire caribou.

Avian scavengers could feed on the carcass after it had been opened by the wolf. A gull began visiting the carcass on the day the wolf arrived. The bird's feeding time increased over the next two days as the wolf's absences from the carcass site increased. By the eighth day, very little remained of the carcass.

Carcass no. 8 was also a caribou carcass but was fed on entirely by avian scavengers (Fig. 13). Meat was still available on this carcass nine days after feeding began. Feeding by all the scavengers at this carcass fluctuated over the days of the carcass, ravens and jaegers showing a higher amplitude than gulls and eagles. Ravens, the first

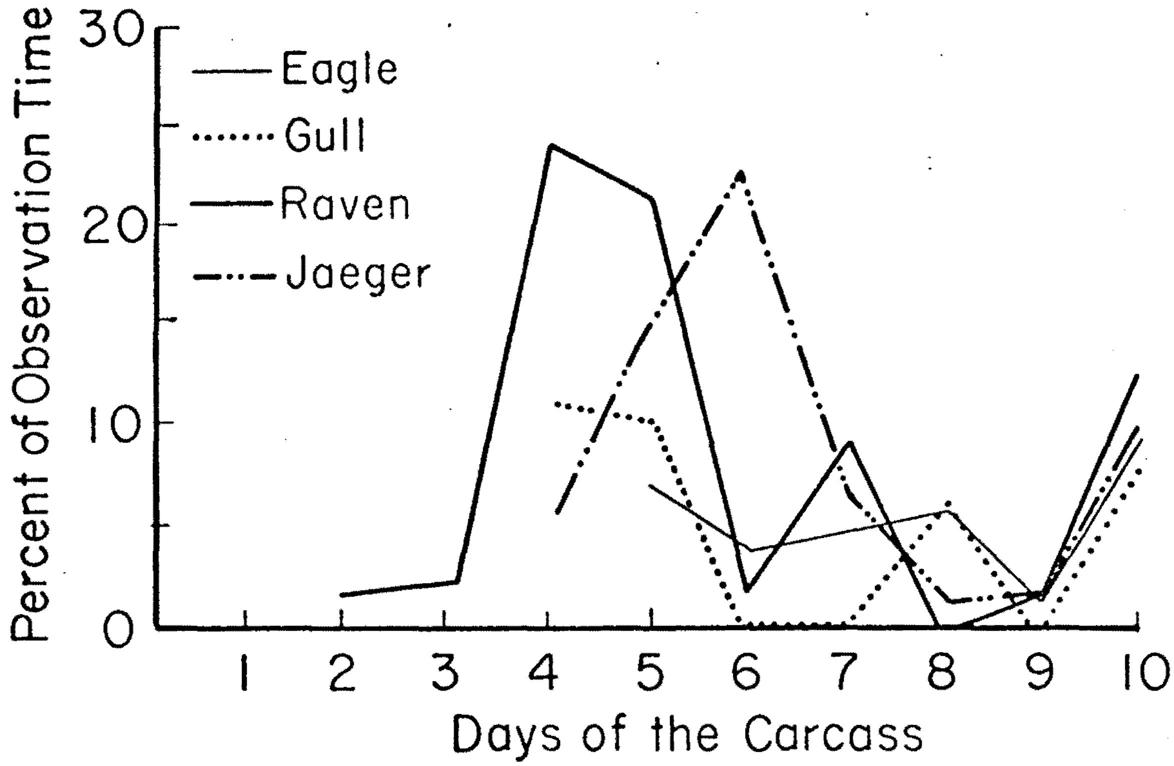

Figure 13. Feeding time of four avian scavengers at carcass no. 8.

Day 1 - Carcass became available at 2230

Day 2 - A raven (R1) arrived at 1115

Day 4 - A gull (G1) arrived at 0945; a jaeger (J1) arrived at 1427; rain most of the day

Day 5 - An eagle (E1) arrived 0327

Day 6 - Observers were at the carcass site during most of the day

Day 7 - Rain and wind from 1200 to 2400

Day 8 - Rain and wind all day

scavenger to arrive, fed extensively on the carcass on the fourth and fifth day, then their feeding activity dropped to a much lower level. My presence near the carcass on the sixth day and rain and strong wind on the afternoon of the seventh and all day on the eighth may have been influencing factors, but ravens fed during a heavy rain on the fourth day when the greatest amount of feeding occurred; I do not feel that rain and wind would seriously deter ravens from feeding on a carcass. Very few observations were made on the ninth day, and the feeding which was observed was probably not representative for that entire day. I do not know why there was increased activity on the tenth day by all the avian scavengers.

The jaeger, despite its subordinance in the company of the other avian scavengers, was able to feed extensively on the carcass because it usually visited the carcass after the other scavengers had left the area. Because it showed no fear of the observers, it fed on the sixth day much more than all the other birds. It would feed on the carcass when I was standing only 10 ft (3.0 m) from it. Reasons for its decline in feeding activity over the remaining days was not evident.

Despite the activity of ravens and an eagle, the gull's feeding time on the fourth and fifth days was greater than for any of the other days of the carcass. The gull would rest or move about the site taking advantage of any opportunity to feed; it also fed undisturbed after the eagle and ravens left. On the sixth day, the ravens and the eagle were able to feed for a short while before the observers arrived at the carcass, but the gull did not have the opportunity to feed. The gull made several attempts to feed on the carcass in the morning of the seventh day, but because a raven kept chasing it, it left the carcass area around 0810; it did not return for the remainder of the day even though there were many opportunities to feed when no other scavengers were present. There was a light rain during all the afternoon, but this would not have discouraged the gull from visiting the carcass. The gull resumed feeding on the eighth day. Heavy rain and wind did not discourage it. The failure of the ravens to visit the carcass that day allowed the gull to feed without interruption.

Minor Activities

Most of a scavenger's activity in the vicinity of a carcass involved feeding, moving, or resting. In addition to or during these activities, however, scavengers were often engaged in minor or short term activities; caching, scraping, drinking, grooming, vocalizing, urinating or defecating, and inter- and intraspecific interactions. Not all of these are directly related to the act of scavenging, but the results for each will be given since they are part of the total behavior pattern of a scavenger near a carcass.

Caching

Only two species of scavengers were observed caching meat from carcasses, the wolf and the raven. During 839 observation periods in which ravens were feeding, these birds made 382 caches or 1 cache per 2.2 observation periods. Wolves made 28 caches in 259 observation periods in which wolf feeding occurred or 1 cache per 9.2 observation periods.

The amount of caching activity is not always the same from one carcass to another. From carcass no. 1, the rate of caching by ravens was one cache per 2.2 observation periods in which feeding occurred; at carcass no. 3 the rate was greater, one cache per 1.3 observation periods, but at carcass no. 8, ravens made only one cache per 4.0 observation periods.

Variation in the rate of caching by wolves is shown by these examples: one cache per 16.7 observation periods in which feeding occurred at carcass no. 12, one cache per 6.7 observation periods at carcass no. 3, and one cache per 3.8 observation periods at carcass no. 7.

Of the total 382 caches made by ravens, 316 were cached away from the carcass (i.e. the raven flew to the caching location) and 66 caches (17%) were made in the proximity of the carcass (i.e. the raven walked, hopped, or glided to the caching location usually within 50 yds (45.8 m) of the carcass) (see Table 10).

Wolves only made 1 of 28 caches (3%) in the proximity of the carcass (i.e. within 50 yds (45.8 m) of the carcass).

Table 10. Number of caches made by ravens and wolves.

Carcass number	Ravens CA*	Ravens CP	Wolves CA	Wolves CP
1	121	8	0	0
2	1	0	3	1
3	81	35	5	0
6	14	7	0	0
7	3	0	9	0
8	65	4	0	0
10	14	12	0	0
12	5	0	8	0
13	12	0	2	0
Total	316	66	27	1

*CA indicates caching away from the carcass and CP indicates caching in the proximity of the carcass.

Raven caches were made in several different types of locations. When a carcass was lying in a riverbed, ravens would often cache meat under pieces of flotsam or cover the caches with sand, small stones, or debris. They were seen caching meat on rocky hillsides, in sedge meadows, and among vegetation on moist slopes. It was not always possible to see whether ravens covered the caches with material, tucked it under vegetation or rocks, or merely left it partly exposed among the vegetation or rocks. But in many cases, ravens were definitely seen covering their caches with material.

Wolves nearly always cached meat in loose soil, usually along streams on sand bars or under willows. One wolf cached a leg bone in a snowbed. The method used to cache meat was typical of many canids. A hole was dug with the forefeet, the meat placed in the hole, and soil or snow pushed over the meat with the nose.

Ravens carried food both in the bill and in a buccal pouch from which they later regurgitated it for caching. Wolves carried meat in the mouth and in the stomach and also regurgitated meat for caching.

Ravens generally made only one or two caches during a caching trip. Ravens at carcass no. 1 were timed during an extensive feeding session to determine the time required for a caching trip. The average for 15 caching trips was 120 seconds with 50 seconds being minimum and 206 seconds being the maximum time observed to complete a caching trip. During 2 of the 15 trips, two caches were made (averaging 172 seconds per trip) and during the remaining 13 trips, only one cache was made (averaging 105 seconds per trip). The actual time to make a cache once the raven was on the ground averaged 28 seconds and ranged from 15 seconds to 56 seconds.

Usually it was difficult to observe wolves caching because they often disappeared into willows or went out of sight behind a hill. On one occasion, one wolf made six separate caches during one caching trip after feeding for 20 minutes. All six caches were completed within 10 minutes after the wolf left the carcass. The caches were dug in sandy soil along the river about 150 yds (137.4 m) from the carcass. All but one were placed beneath willow bushes. At one of the caches, the wolf deposited three to five pieces of meat in the hole before covering it over with sand. At other times, wolves made only one or two caches during one caching trip.

Attempts to estimate the subsequent use of caches by the scavengers that made them or by other scavengers were largely unsuccessful. Only one raven cache was found despite much searching in an area where raven caching was closely watched. One empty cache, probably made by a wolf, was also found. Therefore, in order to arrive at some idea of the subsequent use of caches, I made simulated raven and wolf caches. Fourteen simulated wolf caches were made in 1972 from carcass no. 8. Some were placed along the river bars in sand and some above the river in tributary stream valleys. All were within a half mile of the carcass. When these caches were checked two days later, five were still intact, one had been disturbed but not removed, and three had been removed. Four could not be relocated; these had either been removed by scavengers or I had not been able to relocate the exact spot where the cache had been made. The caching locations were not as obvious to me upon rechecking them as I had thought they would be even though they had been marked with stones and sticks.

Raven caches were even more difficult to relocate since they were so much smaller. Seventeen were made in 1972 from carcass no. 8 much as the wolf caches had been made. A few days later, four were still intact, one was partly eaten, and three had been removed; nine others could not be relocated. Some of these almost certainly had been removed by scavengers. I watched a raven find and eat one of the caches that I had made near the carcass. I do not believe the raven had seen the cache being made. This is the only time I actually saw a scavenger take one of the simulated caches.

Fifteen simulated raven caches were made from fish remains in 1973. These were marked with red flagging. Additional flagging was used in places without caches to reduce the chance that ravens would learn to search for cached meat near the flagging. Even at these flagged caches, the meat was difficult to find when the caches were checked. I covered most of the meat with pieces of vegetation, small stones, or sticks. One had been removed in the first 24-hour period by a ground squirrel. All others were intact. Unfortunately, time did not permit a later check of these caches.

Scraping

Scraping refers to a bear's behavior of covering a carcass with vegetation and dirt scraped from the area around a carcass. Scraping occurred at four of eight carcasses that bears were known to have visited. Scraping was only observed for an extended length of time at carcass no. 1 so no generalizations can be made about this behavior. However, a description of scraping at carcass no. 1 will be given to illustrate some characteristics of this behavior.

A bear was the first scavenger to arrive at this carcass. It fed, rested, and moved about in the proximity of the carcass for 23 hours and 50 minutes before a second scavenger, a raven, arrived at the carcass. No scraping activity had occurred prior to the raven's visit, but immediately upon arrival of the bird, the bear began to scrape litter onto the carcass.

On the day it began scraping, the bear scraped 13 different times averaging about 9 minutes per session of scraping with the longest session being nearly 15 minutes long. The next day it scraped eight times again averaging around 9 minutes each time with the longest session being 20 to 25 minutes long. The third and last day, it scraped five times averaging about 13 minutes per period with the longest being nearly 30 minutes.

The way the bear covered the carcass with litter was usually by standing on the carcass and scraping material onto it or standing beside the carcass facing away from it and scraping material backward onto the carcass. Bears consistently used front feet for scraping.

Of the times the bear was observed scraping material onto the carcass, all but four occurred when a raven or wolf was nearby, and often the bear interrupted its scraping to chase the other species away. All four instances when the bear covered the carcass with litter when no other animal was nearby occurred just after the bear had fed on the carcass and before it began a period of rest.

Drinking, grooming, vocalization, and elimination

The number of times these minor activities were observed are given in Table 11. In most instances, the minor activities were part of the normal behavior of the scavengers whether or not they were at a carcass site. Some of the activities for particular scavengers, however, occurred more frequently than for other scavengers. The relatively large amount

Table 11. Number of times the minor activities were observed.*

Species	Drinking	Grooming	Vocalization In proximity	Vocalization In area	Elimination
Bear	-(0)	21(32)	-(0)	-(0)	1(2)
Wolf	14(16)	9(11)	0(1)	0(1)	40(46)
Eagle	-(0)	4(1)	-(0)	-(0)	9(2)
Raven	1(2)	2(4)	71(128)	111(197)	1(2)
Gull	76(33)	45(19)	5(2)	7(3)	2(1)
Jaeger	3(1)	3(1)	-(0)	14(4)	-(0)

*The first number is the number of times the activity occurred in 1000 observation periods; the number in parentheses is the total number of times the activity was observed.

of drinking and grooming by the glaucous gull was directly related to feeding on a carcass. During an hour of alternating between feeding and grooming, a gull at carcass no. 7 drank seven times during four visits to a nearby river channel. The visits were made at 7 to 23 minute intervals. The intervals between drinking generally increased in length. The gull continued to make visits to the water for grooming purposes and no drinking was observed. While grooming, the gull wiped its bill on the rocky ground 48 times and scratched its bill with its foot 11 times. It would also shake its bill in the water. The gull rarely preened its feathers at the carcass site.

Of the 46 instances of urination and defecation by wolves, at least two were directly related to the scavenging activities. Carcass no. 2 had been partly eaten when the two observers arrived. I could not determine whether two wolves, which subsequently visited the carcass, or some other scavenger had opened the carcass. I had set up two cameras in the vicinity of the carcass, and either the cameras, my scent, or the scent of other scavengers were making these wolves nervous. They urinated nine times in the carcass vicinity, twice directing the urine onto parts of the carcass. The dark-colored wolf had been walking around in the vicinity of the carcass sniffing the ground when it found a piece of meat. It picked the meat up and carried it a few feet then dropped it, urinated on it, and scratched with its hind legs. It then alternately walked and lay near the carcass until the light-colored wolf returned from a caching trip. At this point, the light wolf approached the other wagging its tail. The dark wolf, while lying down, turned its head toward the light wolf and appeared to snarl; the light wolf moved away. It approached the dark wolf again and raised its paw in the air once. At this point the dark wolf stood up with its tail held stiffly in a vertical position. As the light wolf approached the other, the dark wolf jumped away from the carcass. The light wolf then approached the carcass and urinated on it. After this, they both left the area.

The number of vocalizations by ravens was high compared to all the other minor activities. Since ravens are such a vocal bird under most circumstances, I could not say that the carcass was responsible for the high number of vocalizations recorded for this scavenger, but certainly some of the vocalizations were related to their scavenging activity.

Interspecific and intraspecific interactions

A few non-aggressive interactions between scavengers at the carcasses occurred, all of them by conspecifics. For example, the sow at carcass no. 4 nursed her cub while in the carcass vicinity, and these two bears played together. A boar and sow at carcass no. 1 copulated in the area while a larger, more dominant boar was feeding on the carcass. Wolves at carcasses no. 2 and no. 11 greeted each other by touching noses and wagging their tails. However, most inter- and intraspecific interactions at carcasses involved some form of aggressive behavior by a dominant scavenger.

Aggression is loosely interpreted here to mean any action on the part of the aggressor that results in the recipient's loss of a vantage point for scavenging. Aggression included the somewhat passive acts of suddenly raising the head and facing the recipient, lifting the wings, opening the mouth toward the recipient, and changing position resulting in the displacement of the recipient. More active aggressive behavior included a lunge or short chase, a swipe with the front paw, and actual bodily contact.

Table 12 is a record of all aggressive acts observed with the number of times each species was a recipient of the aggressive act. These figures are not meaningful unless the amount of time the aggressor and the recipient were together in the proximity of the carcass is given. This time also appears in Table 12.

For the sake of comparing the frequency of aggression among the pairs of aggressor and recipient, I listed each pair, in descending order, according to the number of aggressive acts expected in 100 observation periods in which the pair were in the proximity of a carcass (Fig. 14). For example, in 173 observation periods that bears and wolves were near a carcass simultaneously, there were 39 aggressive acts by the bear toward the wolf. This is an average of one aggressive act for every 4.4. observation periods or 23 aggressive acts in 100 observation periods. An asterisk was placed before each pair for which the aggressor is the dominant species in the hierarchy given above. This graph clearly shows that most aggression occurred by a species higher in the scavenging hierarchy and that intraspecific aggression was low.

Most aggressive acts by bears towards ravens and wolves involved a short lunge or swipe at the recipient. The first bear to arrive at carcass no. 1 reacted in this manner every time a raven or wolf approached

Table 12. The number of inter- and intraspecific aggressive acts* and the number of observation periods in which the aggressor and recipient were together in the proximity of a carcass.**

RECIPIENTS

AGGRESSORS	Bear	Wolf	Fox	Eagle	Raven	Gull	Jaeger
Bear	7 / 84	39 / 173	0 / 0	33 / 81	0 / 0	0 / 0	0 / 0
Wolf	1 / 173	3 / 87	0 / 0	0 / 0	16 / 113	0 / 1	0 / 0
Fox	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0
Eagle	0 / 0	0 / 0	0 / 0	0 / 3	4 / 11	0 / 7	0 / 5
Raven	0 / 81	0 / 119	0 / 0	0 / 11	12 / 291	12 / 51	2 / 27
Gull	0 / 0	1 / 1	0 / 0	5 / 7	0 / 51	2 / 4	4 / 33
Jaeger	0 / 0	0 / 0	0 / 0	0 / 5	6 / 27	2 / 33	0 / 22
	* / **						

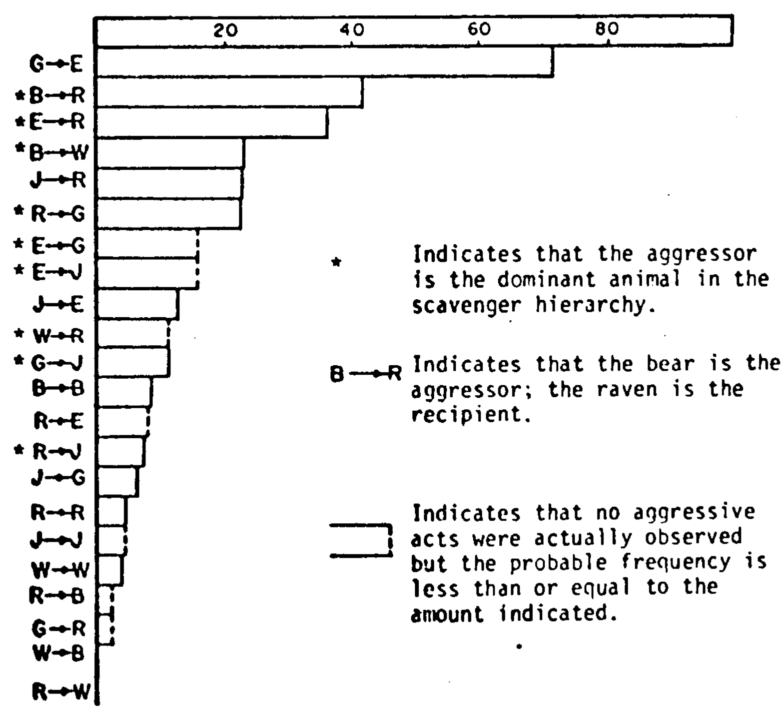

Figure 14. Number of inter- and intraspecific aggressive acts per 100 observation periods in which the aggressor and the recipient occur together in the proximity of a carcass.

the carcass.

A bear sometimes chased a wolf if it approached close to a carcass. Unlike ravens, however, which often attempted to feed on a carcass while the bear was there, the wolf usually just rested nearby. On one occasion, while a bear was wandering around a carcass site, it approached the place where a wolf was lying. The wolf got up and moved away; the bear made no attempt to chase it. One of the bears at carcass no. 2 approached a wolf that was lying down gnawing a bone. When the wolf got up, the bear chased it for a short distance; the wolf was able to avoid the bear with little effort.

Bodily contact between an aggressive bear and another scavenger occurred only once at a carcass; this involved two boars which were both interested in a sow. A medium-sized boar had had possession of a carcass for nearly four days until another and larger boar accompanied by a sow arrived in the area. When they approached the carcass, the sow was leading, but she moved off to the side as the larger boar approached her. The first boar had been watching the two approach; he moved off about 50 yds (45.7 m) as they came closer. The sow went to the carcass as the larger boar was going toward the other boar. The larger boar then changed direction and went to the carcass; the sow ran from the carcass as he approached. The smaller boar began following the sow. The larger boar then left the carcass and moved slowly toward the other boar. The smaller boar did not run but turned toward the larger boar as he approached. They faced each other, half squatting with their mouths open and noses almost touching; they raised themselves up on their hind legs and the larger boar pushed the other down on its back. While the larger boar straddled the other bear for a few moments, he appeared to be biting the muzzle of the smaller boar. When they separated, the larger boar ran back to the carcass, a distance of about 200 yds (182.8 m). When he reached the carcass, a wolf ran from it. The larger boar then remained on the carcass while the smaller boar went after the sow again and eventually mated with her while still in the area of the carcass. Afterward, the sow returned to the carcass and kept circling the carcass from about 10 ft (3.0 m), but she would run off every time the larger boar moved. She finally moved up to the carcass and put her front paws on it while the boar was scraping debris onto it. He then moved off, and the sow began to uncover the carcass while the boar lay about 20 ft (6.1 m) from the carcass. When these two bears returned on another day, they were both seen feeding on the carcass at the same time. There was no active aggression between this boar and sow.

A boar that approached carcass no. 3 while a sow and cub were feeding caused the sow and cub to flee from the carcass site. Even the shouts and motions of the observers could not turn the two fleeing bears from the direction they were headed, uphill towards our campsite. They passed by just below the camp and when last seen, were still running.

Most of the aggression by wolves which I observed was directed towards ravens; the other smaller scavengers did not usually visit a carcass site if a wolf was there. Aggression towards ravens was most often a short lunge at the birds. Sometimes a wolf would merely move in the direction of a raven; this was considered an aggressive act if the raven moved away from the wolf. At other times, when a wolf approached a raven as the bird was caching meat, the wolf would make a short leap at the raven; this did not seem to be an effort to capture the raven as much as an effort to frighten the bird away from the cache. The wolf would always sniff around the site where the cache had been made and sometimes was able to retrieve the meat. On more than one occasion, I have seen a wolf run towards a raven that was just resting on the tundra. When the bird flew, the wolf eagerly sniffed the area where the raven had been sitting, obviously searching for a cache which the raven actually had not made.

I saw a red fox at a carcass only twice during this study, and on one of these occasions, a wolf chased the fox for about a half mile (0.8 km) and nearly caught it. From the appearance of the carcass, a fox had fed on it the first night the carcass was available. A fox fed on the carcass the next day for about 3 minutes, but I did not see a fox again until the seventh day. Wolves and bears had fed on the carcass during the intervening days. On the seventh day, through the heat waves, I could barely make out the shape of a fox as it ran around a knoll above the carcass with a wolf pursuing closely and two eagles flapping behind them.

Aggression by wolves towards other wolves was infrequent. Except on one occasion, the aggressive behavior that did occur simply consisted of baring the teeth if another wolf approached too closely while the first wolf was at the carcass. Wolves usually fed at a carcass at the same time without any evidence of conflict. The one case of active conspecific aggression by wolves occurred at a moose carcass. A single wolf had been moving and resting in the carcass vicinity for about 24 hours while a grizzly was in possession of the carcass. Three wolves traveling together suddenly appeared and, running past the carcass, they pursued the single wolf for about a quarter of a mile (0.4 m) nearly closing with the wolf at one point. They gave up the chase and returned to the carcass. They investigated the bed where the single wolf had been lying and urinated nearby then left the carcass area.

Eagles were not particularly aggressive at a carcass and permitted ravens to feed with them. Ravens were the only species at a carcass that were recipients of aggressive acts by an eagle. An eagle was feeding around the head region of a carcass when a raven attempted to displace another raven which was feeding near the sternum. The eagle flapped its wings as the second raven took over the position at the sternum; this caused both ravens to move away from the carcass. Later, one of the ravens attempted to feed on top of the ribcage, but every time it moved nearer to the eagle, the eagle would flap its wings and the raven would move away. On the raven's third attempt, the eagle merely raised its head and looked at the raven which was enough to make the raven move away. All this time, the other raven fed uninterrupted at the pelvic area of the carcass. Ravens showed little fear of eagles if the eagles were perched on the ground or on the carcass, but an eagle which flew onto a carcass where ravens were feeding caused panicked flight among the ravens.

Aggression by ravens was of a minor nature, mostly consisting of movement toward the recipient, causing the recipient to avoid the immediate vicinity of the dominant raven. However, one instance of bodily contact between two ravens did occur. A raven was feeding at a carcass when two more ravens appeared, one behind the other, and began circling over the carcass site. One of these ravens appeared to be chasing the other. Both landed and the smaller of the two hopped at the other with its feet stretched out toward the other raven. Then they both took off into the air and tangled with their feet together. They fell to the ground with their wings flapping and their beaks open. They were pecking at each other; the raven that had been feeding on the carcass went over and also pecked at one of the fighting ravens. Then the two fighting ravens flew away, reappeared briefly, and eventually one returned alone.

Glaucous gulls were not as aggressive at carcasses as Figure 16 seems to indicate. Aggression toward the eagle and the raven was merely in the form of low passes made over the animals while they were at the carcass. The eagle and the wolf paid little attention to the gull other than to look up at the bird. These were the only times that a gull was in the vicinity of a carcass when an eagle or a wolf was present. Aggression toward the jaeger merely involved movement toward the jaeger, resulting in the jaeger moving away from the gull.

Aggression toward another gull was more intense. One gull flying into the proximity of a carcass chased another gull from the carcass. On another occasion, a gull, which landed at a carcass where another gull was feeding, fought briefly with the other gull but was driven from the carcass area.

Despite its small size and low position in the scavenger hierarchy, the jaeger would occasionally dive at a larger scavenger (raven and gull) from the air while they were at a carcass. This was the only form of aggression by jaegers.

In most instances, subordinate scavengers avoided the area near a carcass or refrained from feeding on the carcass while the more dominant animals were feeding; some of the subordinate scavengers did feed on fragments of the carcass while a dominant scavenger was at or near the main portion of the carcass. In many cases, a subordinate scavenger would wait until a dominant scavenger had finished feeding then make sucessful attempts to feed on the carcass while the dominant scavenger moved about or rested nearby. The amount of time that a subordinated scavenger fed while a dominant scavenger was near the carcass is given in Table 13. Of the 28 pairs of subordinate and dominant scavengers shown in this table, 54 percent of the subordinates did not visit the carcass site or did not attempt to feed at all if the dominant scavenger was near the carcass.

Foxes and eagles usually avoided the carcass site altogether when dominant scavengers were there. Gulls and jaegers would attempt to feed if avian scavengers were the only dominant scavengers present. Ravens were the least likely to refrain from feeding if more dominant scavengers were present.

Some Observations of a Scavenging Ground Squirrel

There were several instances of ground squirrels scavenging carrion

Table 13. Feeding by subordinates while dominant scavengers were in the proximity of the carcasses.*

Dominant	Subordinates: Jaeger	Gull	Raven	Eagle	Fox	Wolf	Bear
Bear	NV	NV	0-1-38 (81)	NV	NV	0-4-1 (173)	16-8-9 (84)
Wolf	NV	NF (1)	2-18-69 (119)	NV	NF	---- (87)	
Fox	NV	NV	NV	NV	NV		
Eagle	0-0-1 (5)	NF (7)	4-6-1 (11)	0-1-0 (3)			
Raven	1-0-1 (27)	15-75 (51)	---- (291)				
Gull	3-4-0 (33)	NF (4)					
Jaeger	---- (22)						

* = Calculations were not made for two wolves, two ravens, or two jaegers feeding together because subordinates and dominants were indistinguishable. These intraspecific pairs fed together without interference with each other.

( ) = No. of observation periods in which the pair was in the proximity of a carcass simultaneously.

1-2-3 = The first numeral is the number of observation periods in which the pair fed together at the carcass; the second is the number of observation periods in which the subordinate fed on carcass fragments while the dominant was in the proximity of the carcass; the third is the number of observation periods in which the subordinate fed on the carcass while the dominant moved or rested nearby.

NV = No visits to the carcass by the subordinate while dominant was present.

NF = No feeding by the subordinate while dominant was present.

in my study area but only one case where a squirrel fed upon a large carcass. The ground squirrel was first observed at a Dall sheep carcass at 1200 on the fifth day after the sheep was killed. At that time, it was scratching vigorously on the hind leg of the sheep. Tufts of hair had been pulled out. It climbed halfway onto the carcass then left. At 1415 on the same day, it was seen again digging at the hide on the hindquarters and at the ground underneath the carcass. At 1423 I lost sight of the squirrel but it reappeared at 1428 from under the sheep. The squirrel's head was covered with blood. It ran into its burrow less than 100 ft (30.6 m) away. The squirrel had found the site of a bullet wound on the underside of the hindquarter where it had begun to feed but had removed only a little meat. Since the observation site was moved farther away later that day, I was not able to gather any more information on the squirrel's activity.

I watched ground squirrels at Neruokpuk Lakes feeding voraciously on the remains of fish which had been caught from the lakes by fishermen. The ground squirrels were noticeably fat and never hesitated to run out from beneath the cabins on the shore of one of the lakes to obtain the fish parts as they were thrown away. They cleaned meat rapidly off the backbones of the fish but did not consume the bones, at least while I was watching them. The heads were usually carried off beneath the cabins out of sight.

I suspected ground squirrels on the Canning River of eating the roe from arctic char which I had left near the stream where I had cleaned the fish. I believe a ground squirrel removed one of the simulated raven caches that I made from parts of a fish.

One of the RRCS biologists told me that she had seen a ground squirrel drag a dead ground squirrel into its burrow and presumed that it eventually fed on the carcass (P. Reynolds, pers. comm.).

I attempted to observe ground squirrels feeding on caribou meat by leaving pieces of a caribou carcass near the burrows of some ground squirrels at one of my campsites, but the squirrels never touched the pieces of meat.

Carcass Disposal and Remains

Usually within two to six days after a bear or wolf had found a carcass of a caribou, sheep, or bear, most or all of the meat had been consumed. Moose carcasses lasted 7 to 13 days. The average disposal time for all carcasses except the moose was about three days. The time depended upon the species and the number of scavengers as well as upon the amount of time the scavengers spent feeding. For example, the bear at carcass no. 6 did not feed for long periods of time and removed very little meat during its first feeding season (see Photo 5), therefore, the disposal time for this carcass was six days, the longest for any carcass except the moose.

The observers were close enough to only one carcass to observe the order in which the carcass parts were eaten; this was carcass no. 7 (see Photo 6), the majority of which was eaten by two wolves. There was no obvious pattern in the order in which the various parts of this carcass were removed; the details are given in Appendix F. The wolves indiscriminately

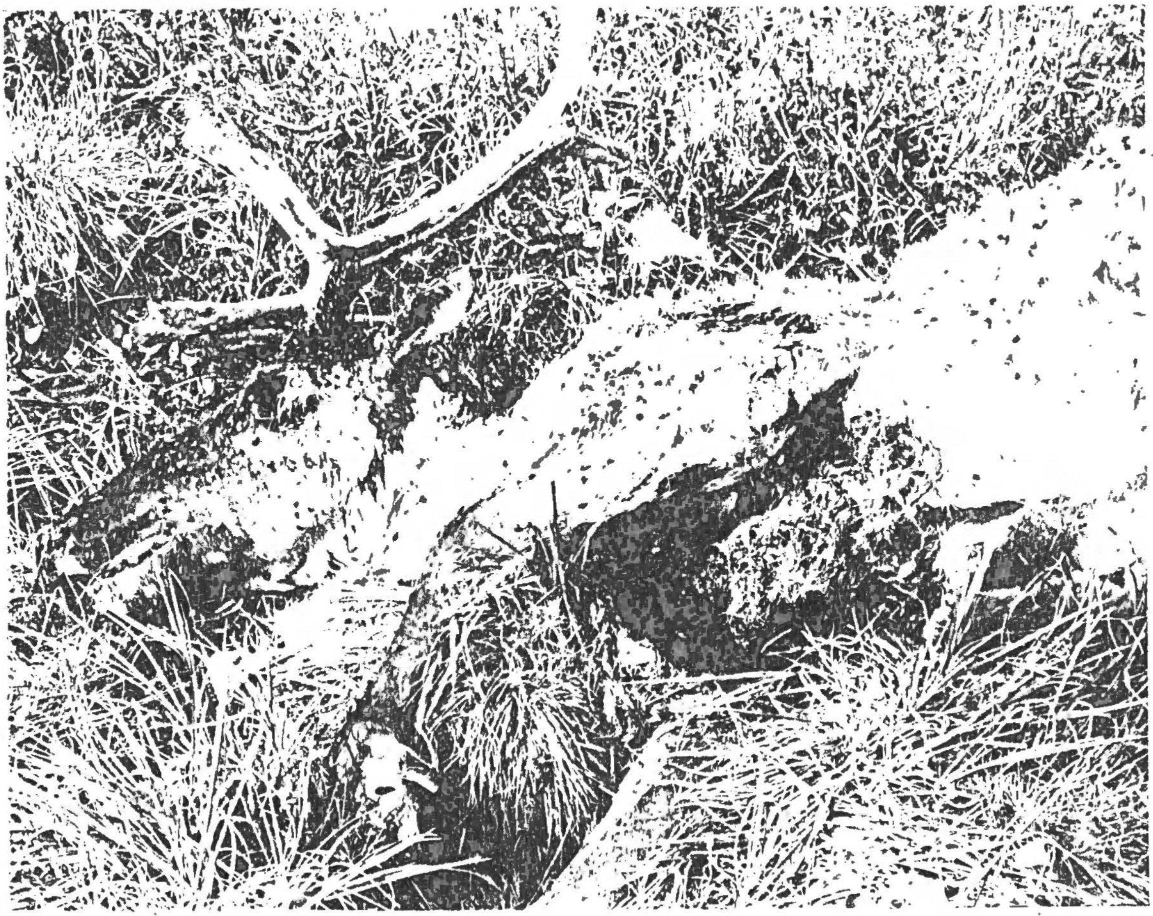

Photo 5. The bear that scavenged at carcass no. 6 ate only a small amount of meat from the chest of the caribou carcass during the first visit to the carcass.

Photo 6. This wolf, which removed the major portion of meat from carcass no. 7, did not appear to show a preference for any particular part of the carcass.

fed on the meat of the backbone and ribcage, legs, and viscera, alternating frequently from one portion to another. The meat of the neck and head was some of the last to be eaten. Pieces of the hide were eaten throughout the duration of the observation time.

The parts of the carcasses that remained at a carcass site after most meat was removed varied from one carcass to another. Table 14 is a list of all the carcasses and the parts that were found at the site. I found no remains at all at carcass no. 1 though I searched the area thoroughly. The odor of decay and of bear excrement was evident. Some areas were found where the bears had scraped dirt and vegetation onto the carcass.

Except for carcass no. 14, none of the carcasses fed on by bears had an intact skull, spinal column, or ribcage, including those checked only two days after the bear began feeding. The bear at carcass no. 14 was shot by hunters before it had removed most of the meat from the carcass.

Those carcasses that were fed on by wolves but not by bears (carcasses no. 3, 7, 11, 12, 13, and 15) had the major portion of the spinal column and ribcage still intact. Even carcass no. 13, a sheep carcass weighing 100 lb (45.4 kg) or less had an intact ribcage after the wolves had removed most of the meat (see Photo 7). All but two of the carcasses also had most of the skull intact. The skull was removed from carcass 15 by hunters. The skull of carcass no. 12 was not visible when the site was checked with a spotting scope; the observers could not reach the site due to high water in the river at that time.

Table 14. Remains of the carcasses.

Carcass number	Major scavengers	Total days of carcass	Number of days the scavengers fed on the carcass	Remains: Pieces of hide	Hair	Legbones-cracked	Legbones-not cracked	Skull intact	Skull in pieces	Lower jawbones	Spinal column intact	Pieces of vertebrae	Ribcage intact	Ribs disconnected	Scapula	Pelvic bones	Remaining meat
1	Bears Wolves	13	12														
2	Bears Wolves	7	4		X	X				X				X	X		N
3	Wolf	5	3					*			*		*			X	S
4	Bears	5	2			X			X			X		X	X		N
5	Bear	No observations			X		X			X		X		X	X		N
6	Bear	10	6	X			X										S
7	Wolves	9	3	X			X	*			*		*				N
8	Avian Scavengers	10	10	X			X	*			*		*		X	X	M
9	Bear	4	2	X			X					X		X		X	N
10	Bear Wolves	5	4	X			X					X		X	X		S
11	Wolf?	No observations		X				*			*		*				N
12	Wolves	2	2								*		*			X	S
13	Wolves	9	2					*			*		*				N
14	Bear Wolves	?	7	X			X	*			*		*				M
15	Wolves	3	3				X				*		*				N

N = No meat remaining.

S = Small amount of meat remaining (less than 10%).

M = Meat still remaining in some quantity (approximately 10-20%).

* = Parts of the carcass remaining nearly intact.

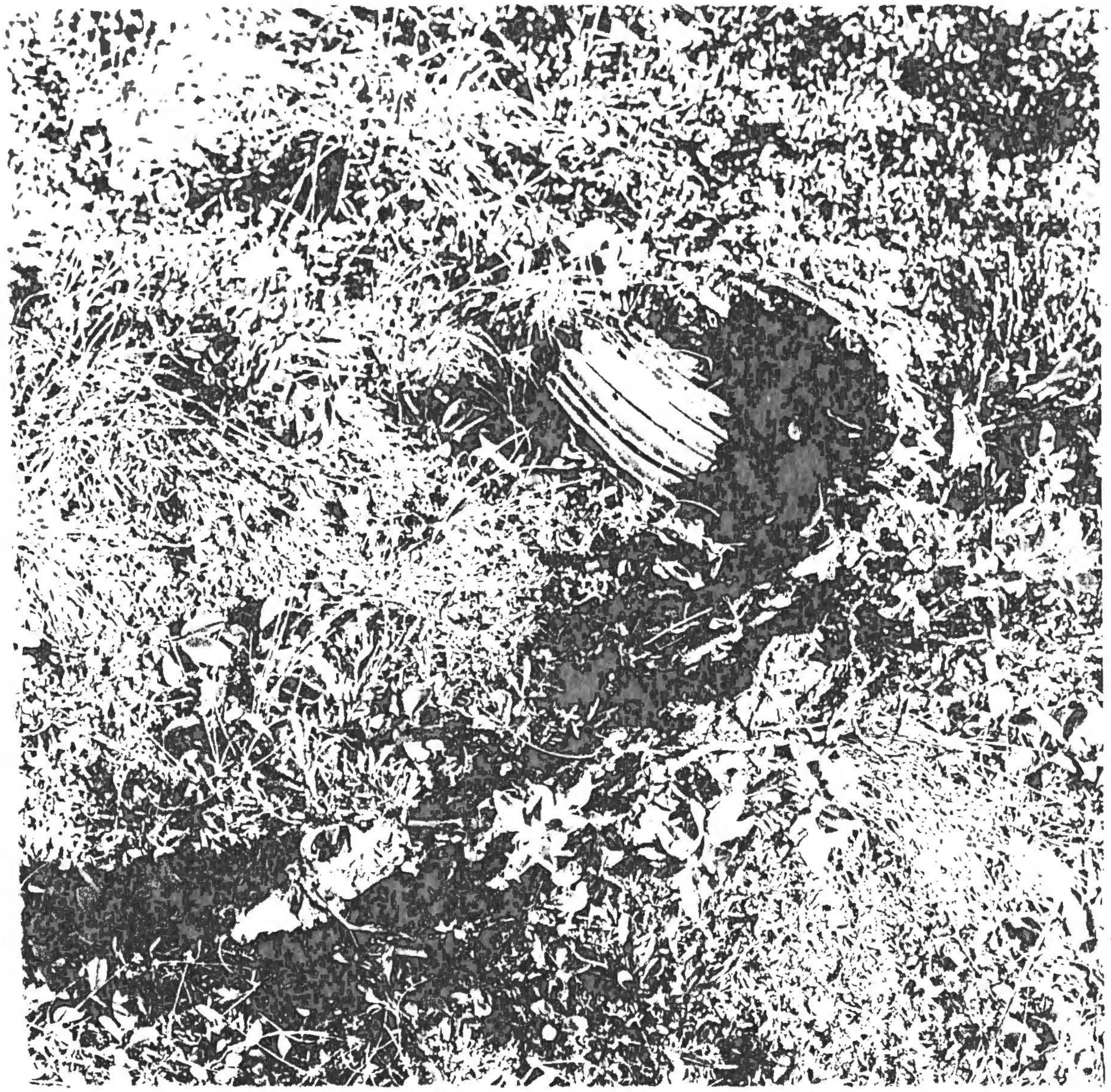

Photo 7. The remains of a Dall sheep carcass after wolves had removed most of the meat included this intact ribcage.

Evidence of avian scavengers included feathers (see Photo 8) as well as tracks and droppings. At carcass no. 8 where birds were the only major scavengers, the intact condition of the carcass (see Photo 9) and the ragged edges of meat still remaining on the bones (see Photo 10) were clear indications that the carcass had supported mostly avian scavengers.

Large mammal carcasses which had been visited only by foxes at the time they were checked provided definite clues to this species visit. Fur lay scattered about the site (see Photo 11) where the fox had attempted to dig into the carcass and meat was removed only around a wound or from the anal region.

It was not feasible to remain at every carcass until all the parts had disappeared, but there is much evidence available to indicate that scavengers continued to visit a site until most of the carcass had been utilized, including skin, hooves, and bones (see Photo 12). I was not able to revisit the carcass sites after an extended period of time; however, every time I found a bone while hiking in the study area, I recorded it in the field notes. Though many bones were found, rarely were more than one or two found at one place to indicate that it had been the site of a carcass. On only one occasion were the remains of a carcass found that had obviously been in place for more than a year and included most of the bones with large portions of the spinal column still intact.

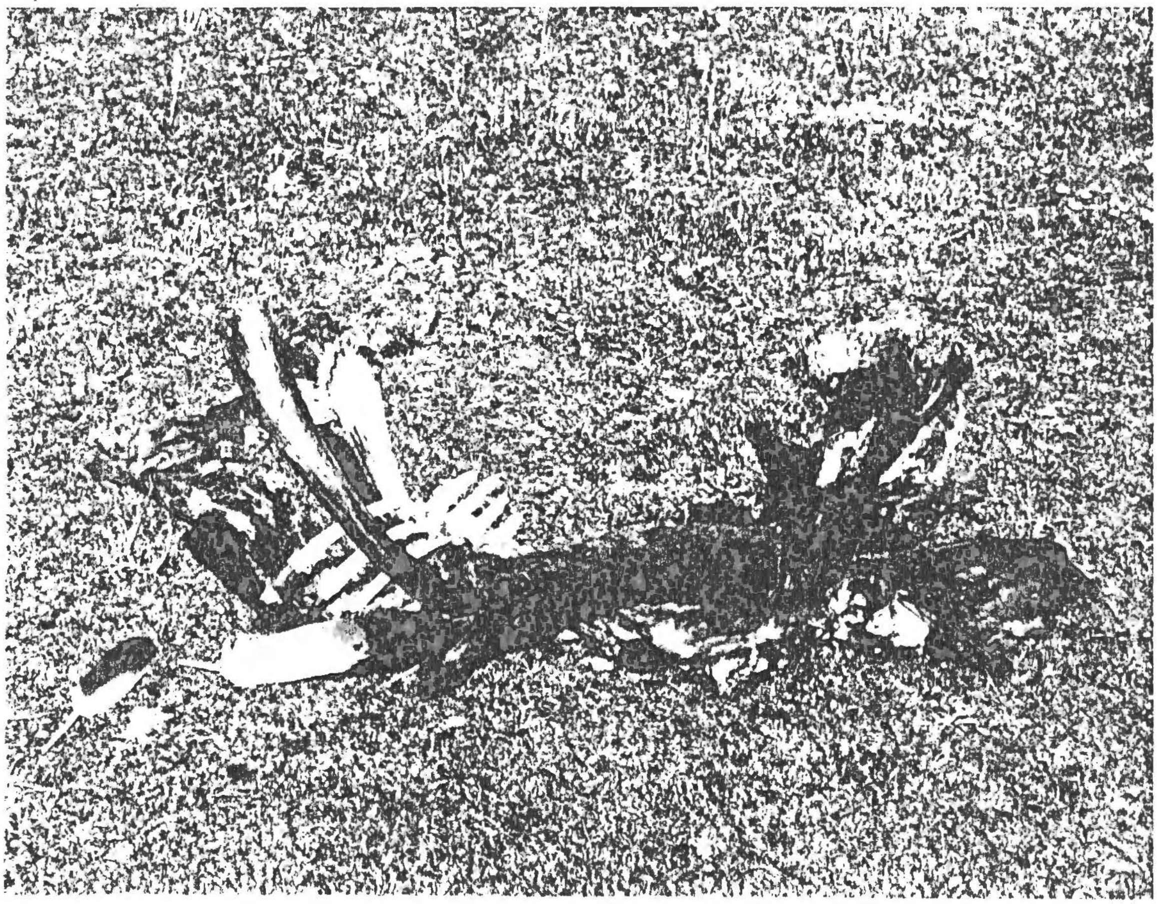

Photo 8. The feathers remaining at the site of carcass no. 11 were evidence of a visit by an immature golden eagle.

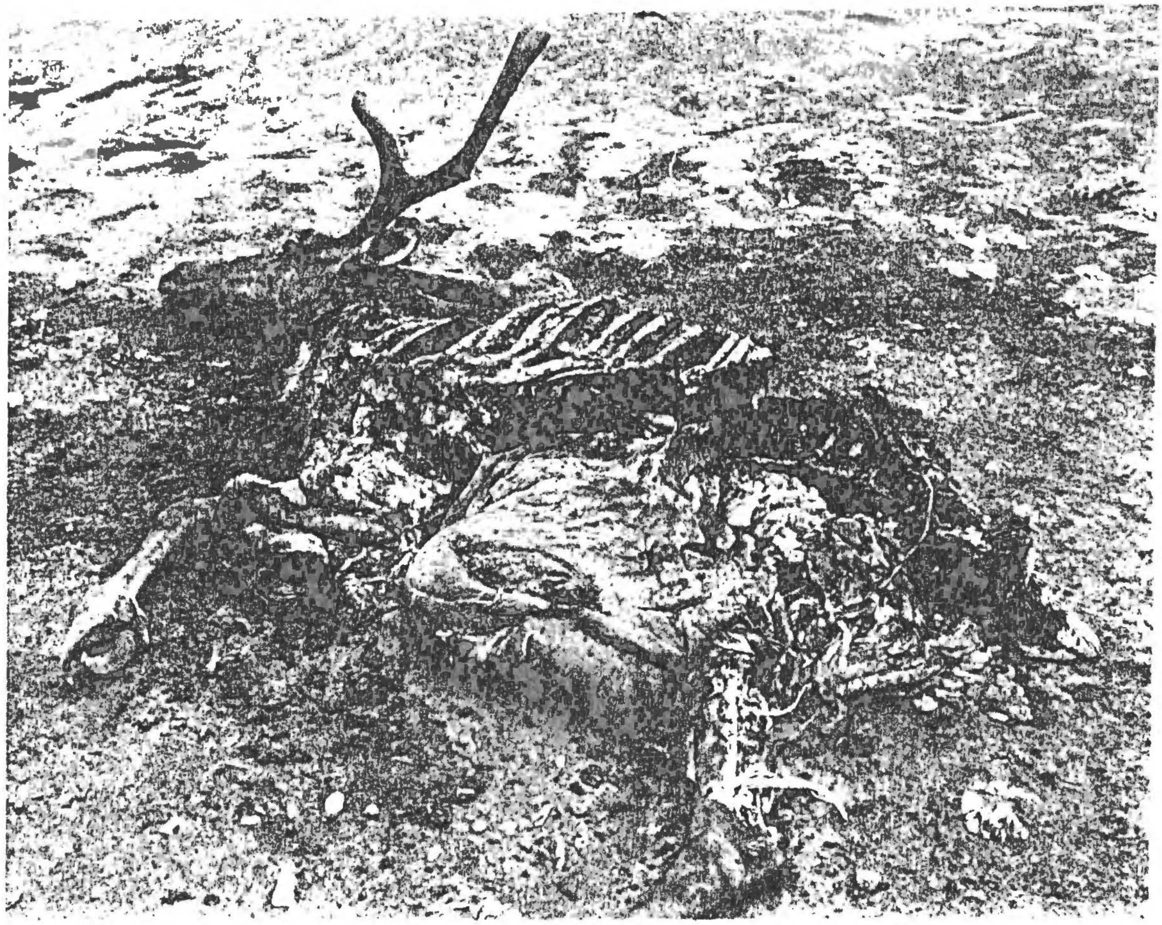

Photo 9. The skeleton of carcass no. 8, having been fed on by avian scavengers only, remained almost entirely intact even after much meat had been removed.

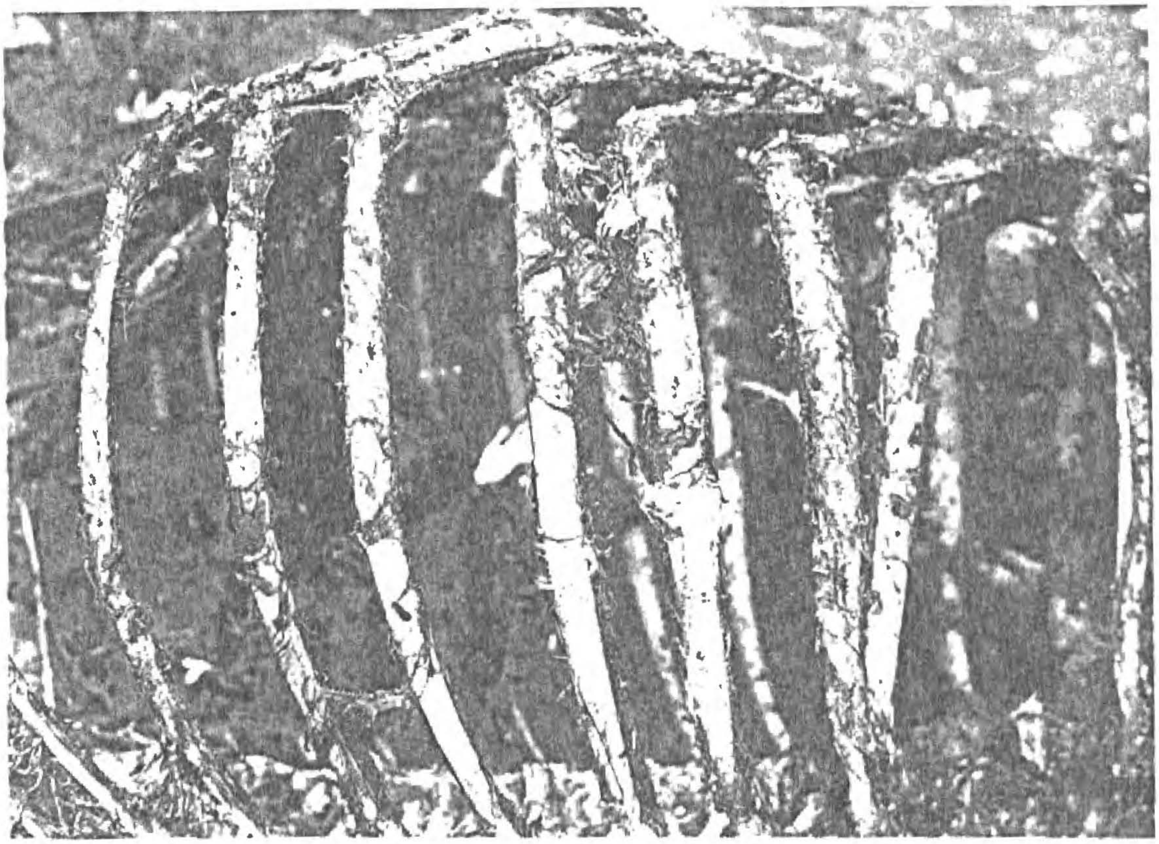

Photo 10. The shredded appearance of meat on the ribcage of carcass no. 8 indicated that it had been fed on by avian scavengers.

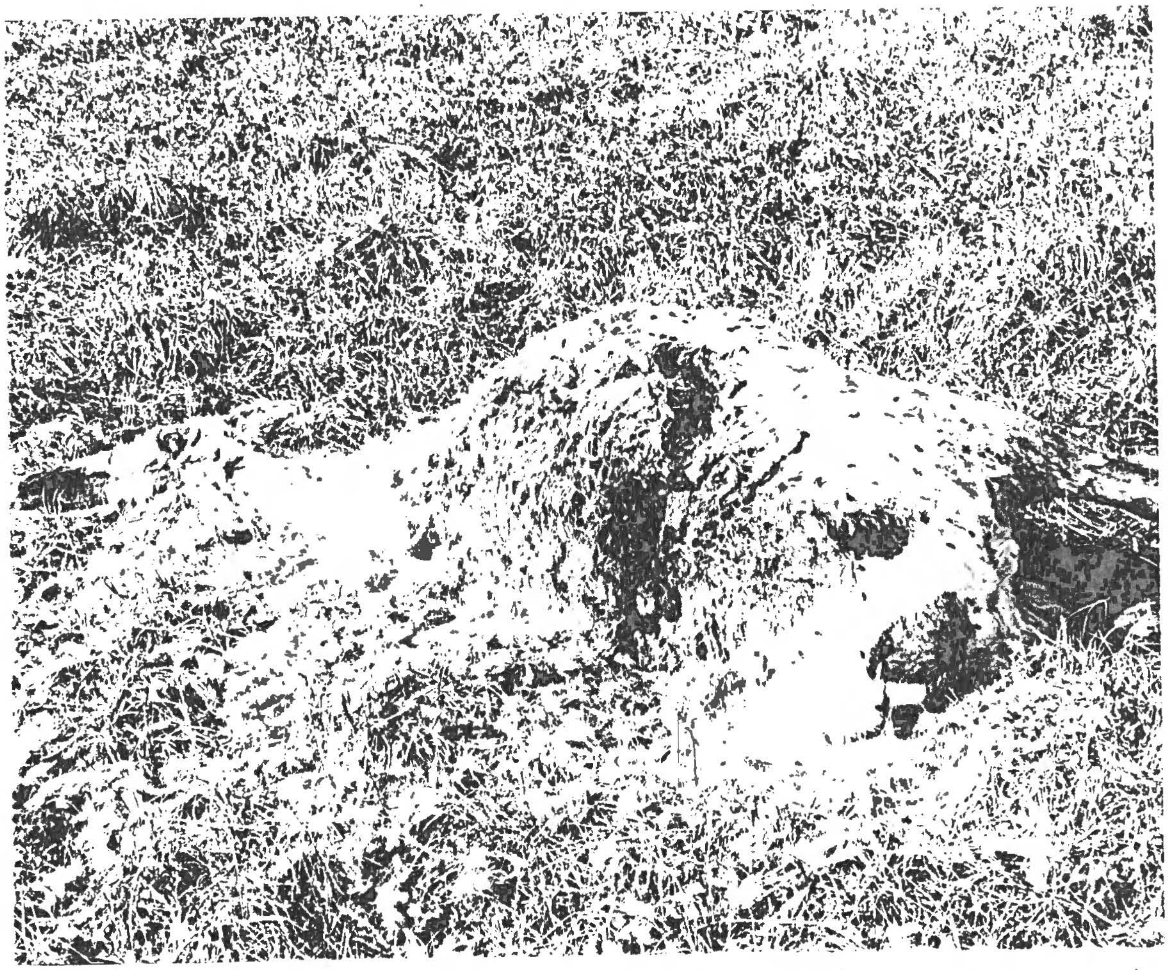

Photo 11. The remains of carcass no. 2 after a red fox had attempted to penetrate the hide on the back of the caribou carcass.

Photo 12. The site of carcass no. 2 was rechecked a month after the observers ended observations; only a few bone fragments still remained.

DISCUSSION

The Scavengers

Grizzly bear

The fact that grizzly/brown bears (*Ursus arctos*) will readily consume carrion has been well-documented in the literature (Cowan 1943, Murie 1944, Storer and Tevis 1955, Meehan 1961, Kistchinski 1972, Craighead and Craighead 1972, Curry-Lindahl 1972, Mundy and Flook 1973) yet not much has been written concerning the importance of carrion in the diet of grizzlies. Some investigators feel that carrion may be a primary food resource for bears in early spring and again in the fall. Craighead and Craighead (1972) found that winter-killed animals formed a large proportion of the early spring diet of grizzlies in Yellowstone Park. Quimby (1974b) stated that observations of bears in the Canning River drainage indicated that "carrion and prey are important food sources during early spring and late fall...." He recorded evidence of bears feeding on 15 ungulate carcasses in my study area between 27 April and 16 October in 1973; nine of these were in the spring (up to mid-June), one in the summer (mid-June to the end of July) and five in the fall. All the bears he observed on carcasses in the spring and fall were males. The only female scavenging was the bear he observed in July. I observed two sows on carcasses, one in spring and one in the summer. The first sow was accompanied by a boar which was dominant at the carcass; the other was accompanied by a cub. The sow and cub hurriedly fled from the carcass site at the approach of a large single bear only an hour after they had arrived at the carcass. The single bear had fed on the carcass the day before and now fed on it again. When the sow and cub returned 5.5 hours later, there was little left of the carcass.

It has been suggested that the pattern of emergence of bears from dens in the spring may be related to the food supply at that time of the year (Linderman 1974, Reynolds et al. 1975). Sows with cubs competing with boars for carcasses probably would not be able to retain possession of a carcass. If bears in the Arctic concentrate their movements in major river valleys during early spring where the availability of moose carrion is highest (Crook 1971), the chances of boars meeting sows and cubs at carcasses would be comparatively high. However, sows with cubs in my study area do not emerge from dens until the third week of May while the first boars or sows without cubs emerge in early April (Quimby 1974b). Bears in the study area begin to utilize root material about mid-May just prior to the time when sows with cubs begin to emerge.

Bears may make spring movements to caribou calving grounds where relatively abundant carrion can be expected. Curry-Lindahl (1972) reported that in Swedish Lapland this is true of brown bears visiting reindeer calving areas, the same bears returning regularly from one year to the next. The Alaska Department of Fish and Game reported that

> the importance of ungulates as a spring food source for brown/grizzly bears is unknown. Bears ... were taking advantage of lowland moose and caribou calving areas in the spring of 1970. Bears appeared to be quite successful at catching calves and finding dead or dying animals. Bears were also observed along the beach ... feeding on whale and seal carcasses which had washed ashore (Glenn 1971).

Grizzly bear behavior at carcasses also appears to be related to the seasonal importance of carrion. If the bear at carcass no. 1 exhibited typical behavior, then, during the spring, one could expect bears to remain with a carcass as long as a quantity of meat is still available. Quimby (1974b) gave evidence of similar behavior by two male grizzlies during the fall. He observed one bear on a moose carcass on 9 October; the bear was there when he revisited the carcass site on 17 October. The other bear was seen on 6 October and again on 16 October at the same site where there appeared to be a carcass covered with debris. According to Curatolo and Moore (1975), an adult male grizzly in the Canning River area "remained on or near a moose carcass nearly two weeks in the fall."

The grizzly's attraction to carcasses during the summer appears to be less intense than in the spring and fall. Bears usually did not remain at summer carcasses except while they were feeding. A bear's hunger state must be at a higher level in the spring and fall when food is considerably less available than in the summer. The large amount of feeding by the first bear to arrive at carcass no. 1 (Fig. 10), a spring carcass, gradually declined over the first five days of the bear's visit and then became sporadic and short in duration. By then, its feeding behavior was probably more typical of the summer scavenging activity of grizzlies. I am not certain that it was not human disturbance which caused the bears to leave summer carcasses after each feeding period; bears reacted noticeably to human scent at these carcass sites. However, I do not believe that this alone accounted for their brief visits to the carcasses. Carcass no. 14 was a moose carcass found by a bear in the spring. The carcass had been handled by humans prior to the bear's arrival. This bear, however, remained for over three days at the carcass site despite human activity nearby and was finally shot by hunters there.

Scraping behavior may also occur less frequently during the summer than in the spring and fall. No scraping occurred at carcasses no. 2, no. 4, no. 5, and no. 6 which were visited by bears during the period 10 June to 20 July. Scraping did occur at carcasses no. 1 (27 May), no. 14 (24 May), no. 9 (16 August), and no. 10 (21 August). Craighead and Craighead (1972) stated that "in the fall when grizzlies dig dens and gather boughs for beds, they also dig to cover carrion or kills more frequently than at other seasons of the year."

Mysterud (1973) offered some preliminary hypotheses about the ecological significance of scraping by brown bears. He suggested that debris covering the carcass may act as a camouflage to prevent visual detection by avian scavengers particularly the raven; the raven "constitutes a potential feeding competitor" and in addition, through their noisy behavior at a carcass, ravens may attract other scavengers.

Secondly, Mysterud suggested that the litter on the carcass may act as a scent inhibitor unless the bear itself releases specific scents, for instance urine and excrement; these scents, however, have a protective value in that they may inhibit other "carrion eating species." He mentioned that wet mosses would be effective in stifling scent from the carcass but added that Wikan (1970) indicated "the use of cover materials which would not be assumed to filter scent so effectively."

In his paper, Mysterud did not present the possibility that scraping is merely a way of hindering access by other scavengers to the flesh of the carcass. Litter which had been scraped onto carcass no. 1 appeared to prevent ravens from feeding on the carcass. Also, a wolf had some difficulty feeding on this carcass because it had to dig through the debris and shake dirt from pieces of meat before it could feed. If the bear had been resting nearby, the wolf would not have had enough time to do this before the bear chased it away.

If the litter were to act as a camouflage, it seems likely that the bear at carcass no. 1 would not have waited nearly 24 hours before covering the carcass; scraping was coincident with the arrival of a raven.

Sites where bears had remained at a carcass and scraped a covering over the carcass were as easy to locate by scent, if not easier to locate, than carcasses which had not been covered with debris. The odor of decomposition may have been partly masked by the debris, but the odor left by the urine and excrement of the bear was very strong and was a definite indication that carrion was present. Since I did not check the sites until the bear had left, I do not know how much time is required to build up the strong odor that accompanied carcasses which were visited by bears, but I saw bears defecating or urinating soon after their arrival at a carcass. Since bears may uncover a carcass several times during the day to feed, the decaying carcass is exposed to the air and the odor is spread around on the debris which would negate any scent-masking value it might have had.

Wolf

Although primarily a predator of large ungulates, wolves are opportunists and will readily eat carrion and even garbage. Mech (1970) made the point that the wolf's propensity for eating carrion was taken advantage of in certain parts of Canada during the wolf-poisoning campaigns. For example, in two and a half months, 59 wolves were poisoned after feeding on bison meat used as bait in Wood Buffalo National Park in the early 1950's (Fuller and Novakowski 1955). Though wolves will readily assume the role of scavenger, they probably have few chances to do so in the study area particularly in summer. The heaviest natural mortality of ungulates, excluding predation, probably occurs in late winter and in the spring. I doubt if a significant number of animals die of disease, injury, or malnutrition during the summer.

Caribou are the most important prey species for wolves in the study area, but during the summer, caribou drift through the study area in small numbers and may be quite scarce in some areas for several weeks. The vulnerability of Dall sheep to wolf predation is likely to be low during summer. The small moose population is no longer concentrated in the major drainages. When prey animals are scarce or difficult to capture, the wolf will have to cover a greater area in search of food; any available carrion would eventually be found and utilized. I believe wolves were making 25 to 40 mile (30.2 to 64.4 km) round trips between carcasses and den sites on some occasions in 1973.

Investigators have recorded evidence that wolves may not fully utilize available carrion if prey is abundant and easy to capture.

In a study of the Kaminuriak caribou herd in Canada, Miller and Broughton (1974) found that

> much of the killing of new-born calves was done without subsequent utilization .... None of the calves that had died from causes other than predation were fed upon by wolves. This, plus the killing of calves without utilization, suggests that carrion was not important to the wolves on the calving ground.

In a study of white-tailed deer in Minnesota, Mech et al. (1971) showed that in a winter of extremely deep snow, there was a higher rate of predation, and the surplus kills were left partly or completely uneaten. Pimlott et al. (1969) found a 44 percent utilization of deer in a year of severe snow conditions and 82 percent utilization in years of much less severe snow conditions; they stated that this probably reflected the ease with which wolves could kill deer in severe winters. A similar situation involving moose on Isle Royale was reported by Wolfe and Allen (1973). Stenlund (1955) also referred to the variation of utilization in different years.

The degree of carcass utilization during this study was undoubtedly related to the availability of prey. During the winter and early spring of 1973, about 2,000 caribou remained in the southern portion of the study area and evidence of wolf kills in that area was numerous. The fact that a bull moose which had died sometime during the winter, before new antler growth had begun, was still intact on 24 May was an indication that carrion was not being fully utilized. About the time the caribou moved out of the area, the wolves found and ate the moose carcass. During the remainder of the summer, wolves utilized 100 percent of the nine carcasses they found.

The frequency with which wolves cached meat from the carcasses may be further evidence that food for wolves in the study area was not abundant. Murie (1961:220) stated that

> when there is an abundant supply, the bother of caching the food is often omitted. I have found calf caribou on the calving grounds left untouched where killed. The wolves were seemingly aware that there was not much point in caching them since food was readily available on all sides.

The frequency at which wolf caching actually occurred in my study area was high, but the number of caches that were made was lower than it could have been. Wolves could have cached all the meat from a carcass before they left the area but they never did. During the time that wolves are away from carcasses, bears, foxes, and avian scavengers might feed on the carcasses. Was the wolves' failure to cache all the meat before leaving the site to return to their dens an indication that the food supply was more than adequate?

The theory that the relative abundance of food may have a bearing on whether or not a carnivore will make the effort to cache excess food items becomes more intriguing after reading Kruuk's (1964) paper on surplus killing of black-headed gulls (Larus ridibundus) by a red fox. Kruuk found that the number of gulls cached did not have an obvious relationship to the number of gulls killed but that the number cached was amazingly constant. This suggests that caching behavior is not controlled by the scarcity or abundance of the food item, but that there is an upper limit to the number of caches or in the amount of time spent caching regardless of the amount of food available. It is to the wolf's advantage to cache portions of a carcass for later consumption; to cache the entire uneaten portion of the carcass may be energetically inefficient since caches are subject to depredation by other scavengers (Murie 1961:221), to destruction by natural forces such as flooding (pers. obser.), and to loss through decay and disintegration (Kruuk 1964).

Red fox

Red foxes rarely visited carcasses during the two summers of the study. This was probably due, in part, to an abundance of rodents, making scavenging unnecessary, and to the aggressive behavior of wolves and bears at carcasses. Evidence from other areas indicates that foxes are hesitant about approaching carcasses on which wolves have been feeding. A red fox in Mount McKinley National Park that found a caribou recently killed and fed upon by a wolf appeared very nervous (pers. obser.). Even though the wolf had left the area, the fox would not approach the carcass; it searched for raven caches for a few minutes, and after finding and eating a few of the caches, it left the area without touching the carcass. When it returned later in the day, it was still very apprehensive even though the wolf had not been back, and it would not feed on the carcass. Chapman (pers. obser.) reported similar behavior by a red fox at another carcass in the park.

Nearly all investigators who have studied the food habits of red foxes refer to the propensity of foxes to scavenge, particularly when prey items are scarce. Korschgen (1959) found that carrion averaged 7.7 percent of the diet of red foxes during a 5-year study in Missouri.

He stated that carrion was taken infrequently, but its use nearly doubled in the last two years of the study substituting for rabbits in the low years and for mice after a decline in their population. Use of carrion was greatest in summer and spring rather than in fall or winter. Hamilton (1935) stated that foxes in New York frequented the vicinity of slaughter-houses where they were able to secure offal and that they will feed on dead stock particularly during winter months. He felt that deer killed by hunters during the fall were favorite food of foxes during the winter in the Adirondack Region, and, in some cases, it is the most important food item in winter. Of the foxes he examined, carrion occurred in 8.3 percent of the stomachs and made up 8.1 percent of the bulk of food in the stomachs. In his paper concerning the food habits of red foxes in Norway, Lund (1962) stated that in inhabited areas, the foxes visit refuse and manure heaps and that this source of food may be of great importance during some winters. He cited several studies of foxes which refer to the scavenging activity of foxes. One of these showed that when small rodent populations were low, carrion constituted an important part of the food of foxes, increasing from none in one winter to 15 percent in the next (Baranovskaya and Kolosov 1935). Scott (1943) felt that carrion made up 16 percent of the food of red foxes. Schofield (1960), in tracking red foxes during winter months in northern Micigan, found that deer (Odocoileus virginianus) shot and wasted by hunters in the fall were the primary food for foxes. He found an average of four deer per square mile in a 24 mi^2 (62.2 km^2) area that had been fed on by foxes. Johnson (1970) found that on Isle Royale, in years when snowshoe hares are not abundant, moose that have been killed by wolves may be the food resource that keeps foxes above the starvation level. Peterson (pers. comm.) stated that in 1972 he saw 10 foxes on a 1-acre area (0.4 hectares) around a moose carcass on Isle Royale. Though the wolves generally chased foxes off a kill, the foxes remained in the area until the wolves had finished feeding.

Since the snowshoe hare population in my study area is always low and ground squirrels, birds, fruits, insects, and eggs are not available to foxes during winter months, ptarmigan and microtines must supply the only food for foxes in winter unless foxes scavenge on carcasses to a greater extent than they did during my study.

Wolves may play an important part in providing food for foxes during certain periods. Foxes are not efficient at opening carcasses of animals that have died from causes other than predation. They are often only able to gain access to the flesh through the anal region particularly with moose. Peterson (pers. comm.) felt that foxes on Isle Royale rely on wolves to break through the tough moose hides. Because populations of microtines and ptarmigan undergo local fluctuations in my study area, foxes may rely on wolves a great deal in some years to supply food during winter months; however, scavenging is probably never a strategy used by foxes in the study area for acquiring a significant amount of food during summer months.

Arctic ground squirrel

Ground squirrels are certainly not an important scavenger of carrion except on a very local scale such as that which occurred at Neruokpuk Lakes. However, that was a man-made situation where a relatively consistent supply of carrion was provided in a small area. Normally, carrion probably does not become available very often to ground squirrels, and it is likely that they seldom actively search for carrion, feeding on it only when it is near their burrows.

Golden eagle

Spoffard (1964) made the statement that "it is now generally known that eagles feed readily and even preferentially upon carrion in cool or cold weather ..." and he referred to many instances of golden eagles in Texas feeding on dead stock animals and on jackrabbits and other animals killed along the roads. Other investigators have seen eagles feeding on wildlife carcasses, some of which were probably obtained as carrion. As many as eight golden eagles, all immature or subadult birds, were seen feeding on a caribou carcass in the Arctic National Wildlife Range (Curatolo, pers. comm.). Two eagles, an immature and an adult, fed on a caribou which had been killed by wolves on the Aichilik River (Roby, pers. comm.). Eagles have been known to kill caribou calves (Skoog 1968), but such cases are probably not common and most often occur during the spring when the calves are very young. The food items most frequently taken by eagles in the study area are probably ground squirrels (which are numerous), birds (I watched an eagle kill and eat a large shorebird), and fish (ravens were observed making a successful attempt to steal what appeared to be a fish from a golden eagle as the bird sat on the ice of the Canning River in late May).

Eagles in the study area appeared to take carrion quite readily, and it may be that carrion figures significantly in the diet of eagles when they first arrive in the spring. A sighting of a golden eagle was made as early as 15 March by RRCS biologists. At this time, most prey items for eagles would be particularly scarce since ground squirrels would not have emerged from their burrows and migratory birds have not even begun to arrive. Caribou calving does not occur in the study area and very few calves were ever observed there. Ice still covers the rivers in most places. Fish would not be readily available. Carrion and ptarmigan would probably be the most readily obtainable food for eagles at this time of year.

All my observations of eagles feeding on carcasses were made during summer months when other food items are available; this probably accounted for the relative infrequency of their visits to carcasses and the long average length of time that passed before they arrived at the carcasses.

Raven

Ravens were highly successful scavengers in the study area. They were able to find 100 percent of the carcasses that were available in an average time of only two days. Since most carrion in the study area probably becomes available to ravens through wolf predation, I expect that the raven's average time for finding a carcass is normally less than two days. All but one of the carcasses which I observed were of large ungulates shot specifically for this study. Ravens had already located the other, a wolf kill, by the time I found it; this was probably less than two hours after the kill had been made. This suggests that the ravens may have been in the area when the wolf made the kill and were attracted by the activity of the wolf or that the ravens had actually been following the wolf that made the kill. In contrast, the shooting of animals for the study was accomplished quickly and with little activity to attract ravens; none of these carcasses were visited by ravens in less than 30 hours. When tracking wolves on Isle Royale in Lake Superior, Peterson (pers. comm.) often encountered ravens doing the same thing. He did not know how far they will follow wolves but has seen them stop and sit in a tree when the wolves lay down to rest. Fresh kills always had ravens associated with them. The only instance of a raven ever closely approaching me as I was hiking through the study area was the one occasion when I had a dog with me; it resembled a wolf very closely. A raven followed us for nearly a mile (1.6 km), often landing ahead on the tundra and waiting while we caught up with it. It would seem advantageous for ravens to keep in close contact with wolves, especially during winter when daylight is so limited in the Arctic that ravens would hardly have sufficient time for a visual search for items such as microtines.

Studies of raven food habits have not been extensive and few are quantitative (Bent 1946, Ratcliffe 1962, Wittenberg 1968, Dement'ev and Gladkov 1970), a notable exception being Rowley's (1973) work on Australian corvids. Most investigators, however, agree that ravens are omnivorous and to a large extent depend on carrion in the form of offal from slaughterhouses, animals killed along roadsides, domestic stock that have died of disease or injury, and animals killed by hunters, trappers, and predators. In addition, ravens readily adapt to feeding at garbage dumps, and in Fairbanks, Alaska, ravens alight in truck beds to feed on garbage and will pillage dog food and garbage from the backyards of local residents and commercial establishments.

Ravens also eat birds' eggs, nestlings, invertebrates, small mammals, berries and other vegetable materials. They have also been known to kill pigeons, chickens, ptarmigan, and reindeer calves.

Many of the food items which are probably eaten by ravens in the study area are only available on a seasonal basis with birds' eggs and nestlings becoming available in late May and June, insects in July and August, and berries in August and September. Small mammals are present all year round, but it is unlikely that ravens could capture enough microtines to subsist during winter months without supplementary food. In many years small mammals are available in significant numbers only as snow is melting in the spring. Lemmings in the Barrow area are most vulnerable during spring melt-off with maximum exposure to avian predators at that time. The arrival of pomarine jaegers generally coincides with spring melt-off, and though snowy owls arrive well before the onset of melt-off, they occur predictably in areas of exposed ground (MacLean, pers. comm.). Glaucous gulls also feed on lemmings during spring melt-off (Maher 1970). In Fairbanks, Alaska, ravens hunt microtines in agricultural fields during melt-off (pers. obser.); this predation on microtines is related to the density of the microtine population, concentration of prey because of standing water and snow, and unfavorable burrowing habitat at the height of melt-off (Hoberg, unpubl. ms.). Besides the gyrfalcon, which is primarily a predator of ptarmigan, the raven is the only avian predator of microtines which remains in the study area during the winter; it is doubtful they are existing primarily on small mammals.

Temple (1974) felt that ravens near Umiat, Alaska "function energetically as half predators and half scavengers during the arctic winter." His assumption was based on a food habits analysis of 684 pellets regurgitated by ravens which roosted at Umiat from early November until mid-March. However, Temple did not discuss the possibility that birds which scavenged on carrion in many cases may produce no evidence of the item in the regurgitated pellets and, in fact, may not produce pellets at all. Carrion may well go undetected or the quantity consumed be difficult or impossible to determine.

> With omnivorous scavenger-predators, such as the Australian corvids, identification of flesh in the stomach is difficult. Not only are the items frequently well-digested but the majority of items lack the clues (such as hair, feathers, wool, or small bones) necessary for complete identification (Rowley 1973).

My own observations of ravens feeding on carcasses indicate that these birds can obtain many meals from a carcass without ever ingesting a portion that might be cast up in a pellet. While it would be relatively easy to determine by pellet analysis the approximate number of microtines eaten, the technique provides poor evidence of the amount of carrion consumed, particularly that of large animals. Temple is likely to have substantially underrated the amount of carrion eaten by ravens, and his estimate must be considered minimal.

I feel that the ravens in my study area are obligate scavengers, at least during a large portion of the year, and that the number of ravens is directly related to the winter supply of carrion. Ravens were not common in the study area and were never seen in groups of over six birds; most often they were seen as singles or pairs. Groups of more than two birds were probably family units. Raven nests comprised less than two percent of the total raptor nests located by Roseneau (1974) on the north side of the Brooks Range between the Shaviovik River and the U.S.-Canadian border. During many hours in search of raptor nests, he found only one raven nest though he was able to locate 9 active gyrfalcon (*Falco rusticolus* Linnaeus) nests, 1 peregrine falcon (*Falco peregrinus* Tunstall) nest, 23 rough-legged hawk (*Buteo lagopus* Pontoppidon) nests, 2 unknown falcon nests, and 15 golden eagle nests. The highest number of ravens he observed in that area was six; these were feeding on a caribou carcass in August. Kessel and Schaller (1960) stated that ravens were not abundant in the area of the Sheenjek River, with a total of 11 birds sighted between 31 May and 14 July. These birds were seen in singles or pairs except for two adults with four fledged young which were seen feeding on a fresh caribou carcass. White and Cade (1971) stated that ravens were also rare breeders along the Colville River which puzzled these authors since the raven "is otherwise so resourceful and successful as a resident arctic species."

Adult breeding ravens probably remain near their nesting sites all year round. White and Cade (1971) suspected that this might be true of ravens along the Colville River in central arctic Alaska.

Ratcliff (1968) stated that the majority of Corvus corax in Great Britain are seen on their territories all year round. Even if ravens do not remain on their territories all year round in the Arctic, they are early breeders and must return to their nesting sites when winter conditions still prevail. Melt-off in the study area did not begin until mid-May in 1972 and late April in 1973. White and Cade (1971) speculated that ravens in the Arctic are incubating eggs by mid-April. Dement'ev and Gladkov (1970) stated that the first eggs in raven nests around Arkhangelsk (latitude 64°30') have been recorded between 15 March and 14 May, depending on the type of spring, and that nestlings hatched between 22 April and 7 June leave the nests by the end of June. I observed juveniles accompanying adult ravens in the study area on 5 July in 1973. Ravens in the Arctic, therefore, are breeding and laying eggs while food resources other than carrion are scarce.

Ratcliff (1962) gives a lengthy discussion of factors which affect the nesting density of Corvus corax, and he arrived at the conclusion that in areas where nesting sites are sufficient, territorialism is the

> factor controlling maximum nesting density by producing a 'proximity tolerance limit' between adjacent nesting pairs. It is believed that such territorialism is not itself an ultimate limiting factor but has evolved in relation to food supply so that numbers of [ravens] are permanently balanced against the factor.

The immediate food supply may be able to support a higher number of birds during some periods but ravens will set up territories that will guarantee an adequate food supply in spite of seasonal and annual variations. Ravens have been known to maintain exactly the same territories through many years of occupation (Ratcliff 1962, Rowley and Vestjens 1973) and though food supply may fluctuate, territories remain the same.

Since carrion appears to be the only consistent source of food for ravens and carrion provided by predators the most dependable supply, I feel that ravens in my study area and within the entire Arctic National Wildlife Range are directly related to the number of predators which provide carrion for these birds. The wolf is probably the most important of these with the gyrfalcon perhaps being second in importance. Peterson (pers. comm.) felt that

> almost all of the winter food supply for ravens [on Isle Royale] is derived from wolf-killed moose or wolf scats, which the ravens recycle. The only exception is during winters when mountain ash fruit has been abundant--then ravens will utilize this food resource.

Even the carcasses of animals which have died of causes other than predation must first be opened by the larger scavengers before the raven can gain access to the flesh. Rowley (1969) stated that the massive bills of the largest raven species in Austrailia "appear very dagger-like and yet they have extreme difficulty in penetrating carcasses" of domestic lambs. My own observations of ravens at carcasses that had not yet been torn open by bears or wolves indicate that ravens may only be able to eat the eyes and perhaps some dried blood that may have resulted from a wound. Removing the eye of a caribou may take as long as 26 minutes (pers. obser.). Even this limited amount of feeding was not attempted in some cases and was never done at carcasses that had exposed flesh.

Ravens on the Colville River may be significantly dependent upon gyrfalcons for carrion (White and Cade 1971). During the spring, I found numerous sites along the Marsh Fork with a pile of ptarmigan feathers. At first I assumed that they were the remains of fox kills, but it is very likely that they were gyrfalcon kills; falcons pluck birds before eating them while foxes tend to eat carcasses without removing the feathers.

In support of my conclusion that predator kills provide the main bulk of raven food in the winter in the Arctic, the remains of caribou (the primary food of wolves) and of ptarmigan (the primary food of gyrfalcons) were the items that occurred most frequently in the winter pellet of ravens at Umiat (Temple 1974).

Caching probably contributes to the raven's success as a scavenger. They have behavioral and morphological characteristics adaptive for food transportation and storage which are similar to those of other members of the family Corvidae (Turcek and Kelso 1968). My autopsy of a raven showed the presence of the antelingual cavity described by Eigelis and Nedrasov (1967) as "an arbitrary increase of the volume of the buccal cavity provided by the extension of the bottom of the buccal cavity and location of the tongue in the extreme backward position." The capacity of the buccal pouch in the autopsied raven was approximately 40 cc or 46 gm of meat. In addition, ravens will sometimes carry extra meat, probably weighing about 10 gm, in the beak. Therefore, a raven on a caching flight might be carrying 40-50 cc or 50-60 gms. An average cache probably contains less than 40 cc. The average flight to a caching site (from 15 flights made at carcass no. 1) was 120 seconds. Schwann (1974) estimated that a 1-hour flight by ravens would require 51 kcal of energy. A gram of moose meat or caribou meat would give an average of 1.2 kcal of energy according to the Cooperative Extension Service, University of Alaska. Given that an average cache weighs 35 gms, an average caching flight would expend 1.6 kcal of energy for the storage of 42 kcal in the cache; this is a net gain, up to this point, of 40.4 kcal. However, one must also consider the energy required to recover the cache as well as energy lost in failing to relocate a cache; this is where information is lacking. The net gain of 40.4 kcal would allow approximately 49 minutes of flying time to retrieve the cache if the raven were to "break even" (even more time if a raven were to walk or hop during retrieval). This seems to be more than enough time to recover a cache particularly if ravens are able to "remember" the locations of their caches. The Eurasian nutcracker (*Nucifraga caryocatactes*) goes directly to the spot where a cache had been made and digs down to the food item without tentative or trial probing (Dulkeit 1960, Mezhennyi 1964, and Reimers 1966 as cited by Turcek and Kelso 1968). Hayman (1958) reported the ability of magpies (*Pica pica*) to go directly to the spot where a cache was made with no searching necessary to recover the hidden food item. Goodwin (1955) reported that the jay (*Garrulus glandarius*) and the carrion crow (*Corvus corone*) recovered food from places where there were no apparent visual clues, and since they went straight to the particular spot of the cache, it seemed that the birds must have remembered the cache location; however, he witnessed occasions when the recovery of caches by jays occurred only after prolonged searching on an apparent trial and error basis, but he stated that, although this may have been due to "forgetfulness" or alteration in the appearance of the terrain, it was more likely a search made by a bird's mate or some other jay.

While it appeared that ravens were able to "remember" the specific site of some of their caches particularly where unique features such as boulders or the base of large willows were the cache site, my observations indicated that they will also use a trial and error search to recover caches. After carcass no. 13 had been almost entirely removed by wolves, a family of six ravens was still in the carcass area. The ravens would fly low back and forth across the hillside above the carcass site and periodically drop to the ground and turn over a piece of vegetation. In a 10 to 15 minute period, one raven had landed five times and appeared to find a cache once. Earlier some of the ravens had been observed walking over the area and appeared to find several caches in that manner.

The trial and error method of searching for caches is not as inefficient as it might seem since ravens appear to concentrate their caches within restricted areas in several locations; this should increase the probability of finding caches. Such areas might include a particular sedge meadow, a rocky hillside, or two or three different gravel bars.

Just how successful ravens are in relocating caches is impossible to say without additional observations. Success rates must vary from one situation to another, and they must decrease with losses of caches due to other scavengers, to deterioration, to "forgetfulness," and to catastrophic events such as flooding rivers which occurred periodically during the summer. In their synopsis of food transportation and storage by Corvidae, Turcek and Kelso (1968) mentioned the proportion of recovered food items for only one species, the Eurasian nutcracker. The proportion varied: 6 to 33 percent (Reimers 1956), 22 to 65 percent (Bibikov 1948), and up to 70 percent (Turcek 1966).

Caching intensity varied between carcasses, between the days of a given carcass, and within a particular day of a carcass. Gwinner (1965) stated that his captive ravens hid more food the longer they had been without food and that during the breeding season, those caring for young hoarded more, particularly of the kind of food they were feeding the young. In my study area, raven feeding and caching activity seemed most intense just after ravens arrived at a carcass on a given day. This may be the result of a higher level of hunger at that time. Goodwin (1955) stated that the carrion crow

> usually hides all the surplus food first and does not eat until the last load is ready for transportation. The eagerness with which it then feeds and the amount eaten often show that the bird must have been in a state of some hunger whilst engaged in storing activities.

The variation in intensity of feeding and caching by ravens in the study area might possibly be explained by this behavior. I was not able to determine when the ravens in the study area were actually feeding or were just preparing to make a cache.

More information is needed to determine whether ravens in the study area cache more often when they are caring for young. It is interesting to note that a cache was made for every 2.2 observation periods of feeding activity at carcass no 1 (early June) and every 1.3 observation periods of feeding activity at carcass no. 3 (early

July) before young ravens were observed foraging with the adult birds, but only once for every 4.0 observation periods of feeding activity at carcass no. 8 (early August) when the juveniles were with the adults and were no longer being fed by the adults. Perhaps an explanation of the variation in caching intensity between carcasses is in part due to the need to care for the young birds.

Feeding and caching intensity usually showed a definite peak over a one or two day period regardless of how long the carcass was available. No one factor or combination of factors could explain why ravens were not making as many caches as the opportunity allowed. In the time between 0600 and 1800 (the most active time for ravens), a raven theoretically would have the opportunity to make 360 caches (at the rate of one cache every 120 seconds). Even at a carcass where other scavengers did not significantly prevent ravens from feeding (carcass no. 8), it did not appear that any raven ever made as many as 50 caches in one day or that the total number of caches from any one carcass ever exceeded a hundred. If they contained 42 kcal of energy, a hundred caches would contain enough food for a raven for over 14 days if a raven's daily requirement is 309 kcal per day as stated by Temple (1974) for ambient temperatures below freezing. Raven caches from one carcass probably provide food for at least a week provided that few caches are lost. It may be that deterioration of the meat causes a high loss of caches if they are left for more than a few days or that losses from other causes increases as the number of caches increases and, therefore, about 50 to 100 caches per carcass may be the most efficient number to make in terms of the return in kilocalories.

In order to fully understand the mechanism behind caching behavior, it is necessary to learn more about the importance of caches in the raven's diet, to determine how long caches will remain before ravens will retrieve them, to determine their success at relocating the caches, to establish the amount of time it takes to recover a cache, and to determine the number of caches that might be lost to other scavengers or through deterioration or catastrophic events thereby, establishing the energy costs of this feeding strategy.

In speaking of the evolutionary aspects of food transportation and storage, Turcek and Kelso (1968) stated that

> it seems most likely that climactic and nutritional variability are factors in the evolution of storage habits in corvids. This is supported by the fact that such behavior is largely confined to species of subarctic, temperate and subtropical zones, or roughly between 20 and 60 degrees geographical latitude.

These authors did not have data on the food storage habits of corvidae at latitudes greater than 60°.

Citing the works of Amadon (1944) and of Keve and Kretzoi (1966), Turcek and Kelso (1968) stated that

> crows are evidently of tropical origin and at present the majority of forms live in subtropical and tropical areas. Only a small proportion of the more specialized forms live in the temperate and subarctic, and boreal zones, and in boreal-alpine altitudes as well.

The authors felt that the adaptation to feeding on seeds, a high energy food item (over four times the kilocalories per unit volume available in carrion), enables corvids to live in temperate and even subarctic zones. The food items most frequently stored by corvids are seeds. However, once the behavioral adaptation to storing seeds had evolved, it seems a logical step to transfer this habit to the caching of carrion where carrion is one of the primary food items. However, carrion has neither a high caloric content nor a long storage life. In addition, supplies of carrion are not seasonally abundant as are seeds and nuts but are available on a limited but consistent basis. Therefore, the need to cache large quantities of food as a store for winter use is not critical to the raven's survival in the Arctic. Rather, caches of meat may serve as temporary food supplies that have their greatest value in being a relatively reliable food source during the periods intervening predator kills.

Glaucous gull

Gulls were rarely seen in any area not associated with large bodies of water, such as the Canning River, the Marsh Fork, Neruokpuk Lakes. Gulls were never seen in the smaller tributaries or over the tundra or in the mountains. All three of the carcasses which were visited by this species were located on the gravel bars of the Canning River. Three other gulls were seen flying along the river past the carcass sites, but they never visited the carcasses. All other carcasses were at considerable distance from large bodies of water and gulls were not observed in the area of these carcasses.

Strang (1973) found that some glaucous gulls on the Yukon-Kuskokwim Delta of Alaska hunt over land. Nearly all these gulls were isolated pairs hunting in the vicinities of their territories; a few were from colonies. The number of gulls that hunt over ground was small when compared to those that flew back and forth to Kokechik Bay to feed. The gulls that do hunt over land spend less than half of their time in the air. Strang estimated that from two-thirds to four-fifths of the hunting time of these gulls was spent standing, usually in elevated or open spots which is not conducive to a scavenging strategy. The gulls in Strang's study area rarely fed on carrion. However, about 35-40 gulls, many of which were immatures, fed on dead animals. Most of the birds in this group were doing some scavenging, but Strang mentions that these gulls were certainly not deriving all their energy from their scavenging activities.

There appears to be little need for gulls to scavenge in my study area. Gulls were often observed fishing in the Canning River. They would stand for long periods of time at the edge of the water and would suddenly crouch down with their heads low to the ground and make a jab at the water with their bills. They were also observed flying after insects and attempting to capture microtines that were along the river. They probably fed on small birds and eggs as well. Strang (1974) stated that birds are considerably more important as a source of food for inland than for sea-edge glaucous gulls, surpassing even fish during the important period of chick rearing. Overall, however, fish make up the bulk of the inland gull's diet. Eggs were less important inland, possibly the result of competition with foxes.

Long-tailed and parasitic jaegers

According to Maher (1974), parasitic jaegers in the Arctic are primarily predators of birds during the breeding season; however, a pair of parasitic jaegers may have been feeding their chick largely on carrion or fish. Breeding long-tailed jaegers took slightly fewer birds and a consistently larger percentage of microtines than parasitic jaegers.

According to Maher's information, all three species of jaegers in the Arctic are primarily predators but when food supplies are reduced, jaegers may increase their scavenging particularly in non-breeding populations. Though both parasitic and long-tailed breed in inland areas, non-breeding birds and birds whose breeding effort have failed usually forage in coastal areas. The non-breeding birds show a greater tendency to be opportunistic in their feeding behavior than the breeding birds.

The tendency toward increased scavenging by non-breeding jaegers is probably, in part, a result of an expanded foraging area. Released from the necessity of defending territories and the responsibility of feeding chicks, non-breeding birds would be able to cover more area in the search for food. Though two to three pairs of jaegers were suspected of nesting in the area of carcass no. 6 and were observed flying over the carcass in pursuit of a golden eagle, no jaegers were ever observed feeding on this carcass. Since they ended the chase just a short distance past the carcass and returned in the direction from which they came, I suspected that the carcass may have been at the limit of their defended territory and that little foraging probably occurred near the carcass site.

The two long-tailed jaegers that fed on carcass no. 4 were probably breeding birds. They were seen flying in the area of the carcass on several occasions. The behavior of the parasitic jaeger at carcass no. 8 suggested that it was not associated with a nest at the time. It appeared on 7 August at the end of the breeding season.

Small mammals and birds were common in the study area, and there was little need for jaegers to scavenge on carcasses. Microtine populations in the foothills do not undergo the dramatic cyclic changes that lemmings do on the coastal plains although fluctuations in their populations do occur. A low in the microtine population would be detected when the jaegers first arrive on the breeding grounds and breeding by long-tailed jaegers might be curtailed with most birds moving onto the coastal plains. Passerine bird populations probably remain fairly stable from year to year so carrion probably does not play an important part in the diet of parasitic jaegers in the study area.

Carcass Disposal and Remains

Wolves as well as bears and most of the other scavengers appeared to feed at the most readily accessible area of the carcass wherever it was possible to remove meat easily and quickly. My own observations do not support evidence presented by Kuyt (1972) that the flesh of the neck and throat, tongue, liver, heart, kidneys, and lungs of caribou are removed first by wolves. However, I do not have sufficient data to state whether or not the pattern of utilization at carcass no. 7 was the normal pattern of wolves in the study area.

If carcasses have been only partially eaten, there may be some indications of the scavenger responsible for missing parts. If only the eye of a carcass has been removed, it is an indication that the raven has been the only scavenger at the carcass. Foxes may gain access to the flesh of a carcass through the soft parts around the anus and usually scatter hair from the carcass. Ravens and other avian scavengers may also start feeding in the anal region.

A carcass which has shredded fragments of meat still remaining on the bones indicates that avian scavengers have been feeding on the carcass. It is likely that some mammalian carnivore had originally opened the carcass since the avian scavengers in the study area were never observed breaking through the hide to reach the flesh of caribou, moose, or Dall sheep.

If a fairly fresh skeleton is found with the skull, vertebral column, and rib cage still intact but most meat removed, it is unlikely that a bear has been feeding on the carcass. Wolves will remove much of the meat without disjointing major portions of the skeleton; often only the legs have been disjointed from the torso, but many of the ribs may have been chewed or broken.

I found it impossible to tell whether bears or wolves had been responsible for the scavenging that occurred at a carcass if the carcass was found when very little meat remained and the bones had been scattered.

Scats, tracks, caches, or scrapings may indicate some of the scavengers which have visited a carcass but even with such evidence available, one cannot conclude that a particular species was the major scavenger at the carcass. Wolves, for instance, may not have left scats near a carcass, and bears do not always scrape debris onto a carcass. The only evidence of the presence of avian scavengers at such a carcass would be the presence of droppings, tracks, or feathers.

The amount of a carcass remaining at the original site is a good indication of the availability of food for the larger scavengers in a particular region. Bears, wolves, and wolverines are more likely to return again and again to a carcass if prey are not abundant. In very little time, not even bones would be left at the carcass site.

CONCLUSIONS

1) Bears and ravens are the major scavengers on the Arctic Slope of the eastern Brooks Range. Wolves have high potential as a scavenger but probably have few opportunities to scavenge on large mammal carcasses in the study area. Red foxes, golden eagles, glaucous gulls, long-tailed and parasitic jaegers, and arctic ground squirrels are among the minor scavengers. Other species such as the wolverine and the gray jay are so few in numbers that they are insignificant scavengers in the area.

2) Because ungulate populations are only sporadically abundant in this area of the Brooks Range, carrion is not plentiful and most frequently becomes available as a result of wolf and occasionally bear predation. Large mammal carcasses which become available from causes other than predation must still be opened by the larger scavenger before the smaller, particularly the avian scavenger, can feed on the flesh.

3) The degree to which carcasses are utilized by the various scavengers is an indication of the scarcity or abundance of prey and alternate food resources.

4) Scraping litter onto carcasses is a means by which bears inhibit other scavengers from gaining access to the flesh of the carcass.

5) Carrion is most important to the grizzly in the spring and fall

and to the raven in the winter; little else is available as food for these species during those seasons.

6) Though ravens are predatory to some extent, most of the flesh in their diet is probably carrion. The numbers of ravens in the area are directly related to the predator population that provides this carrion.

7) Wolves and ravens do not make the maximum number of caches possible from the carcasses they visit; there may be an upper limit to the number of caches these species will make regardless of the scarcity or abundance of carrion. Ravens distribute their caches within several specific areas; they later revisit the areas and relocate the caches through a "trial and error" method of search.

8) Red foxes are not important scavengers during the summer; alternate sources of food are abundant making scavenging unnecessary, and carcasses are avoided due to the potential harassment by wolves. Foxes are likely to scavenge more often during winter months.

9) Carrion is likely to be an important source of food for golden eagles during early spring when they first arrive in the Arctic, but this raptor does not depend on scavenging during summer months. Alternate food supplies are plentiful enough to make scavenging an unnecessary strategy for the glaucous gull. Scavenging by glaucous gulls does not occur in areas away from the larger bodies of water,

and does not appear to be an important method of obtaining food. Jaegers also do not rely on scavenging in the study area but scavenging may be important during some years.

10) The behavior of scavengers at carcass sites is particularly influenced by competition with other scavengers, by human interference, and by alternate food supplies.

SUMMARY

1) The species that visited carcasses were the grizzly bear, the wolf, the red fox, the arctic ground squirrel, the golden eagle, the raven, the glaucous gull, and the long-tailed and parasitic jaegers.

2) There was no activity at carcasses during 70 percent of the observation time.

3) Ravens, wolves, and bears scavenged at over 50 percent of the carcasses, the raven being the first species to arrive at 73 percent of these carcasses.

4) The average number of days which passed before a species arrived at a carcass varied between 1.25 days for the red fox and 4.75 days for the golden eagle.

5) The hierarchy of scavengers corresponded generally with body size, the largest scavenger being more dominant than the smaller.

6) The three major activities at carcass sites were feeding, moving, and resting. The proportion of time which scavengers spent at each of these activities varied considerably from one carcass to another.

7) The average duration of feeding sessions for all scavengers was

around 20 minutes; the average for moving sessions varied from 7 to 17 minutes. The average duration of resting was very different from one species to another, with 10 minutes for the jaeger being the shortest and 60 minutes for the bear being the longest.

8) There was a definite relationship between the time of day and the activity of most scavengers at carcass sites. This relationship was particularly strong for the raven which was most often at the carcasses between 0600 and 1800.

9) The time that scavengers spend feeding at a carcass fluctuates from day to day. The reasons for the changes in feeding time are not always evident, but some of the factors which affected feeding behavior during this study included interspecific competition, human interference, and changes in the hunger levels of the scavengers.

10) Minor activities included caching, scraping, drinking, grooming, vocalizing, urinating or defecating, and inter- and intraspecific interactions. Wolves made one cache per 9.2 observation periods in which feeding by wolves occurred, and ravens made one cache every 2.2 observation periods in which raven feeding occurred. Bears scraped debris onto four of eight carcasses that bears were known to visit. Drinking and grooming by gulls, vocalization by ravens, and elimination by wolves occurred most frequently by those respective species. Aggressive interactions occurred most often between interspecific pairs and was most

often initiated by the dominant member of the pair. In most instances, subordinate scavengers avoided the area near a carcass or did not feed on a carcass while a more dominant animal was feeding.

11) Caribou, Dall sheep, and bear carcasses were usually disposed of within a week after the carcasses were found by bears or wolves; moose carcasses lasted twice as long. The carcass fed on entirely by avian scavengers lasted over 10 days; this carcass had been opened by the investigator. Though the parts of a carcass that remained at a carcass site varied from one carcass to another, a pattern was evident at most sites to indicate the major scavengers. Carcasses visited by wolves but not bears had intact skulls, spinal column, and ribcage after most of the meat had been removed; carcasses visited by bears did not. The carcass fed on only by avian scavengers had the entire skeleton intact and shreds of meat on all the bones.

APPENDIX A.

LIST OF MAMMALS OBSERVED IN THE STUDY AREA

Snowshoe hare, Lepus americanus dalli Merriam

Arctic ground squirrel, Spermophilus undulatus kenicottii Ross

Red-backed vole, Clethrionomys rutilus dawsoni Merriam

Tundra vole, Microtus oeconomus endoecus Rausch

Singing vole, Microtus miurus paneaki Rausch

Brown lemming, Lemmus sibiricus trimucronatus Rausch

Collared lemming, Dicrostonyx groenlandicus rubricatus Richardson

Porcupine, Erethizon dorsatum myops Merriam

Gray wolf, Canis lupus tundrarum Miller

Red fox, Vulpes vulpes alascensis Rausch

Grizzly bear, Ursus arctos horribilis Rausch

Short-tailed weasel, Mustela erminea arctica Merriam

Woverine, Gulo gulo luscus Rausch

River otter, Lutra canadensis yukonensis Goldman

Lynx, Lynx canadensis canadensis Kerr

Moose, Alces alces gigas Miller

Caribou, Rangifer tarandus stonei Rausch

Dall sheep, Ovis dalli dalli Nelson

APPENDIX B.

LIST OF BIRDS OBSERVED IN THE STUDY AREA*

Common loon, _Gavia immer_

Yellow-billed loon, _Gavia adamsii_

Arctic loon, _Gavia arctica_

Red-throated loon, _Gavia stellata_

Red-necked grebe, _Podiceps grisegena_

White-fronted goose, _Anser albifrons_

Mallard, _Anas platyrhynchos_

Pintail, _Anas acuta_

Green-winged teal, _Anas crecca_

American wigeon, _Anas americana_

Lesser scaup, _Athya affinis_

Old squaw, _Clangula hyemalis_

Harlequin duck, _Histrionicus histrionicus_

White-winged scoter, _Melanitta deglandi_

Red-breasted merganser, _Mergus serrator_

Rough-legged hawk, _Buteo lagopus_

Golden eagle, _Aquila chrysaetos_

Marsh hawk, _Circus cyaneus_

Gyrfalcon, _Falco rusticolus_

Peregrine falcon, _Falco peregrinus_

Rock ptarmigan, _Lagopus mutus_

Semipalmated plover, _Charadrius hiaticula_

Appendix B, continued.

American golden plover, <u>Pluvialis</u> <u>dominica</u>

Black-bellied plover, <u>Pluvialis</u> <u>squatarola</u>

Upland plover, <u>Bartramia</u> <u>longicauda</u>

Spotted sandpiper, <u>Actitis</u> <u>macularia</u>

Solitary sandpiper, <u>Tringa</u> <u>solitaria</u>

Wandering tattler, <u>Heteroscelus</u> <u>incarnus</u>

Yellowlegs, <u>Totanus</u> sp.

Baird's sandpiper, <u>Calidris</u> <u>bairdii</u>

Least sandpiper, <u>Calidris</u> <u>minutilla</u>

Northern phalarope, <u>Lobipes</u> <u>lobatus</u>

Common snipe, <u>Gallinago</u> <u>gallinago</u>

Pomarine jaeger, <u>Stercorarius</u> <u>pomarinus</u>

Parasitic jaeger, <u>Stercorarius</u> <u>parasiticus</u>

Long-tailed jaeger, <u>Stercorarius</u> <u>longicaudus</u>

Glaucous gull, <u>Larus</u> <u>hyperboreus</u>

Mew gull, <u>Larus</u> <u>canus</u>

Arctic tern, <u>Sterna</u> <u>paradisea</u>

Snowy owl, <u>Nyctea</u> <u>scandiaca</u>

Short-eared owl, <u>Asio</u> <u>flammeus</u>

Say's phoebe, <u>Sayornis</u> <u>saya</u>

Horned lark, <u>Eremophila</u> <u>alpestris</u>

Cliff swallow, <u>Petrochelidon</u> <u>pyrrhonota</u>

Gray jay, <u>Perisoreus</u> <u>canadensis</u>

Appendix B, continued.

Common raven, Corvus corax

American robin, Turdus migratorius

Wilson's warbler, Wilsonia pusilla

Wheatear, Oenanthe oenanthe

Gray-checked thrush, Catharus minima

Water pipit, Anthus spinoletta

Northern shrike, Lanus excubitor

Boreal chickadee, Parus hudsonicus

Dipper, Cinclus mexicanus

Gray-crowned rosy finch, Leucosticte tephrocotis

Hoary redpoll, Acanthis hornemanni

Common redpoll, Acanthis flammea

Savannah sparrow, Passerculus sandwichensis

Tree sparrow, Spizella arborea

White-crowned sparrow, Zonotrichia leucophrys

Fox sparrow, Passerella iliaca

Lapland longspur, Calcarius lapponicus

Smith's longspur, Calcarius pictus

Snow bunting, Plectraphenax nivalis

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*Scientific nomenclature from Checklist of North American Birds published in 1957 by the American Ornithologist's Union and from the supplement to this work published in Auk 90:411-419, 1973.

APPENDIX C.

EXPLANATION OF THE ACTIVITY CODES

Major Activities:

FCC - Feeding on the carcass continuously - Feeding occurred during the entire 5-minute observation period; it was intensive and uninterrupted by minor activities. An observation period with FCC could contain no other activity for that individual scavenger.

FCI - Feeding on the carcass intermittently - Feeding was interrupted at short intervals (less than 30 seconds) by minor activities; the scavenger usually did not leave the immediate vicinity of the carcass except to cache or to chase other scavengers. Feeding was not intensive, the scavenger often interrupting feeding to look about or move to a new position at the carcass. Since raven caching activity was an integral part of its feeding behavior, a caching flight was not considered termination of a session of FCI unless the raven did not return to the carcass after the normal time had elapsed. If one full 5-minute observation period passed before a cache was made and feeding had been intensive, the feeding during that observation period was considered FCC; FCI was recorded for the observation periods in which caching occurred. The same basic pattern was followed for the wolf's caching behavior and the bear's scraping behavior except that when scraping became long in duration (5 minutes or longer) without any feeding, it was no longer considered part of FCI.

Appendix C, continued.

FCP - Feeding on carcass parts - The same type of behavior as FCI except that feeding was from pieces of the carcass (most often the legs) which had been disconnected from the main portion of the carcass.

FC - Feeding on caches - Eating caches made by ravens or wolves.

F - Feeding on something other than the carcass or parts of the carcass - That is, eating vegetation, microtines, or other items from the carcass site.

MA - Moving in the area of a carcass - Moving around the carcass site close enough to the carcass to be aware of it yet not close enough to affect the behavior of other scavengers at the carcass; often accompanied by minor activities such as grooming, urinating, and vocalizing.

MP - Moving in the proximity of a carcass - Moving around the carcass site close enough to the carcass to affect the behavior of other scavengers at the carcass; usually accompanied by inter- and intraspecific interactions.

RA - Resting in the area of the carcass - Resting in the carcass vicinity close enough to the carcass to be aware of it yet not close enough to affect the behavior of other scavengers at the carcass; anytime an animal was not moving or feeding; could include brief periods of movement for the purpose of changing position.

RP - Resting in the proximity of the carcass - Resting close enough to the carcass to affect the behavior of other scavengers at the

Appendix C, continued.

carcass; could include brief periods of movement for the purpose of changing position or reacting to another scavenger's activity.

RC - Resting on the carcass - Resting directly on the carcass; could include brief periods of movement to change position.

Minor Activities:

AA - Aggressive act in the area of the carcass - A scavenger initiated an aggressive act in the carcass vicinity but not in close proximity to the carcass; description of the types of aggressive acts are given in the text; not always directly related to the presence of the carcass.

AAR - Recipient of an aggressive act in the area of the carcass - A scavenger is the recipient of the above aggressive act.

AC - Aggressive act in the proximity of the carcass - A scavenger initiated an aggressive act near the carcass; almost always directly related to the presence of the carcass.

ACR - Recipient of an aggressive act in the proximity of the carcass - A scavenger is the recipient of the above aggressive act.

CA - Caching away from the carcass - Ravens flew to a caching site usually out of the carcass vicinity or at least further than 50 yds (45.8 m) from the carcass; wolves cached further than 50 yds (45.8 m) from the carcass. If more than one cache was made during one trip, it was counted as more than one cache. If the number of

Appendix C, continued.

caches could not be detected, only one cache was recorded.

CP - Caching in the proximity of the carcass - Ravens walked, hopped, or glided to the caching site usually within 50 yds (45.8 m) of the carcass; wolves cached within 50 yds (45.8) of the carcass.

D - Drinking - The number of times drinking occurred was recorded; more than one session of drinking was recorded in one trip to water if the drinking activity was interspersed with other activities such as grooming.

G - Grooming - The amount of time the animal spent grooming was recorded.

NAA - Non-aggressive interaction - Scavengers were engaged in an activity that had no aggressive overtones (e.g. playing).

S - Scraping - The amount of time the bear spent scraping was recorded.

U - Urinating or defecating - Often the observer was too far away to tell whether the animal was urinating or defecating so both are included in this code. The number of times the activity occurred was recorded.

VA - Vocalizing in the area of the carcass - The animal was not close enough to the carcass to affect the behavior of other scavengers at the carcass but was close enough to be aware of the carcass. The number of times vocalization occurred was recorded.

VP - Vocalizing - Vocalizing in the proximity of the carcass - The scavenger was close enough to the carcass to affect the behavior of the other scavengers at the carcass. The number of times vocalization occurred was recorded.

APPENDIX D.

DESCRIPTION OF THE COBOL PROGRAMS AND A SAMPLE OF THE OUTPUT*

Program Title	Description
ANIMAL	This is the major program. It gives the amount of observation time and totals all the time for each scavenger/activity (e.g. B1FCC) for each group of major activities. For example, it adds up all the FCC, FCI, and FCP to give a total of all feeding. The activity times are also given as a percent of the observation time. One other figure is included, the amount of time the activity occurred while other scavengers were at the carcass (combination). A grand total of the activity time for all the days of the carcass is also given.
COMBTIME	This program totals the amount of time two or more scavenger/activities occurred at the same time. In the sample below, the activities B2FCC (bear no. 2 feeding on the carcass continuously) and B3MA (bear no. 3 moving in the area) occurred simultaneously for 20 minutes during the third quarter of the day on day no. 10 and for 10 minutes during the third quarter of the day on day no. 11. The total amount of time that these two activities occurred for this carcass (carcass no. 1) was 35 minutes.
CONSEC	This program lists all the scavenger/activities alphabetically with each of the 5-minute observation periods in chronological

Appendix D, continued.

Output

ANIMAL

CARCASS NUMBER - 01
ACTIVITY - FEEDING
SPECIES - BEAR
INDIVIDUAL - 1

TIME OBSERVED IN ACTIVITIES
TIME - HRS.MINS
* - PERCENTAGE OF OBSERVATION TIME
(COMBINATIONS)

TOTALS FOR BREAKDOWN
OF SUB-ACTIVITIES

PAGE 9

DAY OF CARCASS	TIME WATCHED	BIFCC	BIFCI	BIFCP	TOTAL ALL ACTIVITIES	FC	FCX
03							
B	6.00	0.50 * 13.8 (00.05)	0.05 * 1.3 (00.05)	0.05 * 1.3 (00.00)	1.00 * 16.7 (00.10)	01.00 * 16.6 (00.10)	01.00 * 16.6 (00.10)
C	6.00	0.30 * 8.3 (00.00)	0.10 * 2.7 (00.05)	-	0.40 * 11.1 (00.35)	00.40 * 11.1 (00.05)	00.40 * 11.1 (00.05)
D	6.00	0.25 * 6.9 (00.25)	0.10 * 2.7 (00.10)	-	0.35 * 9.7 (00.35)	00.35 * 9.7 (00.35)	00.35 * 9.7 (00.35)
03 - DAY TOTALS	24.00	2.50 * 11.8 (00.30)	0.35 * 2.4 (00.20)	0.05 * .3 (00.00)	3.30 * 14.5 (00.50)	03.30 * 14.5 (00.50)	03.30 * 14.5 (00.50)

SUMMARY OF TIMES INDIVIDUAL
WAS ENGAGED IN ACTIVITIES
DURING THE PERIOD

PAGE 14

SUB-ACTIVITIES FOR PERIOD

TOTAL TIME WATCHED	BIFCC	BIFCI	BIFCP	TOTAL ALL ACTIVITIES	FC	FCX
228.30	7.20 * 3.2 (01.20)	4.30 * 1.9 (01.25)	0.10 * .0 (00.35)	12.00 * 5.2 (02.50)	12.00 * 5.2 (02.50)	12.00 * 5.2 (02.50)

Appendix D, continued.

COMBTIME

```
CARCASS NUMBER - 01                                                    PAGE   55

SPECIES TYPES IN COMBINATION - B2FCC     B3MA

 DAY OF CARCASS

      08
          A       0 HRS  00 MINS
          B       0 HRS  00 MINS
          C       0 HRS  00 MINS
          D       0 HRS  00 MINS

          TOTAL FOR DAY 08  -   0 HRS  00 MINS

      09
          A       0 HRS  00 MINS
          B       0 HRS  00 MINS
          C       0 HRS  00 MINS
          D       0 HRS  00 MINS

          TOTAL FOR DAY 09  -   0 HRS  00 MINS

      10
          A       0 HRS  00 MINS
          B       0 HRS  00 MINS
          C       0 HRS  20 MINS
          D       0 HRS  00 MINS

          TOTAL FOR DAY 10  -   0 HRS  20 MINS

      11
          A       0 HRS  00 MINS
          B       0 HRS  00 MINS
          C       0 HRS  10 MINS
          D       0 HRS  00 MINS

          TOTAL FOR DAY 11  -   0 HRS  10 MINS

 TOTAL FOR CARCASS 01  -   0 HRS  35 MINS
```

Appendix D, continued.

CONSEC

```
REC     890   DATA    22          18813C7161C R2VA   1
* * * * DEVICE  281  SYS001.  MODE CC              BLOCK   89   DATA   220                                  * * * *
REC     881   DATA    22          18813071615 R2VA   1
REC     882   DATA    22          18813071620 R2VA   1
REC     883   DATA    22          18813071625 R2VA   1
REC     884   DATA    22          18813C7163C R2VA   1
REC     885   DATA    22          18813C71635 R2VA   1
REC     886   DATA    22          1881307164C R2VA   1
REC     887   DATA    22          18813C71645 R2VA   1
REC     888   DATA    22          18813C7165C R2VA   1
REC     889   DATA    22          18813C71655 R2VA   1
REC     890   DATA    22          18813C717CC R2VA   1
* * * * DEVICE  281  SYS001.  MODE CC              BLOCK   90   DATA   220                                  * * * *
REC     891   DATA    22          18813C71705 R2VA   1
REC     892   DATA    22          18813C71710 R2VA   1
REC     893   DATA    22          18813C71715 R2VA   1
REC     894   DATA    22          18813C7172C R2VA   1
REC     895   DATA    22          18813071725 R2VA   1
REC     896   DATA    22          18813C71730 R2VA   1
REC     897   DATA    22          18813071735 R2VA   1
REC     898   DATA    22          18813C7174C R2VA   1
REC     899   DATA    22          18813071745 R2VA   1
REC     900   DATA    22          1881307175C R2VA   1
* * * * DEVICE  281  SYS001.  MODE CC              BLOCK   91   DATA   220                                  * * * *
REC     901   DATA    22          18813C71755 R2VA   1
REC     902   DATA    22          18813C718CC R2VA   1
REC     903   DATA    22          19013090425 R2VA   1
REC     904   DATA    22          19013090455 R2VA   1
REC     905   DATA    22          19013C90535 R2VA   1
REC     906   DATA    22          19013090720 R2VA   1
REC     907   DATA    22          19013C9C85C R2VA   1
REC     908   DATA    22          19013090920 R2VA   1
REC     909   DATA    22          19013C91120 R2VA   1
REC     910   DATA    22          19013C91125 R2VA   1
* * * * DEVICE  281  SYS001.  MODE CC              BLOCK   92   DATA   220                                  * * *
REC     911   DATA    22          19013C9115C R2VA   1
REC     912   DATA    22          19013091155 R2VA   1
REC     913   DATA    22          19013C912C0 R2VA   1
REC     914   DATA    22          19013C912C5 R2VA   1
REC     915   DATA    22          19013091210 R2VA   1
REC     916   DATA    22          19013091525 R2VA   1
REC     917   DATA    22          19013C91625 R2VA   1
REC     918   DATA    22          19013C91900 R2VA   1
REC     919   DATA    22          19113100400 R2VA   1
REC     920   DATA    22          19113102C00 R2VA   1
* * * * DEVICE  281  SYS001.  MODE CC              BLOCK   93   DATA   220                                  * * *
REC     921   DATA    22          19213111000 R2VA   1
REC     922   DATA    22          1921312C40C R2VA   1
REC     923   DATA    22          1921312C83C R2VA   1
```

Appendix D, continued.

Program Title	Description
	order so that one can determine the duration of an activity session by scanning for the beginning and ending time. For example, in the sample below, raven no. 2 was vocalizing in the area of carcass no. 13 (R2VA) from 1615 to 1800 on day no. 7, a total of 22 observation periods. It vocalized sporadically on days no. 9 and no. 10 for one to three 5-minute periods.
AUDREY	This program permits the investigator to designate a print-out of all cards containing a given scavenger/activity for a given carcass. In the sample below, the print-out of all W1FCC that occurred at carcass no. 7 was requested.
TIME THERE	This program totals the amount of time a particular scavenger species was at a carcass for each day of the carcass.
ACT-TOT	This program totals the number of times an activity occurred and the amount of time in which it occurred and gives the amount of time the activity occurred while some other scavenger was at the carcass (combination time).

*Copies of these programs can be obtained by writing the Alaska Cooperative Park Studies Unit, University of Alaska, College, Alaska 99701.

Appendix D, continued.

AUDREY

CARDS FOR SPECIES TYPE - W1FCC

```
2120706 0720 0735 W1FCC
2120706 0540 0550 R1RA   1  W1FCC  1
2120706 0555      R1MA   1  W1FCC  1  E1MA   1  R1VA   1
2120706 1000      G1AC 1 1  W1ACR1 1
2120706 1000      R1RA   1  R1VA   1  E1RA   1  W1FCC  1  G1MA   1  G2MA   1
2120706 1005      G2VA   1  E1RA   1
2120706 1005      W1FCC  1  R1RA   1  R1VA   1  G1MA   1  G1VA   1  G2MA   1
2120706 1425 1440 W1FCC
2120706 1740 1800 W1FCC
2130707 0140 0155 W1FCC
2130707 0220 0225 W1FCC
2130707 0625      W1FCC  1  W2FCC  1
2130707 0630      W1FCC  1  W2FCP  1  W2D    1
2130707 0635 0640 W1FCC  1  W2FCC  1
2130707 0645      W1FCC  1  W2FCP  1  W1AC 1 1  W2ACR1 1
```

TIME THERE

CARCASS NUMBER 06

TOTAL TIME BY DAY OF CARCASS THAT SPECIES WAS PRESENT AT CARCASS NUMBER 06.
ALL ACTIVITIES COMBINED. MULTIPLE ACTIVITIES BY SAME SPECIES IN SAME TIME UNIT ELIMINATED.

DAY NUMBER	SPECIES	HOURS-MINUTES
01		09 HRS 05 MINS

DAY NUMBER	SPECIES	HOURS-MINUTES
02		04 HRS 35 MINS
02	E	00 HRS 05 MINS
02	J	00 HRS 30 MINS
02	R	00 HRS 15 MINS

DAY NUMBER	SPECIES	HOURS-MINUTES
03		16 HRS 15 MINS
03	B	02 HRS 30 MINS
03	J	00 HRS 10 MINS
03	R	00 HRS 30 MINS

Appendix D, continued.

ACT-TOT

ACTIVITIES FOR CARCASS NUMBER 01

DAY-OF-CARCASS	SPECIES/ACTIVITY	HOURS-MINUTES	TOTAL ACTS	COMBINATION TIME
03	NOT WATCHED	13 HRS 10 MINS		
	RICP	00 HRS 20 MINS	0004	00 HRS 15 MINS
06	NOT WATCHED	23 HRS 50 MINS		
	RICP	00 HRS 10 MINS	0002	00 HRS 10 MINS
11	NOT WATCHED	12 HRS 55 MINS		
	RICP	00 HRS 05 MINS	0001	00 HRS 05 MINS

APPENDIX E.

DETAILED DESCRIPTION OF TWO WOLVES FEEDING ON CARCASS NO. 7

30 July 0715 W1 began feeding at the left hip

Pulled a piece of skin off and ate it

Fed on the backstrap

Ate the tail

Pulled large chunks of meat from the haunch and ate them

0725 Ate some of the stomach contents

Chewed some skin off the ribs

Pulled off two ribs and ate them

0727 Pulled at the integument of the stomach

Pulled out a kidney and dropped it

0729 Pulled out the small intestines and ate a little of them

Chewed on some of the large intestine

Cut the intestines with its carnassials and dropped the remainder

0731 Carried a kidney to the edge of the river then ate it

Went back and chewed on the small intestines

0733 Began a caching trip

0750 Began a period of moving and resting

0945 W1 fed at the back of the carcass from above and below removing most of meat from the backbone

Began feeding on the ribcage

0949 Swallowed large chunks of meat from the left haunch

Appendix E, continued.

Pulled out a lung and ate it

Carried part of the other lung for a short distance then ate it

Fed on the right hind leg

1000 Ate meat from the ribcage

Ate meat from the left hind leg

1010 Began moving around the carcass site

1019 Left the carcass site

1425 W1 tore some skin off the right side of the carcass

Pulled meat off the ribs

Pulled more skin off and ate it

Disjointed the hindquarters

Pulled a large piece of skin off the ribcage

Fed on the hindquarters

Fed on the ribcage

Chewed on a rib but dropped most of it

Fed near the brisket

1442 Fed around the ribs

1443 Began a period of moving and resting

1736 Fed on the mesentery of the viscera

1744 Fed around the backbone

Fed at the ribs and pulled the skin off toward the head

Broke off ribs and chewed them down

Appendix E, continued.

		Chewed at the brisket; broke part of it off and swallowed it
		Pulled on some skin
		Fed at the ribs again
	1750	Pulled the skin off at the shoulder
		Chewed at the brisket again
		Pulled off a piece of bone from the brisket and chewed it in pieces before swallowing it
	1755	Pulled piece of the lungs away from the body cavity
		Pulled the pericardium from the heart
		Ate the top of the heart and a piece of lung
		Left the remainder of the lung and pulled on the heart
	1759	Began caching the heart
	1802	Began caching regurgitated meat
	1803	Left the carcass site
31 July	0140	W1 fed on a hindquarter and a foreleg
		Tore off large chunks of meat and cached it
	0154	Removed a piece of meat and cached it
	0155	Began caching regurgitated meat
	0205	Began moving about the carcass site
	0216	Fed on the neck and a hindleg
	0225	Began caching
	0235	Left the carcass site
	0622	W1 fed on the forequarters

Appendix E, continued.

W2 fed on the hindquarters (not continuously)

0635 The wolves reversed positions

0640 W2 stopped feeding

0647 W1 stopped feeding

0648 Both wolves left the carcass site

0737 W2 chewed on the ribcage

0747 Fed on the head

Fed on the ribs

0754 Fed on the rumen and mesentery

0758 Began caching regurgitated meat

0813 Left the carcass site

1923 W2 fed on some meat still remaining along the backbone and ribs

1937 Began moving about the carcass site

2011 Left the carcass site; the bones (with almost no meat left on them) were dragged away within three days

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