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WOLVES (CANIS LUPUS L.)

University of Alaska, M.S., 1977 Zoology

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THE EFFECTS OF HUMAN DISTURBANCE ON WOLVES (CANIS LUPUS L.)

Α

THESIS

Presented to the Faculty of the
University of Alaska in partial fulfillment
of the Requirements
for the Degree of

MASTER OF SCIENCE

Вy

Richard Charles Chapman, A.B.

Fairbanks, Alaska May 1977

THE EFFECTS OF HUMAN DISTURBANCE ON WOLVES (CANIS LUPUS L.)

RECOMMENDED:	
Philip S. Lesson	
Rale Quitino	
Fullenia Cean CHAIRMAN, ADVISORY COMMITTEE	
CHAIRMAN, ADVISORY COMMITTEE	
Lulerich C. Dewn ACTING CHAIRMAN, PROGRAM IN WILDLIFE AND	
ACTING CHAIRMAN, PROGRAM IN WILDLIFE ANI FISHERIES)
ACTING DIRECTOR, DIVISION OF LIFE SCIENCE	ES
•	
APPROVED:	
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ACTING DEAN, COLLEGE OF ENVIRONMENTAL SCIENCES	
ACTING DEAN, COLLEGE OF ENVIRONMENTAL SCIENCES	
April 12,1577	
-	
VICE-CHANCELLOR FOR RESEARCH AND ADVANCED STUDY	
VICE-CHANCELLOR FOR RESEARCH AND ADVANCED STUDY	
April 21, 1977	

ABSTRACT

National Park Service concern for denning wolves initiated a review of over 100 published and unpublished accounts of wolf reaction to disturbance, observation exceeding 1800 hours, and experimental disturbance of three packs in northern Alaska.

Wolves characteristically respond to humans near their pups by barking or howling, leaving the area, and/or moving the pups. Natural summer mortality of pups older than 3 weeks is rare. Neither reduced growth from disrupted feeding regimes or forced moves to poorer prey situations nor indirect pup mortality has been reported to result from human activity. Low intensity disturbance seems unlikely to cause significant pup mortality.

The seriousness of human disturbance effects is a judgment conditioned by management objectives. Minimally adequate protection should be afforded by areas with 2.4 km radius around homesites; these should be closed around all traditionally active dens from 4 to 5 weeks before whelping until inactivity has been confirmed.

ACKNOWLEDGMENTS

Many people have contributed to the success of this study. I thank Rick Sinnott, Catherine Curby, Raymond Wiggs, Harold "Chip" Downing, and Elissa Mannheimer, my field assistants; James Curatolo, Robert Ritchie, and David Roseneau of Renewable Resources Consulting Services, Ltd.; Robert Stephenson of the Alaska Department of Fish and Game; bush pilot Walt Audi; and Gary Brown and Steven Buskirk of the Mount McKinley National Park staff.

Drs. Frederick Dean and Peter Lent provided direction throughout the study. Dr. Philip Gipson's help during preparation of the final draft of this thesis is greatly appreciated. I thank Robert Stephenson and James Curatolo for critically reviewing early drafts of parts of this manuscript. Special thanks to my committee members Dr. Peter Lent, my committee chairman until he left the University in 1976; Dr. Frederick Dean, my committee chairman; Dr. R. Dale Guthrie; and Dr. Philip Gipson. Special thanks to Catherine Curby for helping at all stages of preparation of this thesis, and to other fellow graduate students, in particular Audrey Magoun and Patrick Valkenburg, for field advice and encouragement.

The National Park Service funded this project in its entirety.

I am grateful to Averill Thayer, Refuge Manager, and the U.S.

Fish and Wildlife Service for permitting us to work in the Arctic National Wildlife Range.

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INTRODUCTION

The Mount McKinley National Park management staff closed areas near active wolf dens in 1973 following several reported cases of human disturbance at active wolf dens in the Park. In 1974 the National Park Service (NPS) in Alaska initiated this study of the effects of human disturbance on wolves (Canis lupus).

The NPS was concerned that repeated disturbance of wolves in Mount McKinley National Park might result in wolves abandoning their traditional den sites for more remote areas, thus possibly reducing visitor opportunities to view wolves, and that significant changes in ecological processes might occur if wolves were excluded from portions of the Park. A study like this one was needed because human use of National Parks is increasing and wolves in some areas, e.g. Minnesota, are endangered.

One objective of this study was to determine the effects of human presence on pup rearing activities and on pup survival. This was accomplished by combining the results of 3 summers of field research with an extensive literature review (Parts I-IV).

When this study began, NPS policy was to protect wolf denning areas in Mount McKinley National Park with temporary closed areas approximately 85 km² in size. Practical considerations dictate that closed areas protect denning wolves from human disturbance, that they not pinpoint wolf homesites, and that they be manageable. An

important objective of this study was to define realistic criteria for such closed areas (Part V).

STUDY AREAS

Wolves on the tundra can probably detect humans near their homesites more readily and at greater distances than wolves in brushy or forest regions. Theoretically, therefore, a closed area needed to protect wolves denning in tundra regions should be more than sufficient to protect wolves denning in brushy or forest regions. The study areas were chosen with this in mind.

Mount McKinley National Park

Most of Mount McKinley National Park lies on the north slope of the Alaska Range. The Park varies from 48 to 56 km in width and is 7,757 km² in area. Access is provided by a road running east-west through the eastern two-thirds of the Park. Most known wolf dens can be reached easily by hiking from the road.

During summer 1974 we observed a pack of wolves that denned on the East Fork of the Toklat River (Figures 1, 2, and 3). This area has been described in detail by Murie (1944), who observed wolves that whelped pups in a den approximately 0.3 km from the 1974 whelping den. The den observed by Murie was used as a secondary den in 1974.

The East Fork dens lie between two lateral ridge systems, the outer range to the north with maximum elevations of about 2,000 m, and the main Alaska Range to the south with Mount McKinley (elev.

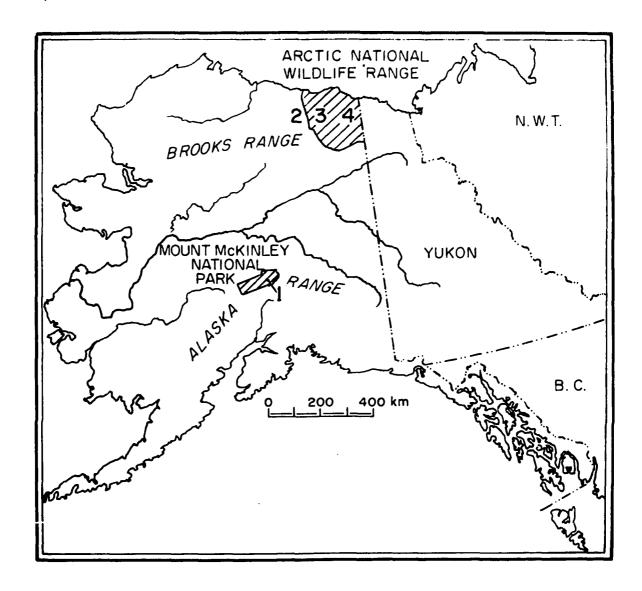


Figure 1. Study areas: (1) East Fork of the Toklat River; (2) Echooka River; (3) Hulahula River; (4) Kongakut River.

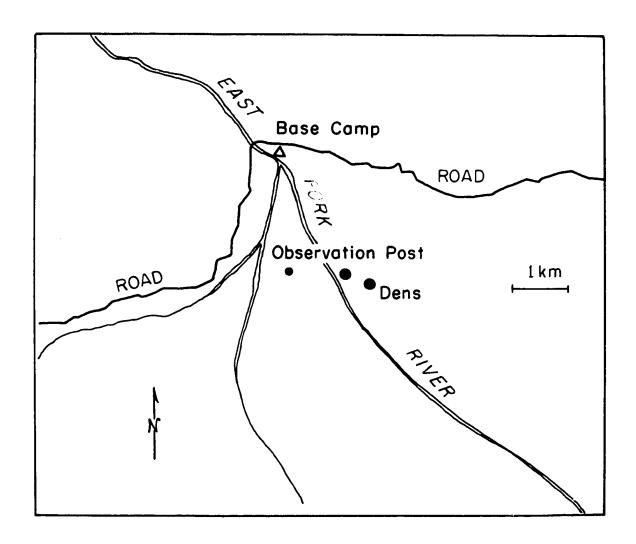


Figure 2. Schematic diagram showing the locations of dens, observation post, and base camp in the East Fork River valley.



Figure 3. Photograph showing the two East Fork dens as viewed from the observation post. The den on the right was the whelping den.

6,194 m) the highest peak. This valley has been used by caribou (Rangifer tarandus) in their seasonal migrations. Tundra vegetation is dominant in the area. Shrubs, principally Salix spp. and Betula spp., are common. The 1974 whelping den was located in a small stand of Populus spp.

Temperatures and precipitation were recorded at Park headquarters 45 km northeast of the East Fork dens. The coldest month was January with a mean temperature averaging -20°C in 1974-76. The warmest month was July with a mean temperature averaging 12°C in 1974-76 (Anonymous 1974-76). The mean annual precipitation was 37 cm, slightly over half falling in June, July, and August (Murphy 1974).

Major prey species were caribou, Dall sheep (<u>Ovis dalli</u>), and moose (<u>Alces alces</u>). Also available were arctic ground squirrels (<u>Spermophilus undulatus</u>), beavers (<u>Castor canadensis</u>), hoary marmots (<u>Marmota caligata</u>), and small rodents. Other studies of wolves in Mount McKinley National Park were conducted by Murie (1944) and Haber (1968, 1973a, 1973b, and unpublished).

Northeastern Alaska

In 1975 the study was shifted to the North Slope of the Brooks
Range in northeastern Alaska because NPS policy prohibited disturbance
of wolves at dens in National Parks. Access to the area was by
Piper Supercub or Cessna-180 aircraft. Gravel bars or overflow ice
were used as landing areas.

During summer 1975 we observed a pack of wolves that denned in

the Echooka River valley (Figures 1, 4, and 5). During summer 1976 we studied two wolf packs, one that denned in the Kongakut River valley (Figures 1, 6, and 7), and one that denned in the Hulahula River valley (Figures 1, 8, and 9). The dens observed in 1976 lie within the Arctic National Wildlife Range.

The habitat for these three dens was typical of river valleys coursing the North Slope of the Brooks Range. The valleys were from 1.6 to 4.8 km wide, and the mountains rarely exceeded 2,400 m in elevation. Plant communities characteristic of the area were described by Churchill (1955), Bliss and Cantlon (1957), and Spetzman (1959). Stephenson (1974) described the physiographic and vegetational characteristics of wolf den sites on the North Slope. The North Slope was much less brushy than Mount McKinley National Park, and trees (Populus spp.) were rare.

Temperatures have ranged from -51°C in winter to over 32°C in summer on the North Slope (Searby and Hunter 1971). The mean January temperature recorded at Happy Valley Camp some 160 km west of the Hulahula River averaged -29°C in 1975-76. The mean July temperature averaged 11°C in 1974-76 (Anonymous 1974-76).

Temperatures were recorded hourly at our observation posts while the Hulahula homesites were observed. Figure 10 indicates the daily mean and range of temperatures between 11 June and 1 August. Figure 11 shows the mean and range of temperatures recorded for each hour of the day during this period. Precipitation was light on the North Slope compared to Mount McKinley National Park. Snow fell in each

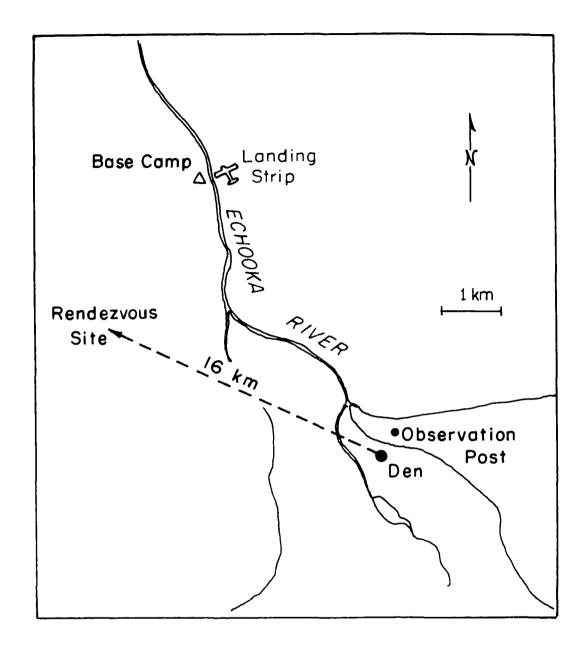


Figure 4. Schematic diagram showing the locations of the den, rendezvous site, observation post, base camp, and landing strip in the Echooka River valley.



Figure 5. Photograph showing the Echooka den as viewed from the observation post.

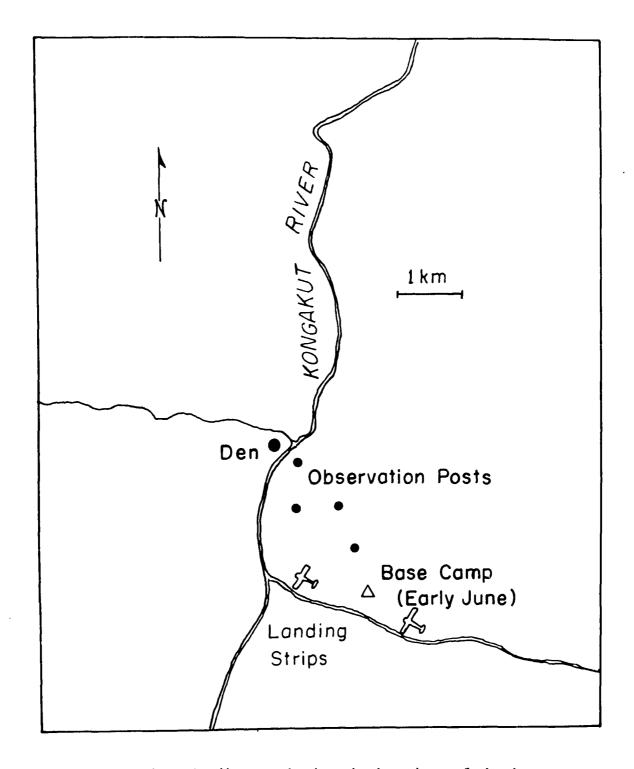


Figure 6. Schematic diagram showing the locations of the den, observation posts, base camp, and landing strips in the Kongakut River valley.



Figure 7. Photograph showing the Kongakut dens as viewed from one of the observation posts. The dens are approximately 60 m apart. The den on the left was the whelping den.

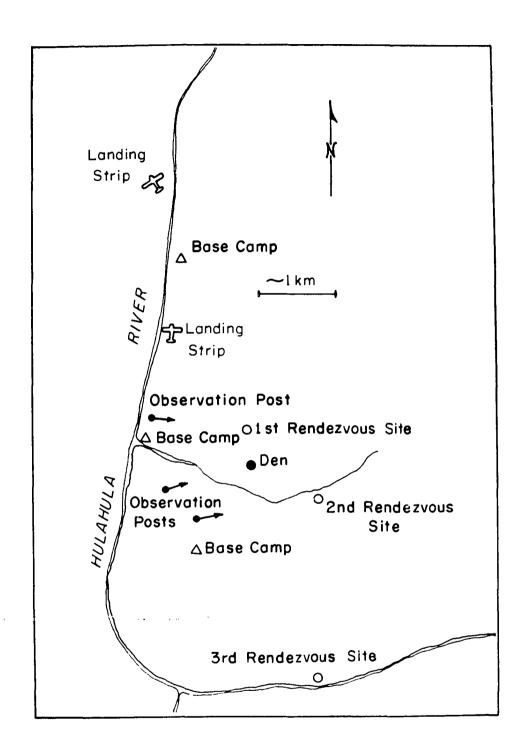


Figure 8. Schematic diagram showing the locations of the den, rendezvous sites, observation posts, base camps, and landing strips in the Hulahula River valley.



Figure 9. Photograph showing the Hulahula den as viewed from the observation post.

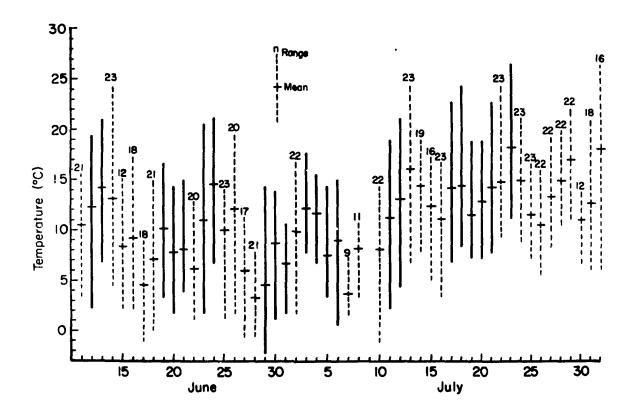


Figure 10. Daily mean and range of temperatures recorded hourly in the Hulahula River valley in summer 1976. Solid lines indicate days in which 24 hourly measurements were taken.

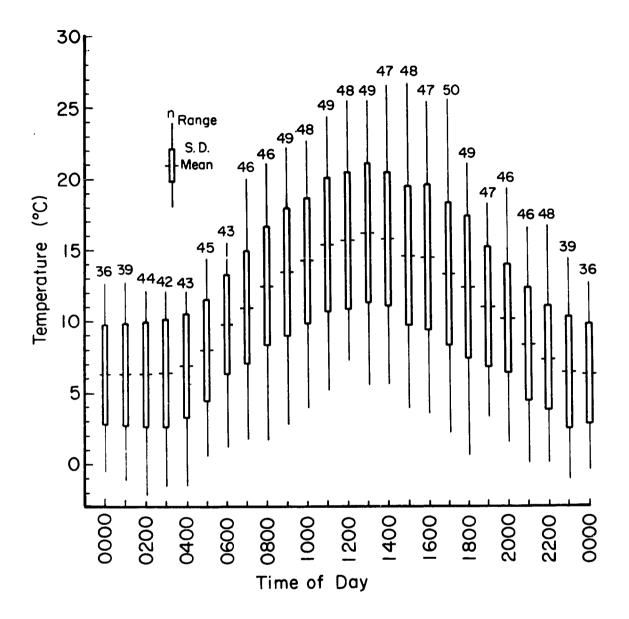


Figure 11. Mean and range of the daily temperature cycle in the Hulahula River valley between 11 June and 1 August 1976.

month. Fog from the arctic coast frequently extended up the river valleys during summer. The gaps in observation time up to 26 July for the den on the Hulahula River represent periods of ground fog or, less frequently, snow (Figure 12). Winds blew up or down the river valleys; generally from the north during the day, and from the south in the morning. Wind velocities varied greatly. Maximum velocities measured with a wind meter in 1976 were approximately 72 kmph. On most days the wind velocity did not exceed 32 kmph.

Major prey species were caribou and Dall sheep for the three wolf packs studied in northeastern Alaska. Moose, arctic ground squirrels, and small rodents were also available. Important non-prey species were red foxes (<u>Vulpes vulpes</u>), grizzly bears (<u>Ursus arctos</u>), wolverines (<u>Gulo gulo</u>), porcupines (<u>Erethizon dorsatum</u>), golden eagles (<u>Aquila chrysaëtos</u>), and common ravens (<u>Corvus corax</u>). Information on wolves in northeastern Alaska has been gathered by Bee and Hall (1956), Valkenburg et al. (1972), Magoun and Valkenburg (1973), Quimby (1974), Quimby and Snarski (1974), Stephenson (1974), Stephenson and Sexton (1974), and Magoun (1976).

METHODS AND MATERIALS

The general plan of this study was to experimentally disturb wolves at homesites to permit an assessment of the circumstances surrounding each case of human disturbance. Initially, we intended to observe denning wolves for periods of several days in a manner that did not disturb them. Following this we allowed wolves to detect human presence at various distances, and documented their esponse to disturbance. Table 1 shows the characteristics of the pack using each den, the observation distances, and the number of hours homesites were observed for wolf activity. Figure 12 indicates the distribution of observation time at each homesite. Our observation posts were usually crosswind from the homesites. Methods of assessing the activity status of known wolf dens is discussed in Part V. Times for this study are reported in Alaska Standard Time.

East Fork dens

National Park Service policy does not permit intentional disturbance of active wolf dens within Park boundaries, and this restriction was not waived for this study. In 1974 a field assistant and I used binoculars and a variable power (20x-60x) spotting scope to observe wolves at the East Fork dens (Figures 2 and 3). Since our observation post could be seen from the road, we were not

Table 1. - Observation times and distances, and characteristics of observed wolf packs, dens, and rendezvous sites.

Homesite	Elevation (m)	Observation Dates	Hours ^a of Observa- tion	Observa- tion Distances (km)	Number of Adults	Number of Pups
East Fork whelping den	1,000	22 June-1 July	116	1.0	3	3
Secondary den	1,000	l July-26 July	219	0.8		
Echooka whelping den	700	29 June-8 July	187	0.4	<u>></u> 3	5
Rendezvous site	490	11 August	4	0.4		
Kongakut whelping den	360	4-9 June 28 June-2 July 26-29 July	15 61 41	1.6 0.4-1.2 0.4	<u>>2</u>	7 ^b
dulahula whelping den	910	5-23 June 25 June-14 July	374 ^c 379	1.2	8	4
First rendezvous	940	23-25 June	45	1.2		
Second rendezvous	1,070	14 July-1 August	400	1.6		
Third rendezvous	850	2 August	1	0.3		

^a See Figure 12.

b One pup died between 15 and 26 July (see Part IV).

^c Includes 4 hours of observation by Robert Ritchie on 1 June (pers. comm.).

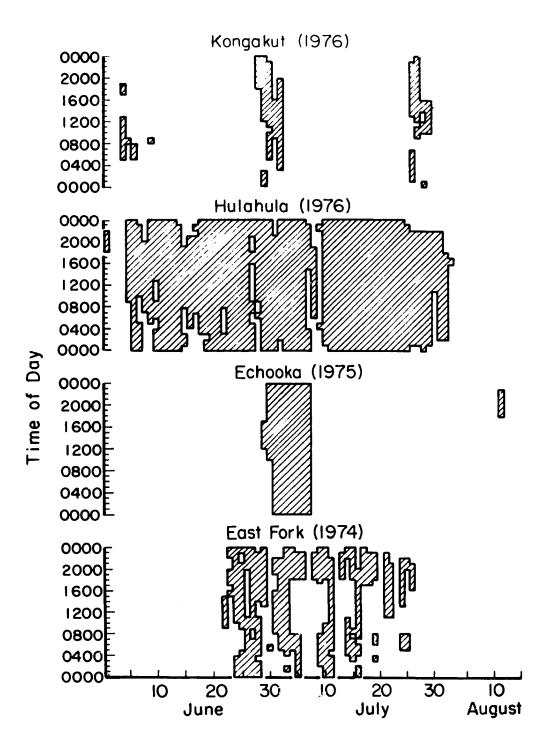


Figure 12. Distribution of observations at wolf dens and rendezvous sites.

permitted to use a tent as a blind or shelter. Consequently, total observation time was limited. Wolf behavior was recorded in notebooks or, when necessary, with a small, portable voice-recorder. We were in the field between 18 June and 1 September 1974. Additionally, I was in the Park in late August and early September in both 1975 and 1976.

Echooka den and rendezvous site

On 30 June 1975 we disturbed wolves at the Echooka den (Appendix A, Case History 1) by placing our observation tent approximately 0.4 km from the den (Figures 4 and 5). The tent was a two-man, navy blue, backpacking tent. The mosquito netting at the back of the tent was modified so that a variable power (15x-60x) spotting scope could be used to observe wolves at the den while the observer remained in the tent. With practice, it was possible to use binoculars to watch a fairly large area for signs of activity while remaining in the tent. By placing the entrance of the tent away from the den we were able to enter and leave the tent without being seen by wolves at the den. These methods minimized visible human activity and, therefore, disturbance; and wolves could be observed regardless of weather. As in 1974, wolf behavior was recorded in notebooks or by using a voice-recorder. One field assistant and I alternated 8, 4, 4, and 8 hour shifts to observe the den area. We were in the field between 2 May and 22 August in 1975.

Kongakut den

Two field assistants observed the den in early June 1976

(Figures 6 and 7). In late June and late July I was the only observer. I disturbed the wolves at the Kongakut den (Appendix B, Case History 1) by hiking to the den entrance on 26, 27, and 28 July. Wolf behavior was recorded in notebooks.

Hulahula den and rendezvous sites

We disturbed wolves at the Hulahula whelping den and subsequent rendezvous sites in several ways (Appendix A, Case Histories 2a-2h). Approximately 90 percent of our activity was within 1.6 km of the whelping den. Our observation tents were placed 1.2-1.6 km from the homesites (Figures 8 and 9). One base camp was located 1.4 km from the den between 4-24 June. Between 24 June and 14 August this camp was in a new location but still 1.4 km from the den. Another camp was located 3.4 km from the den between 9 June and 3 August. Between 14 and 26 June a small tent, usually unoccupied, was placed northwest of the den at diminishing distances of approximately 2.0, 1.6, 1.2, and 1.0 km. It was left at each location for 2, 2, and 6 days respectively. Lastly, on several occasions I was detected by wolves when I approached within 0.2 km to photograph them. same two-man observation tent and spotting scope used in 1975 were used at this den. Two field assistants and I alternated 6 hour shifts to observe wolves. Wolf behavior was recorded in notebooks. were in the field between 22 May and 20 August in 1976.

Case histories of human disturbance

A thorough literature review was conducted in addition to the field work. Cases of human disturbance (hikers, aircraft, and vehicles) at wolf homesites obtained from this study, from personal communications, and from the literature are summarized in Appendices A, B, C, and D.

RESULTS AND DISCUSSION

PART I. SUMMER HOMESITES OF WOLVES

Wolf dens

Wolf dens may be burrow systems, hollow logs, spaces between roots of trees, caves or crevices in rocks, abandoned beaver lodges, or expanded red fox, arctic fox (Alopex lagopus), badger (Taxidea taxus) or marmot (Marmota spp.) burrows. Pups have also been whelped in excavations in snow (Kelsall 1960), on surface beds at the base of spruce trees (Soper 1942), and in very shallow "pit dens" (Stephenson 1974:17). In the present study the dens on the East Fork, Echooka, and Kongakut Rivers were burrow systems. The den in the Hulahula River valley was a burrow whose triangular shaped entrance was defined on two sides by large rocks (Figure 13).

Characteristics of dens

Wolf dens usually have common characteristics although they have been found in a variety of situations. Most dens face south or near south; their exposure to sun and wind is such that the den area is usually snow-free at the onset of denning (Clark 1971, Stephenson 1974). Banfield (1954), however, noted one den where the burrow length included about 1 m of snow. Haber (1968) hypothesized that



Figure 13. Entrance of the whelping den on the Hulahula River. This den was hordered on two sides by large rocks.

dens in Mount McKinley National Park were located on south- and east-facing slopes to protect the dens from cold northerly and westerly winds.

Some dens provide visibility of the surrounding area, and most are located where there is good drainage. Mech (1970), Carbyn (1974b), and Stephenson (1974) indicated that good visibility may usually be a result of selection of den sites with good drainage. On 2 June 1976, 10 cm of water was standing in the inactive Echooka den. A den on the lower Kongakut River, used in 1975, was flooded by the river on 1 June 1976. Either the year was exceptionally wet (spring breakup was rapid), or these two dens are not usually used as whelping dens. Adult wolves were seen near the den on the Kongakut River later in summer (Curatolo pers. comm.).

There is generally a source of water near dens (Joslin 1967, Haber 1968, Clark 1971, Voigt 1973, Carbyn 1974b, Stephenson 1974).

The dens on the Hulahula and Kongakut Rivers were within 200 m of water. The Echooka den was approximately 85 m from water. It seems to me, however, that almost any location in Mount McKinley National Park and the Brooks Range, within the elevational range of wolf dens, is near (within 400 m) a permanent or semi-permanent source of water. No one has yet demonstrated that sites near water are selected over sites far from water.

Longevity of dens

The longevity of wolf dens is not known. Macpherson (1969)

calculated that arctic fox dens would last about 330 years.

Clark (1971:68) noted that the "large-scale burrowing activities of wolves would lead to a more rapid degradation of the sites than would the burrowing of foxes." Stephenson (1974:11) noted that longevity would probably vary from site to site since some dens are constructed in substrates that are more stable than others. Rock dens could be "unchanged for decades or even centuries." Stephenson noted that extreme dryness caused the collapse of dens in sandy soil, and extreme wetness hastened collapse of those in clay soil.

Stephenson (1974) examined a den completely filled with soil that may have been filled by ground squirrels. I examined the Echooka den thoroughly on 17 August 1975. The next day I returned to the site to take pictures, and surprised a ground squirrel in the den. It had just tunneled in and left a fresh pile of soil.

Figures 14, 15, and 16 show the 1974 East Fork whelping den.
The photographs were taken in successive years. The den was cleaned out and used by wolves in 1974 (Figure 14), it collapsed in 1975 (Figure 15) and in 1976 the den was again cleaned out, apparently by foxes, though it did not appear to have been used (Figure 16).
Figure 17 shows the partial collapse of the entrance to a den near the Sanctuary River in Mount McKinley National Park which was active in 1975. The photograph was taken in late August. Figure 18 was taken approximately 1 year later. The part of the den that was about to collapse in 1975 did collapse. The den was not used in 1976.

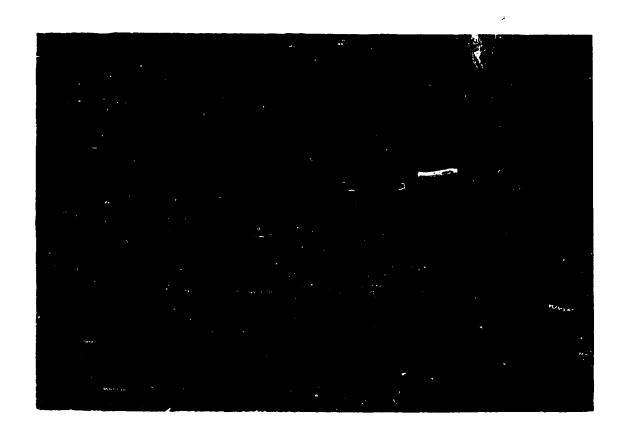


Figure 14. Entrance of the 1974 East Fork whelping den in late summer 1974.



Figure 15. Entrance of the 1974 East Fork whelping den in late summer 1975 showing collapse of the den.



Figure 16. Entrance of the 1974 East Fork whelping den in late summer 1976. This den was apparently cleaned out by foxes, though it did not appear to have been used.



Figure 17. Entrance of a den near the Sanctuary River in Mount McKinley National Park in late summer 1975 showing partial collapse of the entrance. This den was active earlier that summer.



Figure 18. Entrance of a den near the Sanctuary River in Mount McKinley National Park in late summer 1976. The den was active in 1975 but not in 1976. The part of the den that was about to collapse in 1975 did collapse.

Distances between dens

The den sites within a given pack's home range may be concentrated in a relatively small area, e.g. five dens within a 15 km² area (Carbyn 1974b). Often two or more dens may be located within a few hundred meters of each other with other dens several kilometers away (Banfield 1954, Clark 1971). In Mount McKinley National Park there are pairs of dens approximately 0.2, 0.3, and 0.4 km apart.

In those few reported cases where single packs had two litters of pups, the dens were located 6.4 km (Murie 1944) and 3.2 km (Clark 1971) apart. Haber (1968) thought two litters were whelped in the same den, but the data he presented were inconclusive.

The distances between active dens of adjacent packs has been recorded in a few cases (Table 2). In areas where packs are territorial, these distances are probably to some degree a function of territory size. Figure 23 shows the relative sizes of summer home ranges for wolves of different regions based on mean distances between active dens. It is not known whether distance between active dens is a realistic criteria for determining size of summer home range in arctic regions.

Secondary homesites

In 1975 wolves that used the Echooka den were found on 11 August at a rendezvous site (see Table 3 for terminology) on the Echooka

Table 2. - Distances between active dens of adjacent packs.

Locale	Distance (km)	Source	
Northwest Territories	10	Banfield (1954)	
Baffin Island	37-93 (ave=61, n=4)	Clark (1971)	
Brooks Range	26-54 (ave=33, n=5)	Stephenson and Sexton (1974)	
Mount McKinley N. P.	24, 24	Murie (1944)	
Mount McKinley N. P.	47	Haber (1968)	
Mount McKinley N. P.	35	Present study (1975)	
Mount McKinley N. P.	15, 33	Present study (1976)	
MOUNT McKINLEY N. P.	ave=30		

Table 3. - Wolf homesite terminology.

Term	Source		
First homesite			
Whelping den, den, or den site	Murie (1944), Young and Goldman (1944), Joslin (1967), Clark (1971), Carbyn (1974b), Stephenson (1974), Present study		
Breeding den	Seton (1937)		
Nursery den	Haber (1968)		
Secondary homesites			
Secondary dens	Present study		
Summer den	Clark (1971)		
Auxiliary den	Haber (1968)		
Nursery den	Seton (1937)		
Rendezvous sites ^a	Murie (1944), Joslin (1967), Voigt (1973), Carbyn (1974b), Peterson (1974), Present study		
Loafing area	Young and Goldman (1944)		
Rearing area	Garceau (1960)		
Resting area	Rutter and Pimlott (1968)		

a "Rendezvous site" can be used in two contexts. First, it is an area where pups are left during summer when adults are hunting. Second, when pups are capable of travelling with the pack in winter, wolves may rendezvous at a particular site. As used here, the former meaning is implied.

River (Figure 4). The areas of use appeared to be small, grassy areas and portions of the gravel bar. Both types of areas were bordered by tall willows. Sources of water were within 50 m of the site.

Wolves that used the Hulahula whelping den in 1976 were found at three rendezvous sites. The first site (Figures 8 and 19), occupied for 2 days when the pups were approximately 5 weeks old, was centered in a stand of large willows near a rock outcrop approximately 100 m above the valley floor (Figure 20). The second site (Figures 8 and 21), occupied for 17 days, was near a small creek bordered by willows and was centered around a large rock (Figure 22). The primary area of use was characterized by low-growing tundra plants. We were unable to determine the center of the third rendezvous site (Figure 8). Pups were seen, however, near a small outcrop of jumbled rocks, on the gravel bar, and near small stands of willows.

In other regions, rendezvous sites are characteristically centered near open, grassy areas that are bordered by trees or thickets (Murie 1944, Joslin 1967, Pimlott et al. 1969, Voigt 1973, Carbyn 1974b, Peterson 1974, Van Ballenberghe et al. 1975).

Pimlott et al. (1969) suggested that rendezvous sites could serve as sites for future whelping dens. An interesting point is that some of the rendezvous sites in forest regions described by Pimlott et al. (1969), Carbyn (1974b), and Peterson (1974) contained burrows of various sizes. Peterson (1974) suggested that such burrows were dug by pups. In over 1,800 hours of observation in the



Figure 19. Photograph from an observation post showing the location of the first rendezvous site (arrow on the left) in relation to the location of the whelping den (arrow on the right) in the Hulahula River valley.



Figure 20. The first rendezvous site in the Hulahula River valley.



Figure 21. Photograph showing the second rendezvous site in the Hulahula River valley as viewed from the observation post.

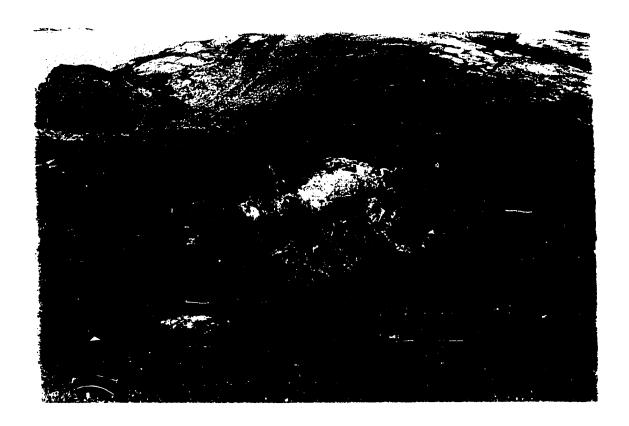


Figure 22. The second rendezvous site in the Hulahula River valley.

present study and over 1,100 hours by Clark (1971), no pups were observed digging. Adults were commonly seen digging at the East Fork den in 1974, and at the Hulahula and Kongakut dens in 1976. Clark (1971) also observed adults digging, and in some cases they dug pup-sized holes. Small holes were present at the second rendezvous site used by wolves on the Hulahula River in 1976. It is possible that some of these holes were dug by ground squirrels or by foxes. In many cases secondary homesites were described as dens (Table 3).

The difference between "rendezvous site" and "secondary den" may be more semantic than functional. Apparently the only requirements that wolves have for secondary homesites are cover (den or thicket), an open area, and a source of water.

PART II. DENNING ACTIVITIES OF WOLVES

Pre-whelping activities

Wolves visit and prepare one to several den sites within their home range as much as 4-5 weeks prior to whelping (Young and Goldman 1944, Jordan et al. 1967, Haber 1968, Clark 1971, Stephenson and Johnson 1973). As parturition nears, the pregnant female probably remains in the vicinity of a selected den (Young and Goldman 1944, Mech 1970).

Selection of dens

The denning area of a wolf pack in Jasper National Park was located near elk (Cervus elaphus) calving grounds and several mineral licks (Carbyn 1974b). From Carbyn's (1974b:21-23) maps of seasonal distribution and movements of ungulates, it appears that wolves in the Park could not have picked a better area in which to den. In Mount McKinley National Park, Haber (1973b) watched wolves prepare dens in an area where moose traditionally calved. Deep snows delayed the movement of moose to the calving grounds, and the wolves utilized a den farther east where caribou were more readily available.

Migratory wolves in Canada (and possibly in Alaska) probably select den sites to maximize chances of obtaining caribou. Most migratory wolves den near tree-line; these areas are without

caribou for the shortest period, and straggler caribou will always be found (Parker 1972). Kuyt (1972) and Clark (1971) noted that migratory wolves will often move to denning areas before caribou begin to migrate through. They also found that wolves usually denned along the major caribou migration routes. Those that did not den along the migration routes had smaller litters and lighter weight pups which indicated a higher pup mortality rate (Kuyt 1972, Stephenson and Johnson 1973).

Wolves that den near traditional migration routes probably suffer high pup mortality when caribou alter their migration routes. In such cases, wolves may choose new denning areas that reflect the changes in prey availability. If this happens, it suggests that wolves may choose dens based on prey availability of the previous year. An important factor may be that new dens are probably dug in summer in arctic regions, since the ground is usually still frozen when parturition occurs. As noted in the section "Secondary homesites", adult wolves were frequently observed digging in summer (Clark 1971, Present study). Thus, if wolves choose to whelp in a new area, they need to dig a den the previous summer. There is an alternative hypothesis. Some wolves den in marginal habitats even when caribou are using traditional migration routes (Kuyt 1972). Perhaps this portion of the wolf population experiences "good times", while wolves denning in previously good habitat decline following a change in caribou migratory patterns.

Nothing is known of the mechanisms by which wolves recognize

suitable homesites. Biologists at present can only speculate on the relative importance of the common features of the selected areas. There are usually several potential den locations within the home range of a pack that fulfill the requirements of suitable substrate and exposure, good drainage, and a source of water. In fact, no one has demonstrated that such areas are in short supply. One of these potential dens is chosen in which to whelp pups. It would seem logical, particularly from an energetics point of view, that in areas where wolves have large summer ranges and prey are clumped, that availability of prey would be the principal influence in final den selection.

Whelping dates

Pups are usually whelped during the first 2 weeks of May in Mount McKinley National Park (Murie 1944, Haber 1968, Buskirk pers. comm.). In the Arctic most pups are whelped between mid-May and early June (Kuyt 1962, Kelsall 1968, Clark 1971, Lentfer and Sanders 1973, Stephenson 1974). Pups first ventured outside the Hulahula den on 8 June, which indicates a birth date between 18 and 25 May. Physical development of pups at the Kongakut and Echooka dens was similar to that of pups at the Hulahula den, which suggests similar birth dates.

At more southerly latitudes whelping occurs during late April to early May in southeast Alaska (Garceau 1960), early to mid-April in Wood Buffalo National Park (Soper 1942), early to mid-May in

Algonquin Provincial Park (Rutter and Pimlott 1968), mid-April to mid-May in Jasper National Park (Carbyn 1974b), and mid- to late April in Isle Royale National Park and in Minnesota (Van Ballenberghe and Mech 1975).

In general, most whelping occurs during a 2-3 week period in any given area (Rausch 1967, Van Ballenberghe and Mech 1975).

Physical development of pups

The eyes of pups open between 11 and 15 days of age (Mech 1970). Mech (1970) reviewed the meager data on the age of pups first emerging from whelping dens and concluded that at approximately 3 weeks of age pups may venture short distances from the den entrance. Clark (1971) found, however, that pups, even with unopened eyes, could be seen outside the den at 10-13 days of age on Baffin Island. He attributed this to a rapid behavioral and physical development of pups in arctic regions.

Weaning can begin by the 19th day of age (Clark 1971), and can be completed between 30 and 35 days of age (Schönberner 1965, in Carbyn 1974b; Mech 1970; Clark 1971). Females lactate for 34-51 days (Ognev 1931, Kuyt 1972), with older females lactating longer than primiparous females.

In the field it is difficult to assess the physical capabilities of wolf pups of various ages. On 23 June 1976 at the Hulahula den, when the pups were approximately 34 days old (assuming a 20 May birth date), the mother led all four pups from the den to a rendezvous site 0.5 km from the den. Actual distance covered was close to

0.6 km. The pups ran the entire way and covered the distance in 25 min - a speed of 24 m/min. Prior to this the pups were never more than about 50 m from the whelping den. On 27 July when they were 68 days old the pups easily trotted 0.7 km uphill through an elevational change of about 50 m in 15 min - a speed of 47 m/min. On 2 July 1975 at the Echooka den, when the pups were approximately 43 days old (assuming a 20 May birth date), two adults led three pups the first 1.6 km of a probable 16.0 km move from the den in 33 min - a speed of 48 m/min. Clark (1971) concluded that from the 4th week of age pups are capable of undertaking long trips (11.0 km) without being carried. Pups younger than 4 weeks are generally carried when homesite changes are made (Bailey 1930, Banfield 1954, Clark 1971, Stephenson 1974).

Whelping den abandonment

Whelping dens are used by wolves for varying lengths of time.

In Mount McKinley National Park most recorded dates for the movement of pups to a secondary den or a rendezvous site are between early June and early July, when pups are 4-8 weeks old (Murie 1944, Haber 1968, Present study). In 1976, however, a whelping den was used until approximately 24 August (Buskirk pers. comm., Linkswiler pers. comm.).

Arctic wolves usually leave whelping dens in July, but moves have been reported in early June and in August (Kuyt 1962, Stephenson and Johnson 1972, Stephenson 1974). On Baffin Island the abandonment of whelping dens occurred between early July and

early August, when pups were 4-9 weeks old (Clark 1971). In the present study at least one pup remained at the Kongakut den on 29 July when observations were terminated. Pups were moved from the Hulahula whelping den on 23 June, but three were returned on 25 June and a fourth 8 hours later on 26 June. The whelping den area was abandoned for the season on 14 July when the pups were 7-8 weeks old.

In southern Canada and in Minnesota it is probably unusual for pups to remain at whelping dens beyond 1 July (Mech 1970). In Jasper National Park pups were moved between late May and mid-June, when they were 3-6 weeks old (Carbyn 1974b). One den in Algonquin Provincial Park, however, was vacated on 8 July (Voigt 1973).

In some cases, wolves may take several hours or even days to vacate a homesite (Banfield 1954, Stephenson 1974, Peterson 1974). In 1974 at the East Fork den one of three pups was moved 2 days after the others. In 1975 at the Echooka den three of five pups were moved on 2 July, the other two on 8 July. In 1976, 8 hours were required to remove all four pups from a second homesite and return them to the whelping den on the Hulahula River. Quimby (1974) reported that in northeastern Alaska a pack of four adults took 15 days to remove 11 pups from one homesite and bring them to another.

Relocation movements of litters

Reported movements of pups from whelping dens to secondary

dens averaged 3.0 km (n=14) and ranged from 0.3 to 11.2 km (Table 4). Reported pup moves from dens to rendezvous sites, and between rendezvous sites, averaged 2.9 km (n=44) and ranged from 0.5 to 11.2 km (Table 4). Between 8 July and 11 August in 1975 tracks of pups from the Echooka den were observed as far as 21 km from the whelping den. Figure 23 shows the distance pups are moved relative to the sizes of summer home ranges. Movements to rendezvous sites early in summer are usually shorter than those late in summer. In 1976 pups on the Hulahula River were moved increasingly greater distances as summer progressed (0.5, 0.5, 0.8, 2.4 km). Early moves recorded by Joslin (1967), Carbyn (1974b), and Peterson (1974) were shorter than succeeding ones.

Duration of occupancy of secondary homesites is quite variable and has ranged from 2 to 90 days (Table 5). Period of occupancy tends to be longer early in summer when pups are relatively small. Termination of rendezvous site use apparently occurs during September or October at all latitudes (Murie 1944, Haber 1968, Pimlott et al. 1969, Clark 1971, Voigt 1973, Peterson 1974, Quimby 1974, Van Ballenberghe et al. 1975).

Reasons for moving pups to secondary homesites

Wolves may move their pups to a new homesite for a variety of reasons: pups may be moved in response to changes in prey availability (Clark 1971, Kuyt 1972); to combine litters (Murie 1944, Clark 1971); in response to human disturbance (see Part III); in

Table 4. - Relocation movements of wolf litters in summer.

Locale	Distance (km)	Source
MOVEMENTS BETWEEN WHEL	PING AND SECONDARY DENS	
Yellowstone N. P.	1.6	Bailey (1930)
Jasper N. P.	0.3	Carbyn (1974b)
Northwest Territories	1.2	Banfield (1954)
Northwest Territories	<1.6	Kelsall (1960)
Baffin Island	1.6	Wayman (1967)
Baffin Island	1.6, 2.4	Clark (1971)
Brooks Range	3.2	Stephenson (1974)
Mount McKinley N. P.	6.4, 1.6, 0.5	Murie (1944)
Mount McKinley N. P.	4.8, 11.2	Haber (1968)
Mount McKinley N. P.	0.3	Present Study (1974)
MOVEMENTS FROM DENS TO	RENDEZVOUS SITES, AND BI	ETWEEN RENDEZVOUS SITES
Isle Royale N. P.	1.0-6.7 (ave=4.2, n=3)	Peterson (1974)
Jasper N. P.	1.8-6.0 (ave=4.0, n=6)	Carbyn (1974b)
Algonquin P. P.	1.0-6.4 (ave=2.4, n=9)	Joslin (1967)
Algonquin P. P.	0.8-8.0 (ave=4.0, n=9)	Joslin (1967)
Algonquin P. P.	0.5-2.4 (ave=1.5, n=9)	Voigt (1973)
Ontario	0.8	Kolenosky and Johnston (1967)
Baffin Island	11.2	Clark (1971)
Mount McKinley N. P.	0.5, 3.2	Murie (1944)
Brooks Range	0.5-2.4 (ave=1.1, n=4)	Present Study (1976)

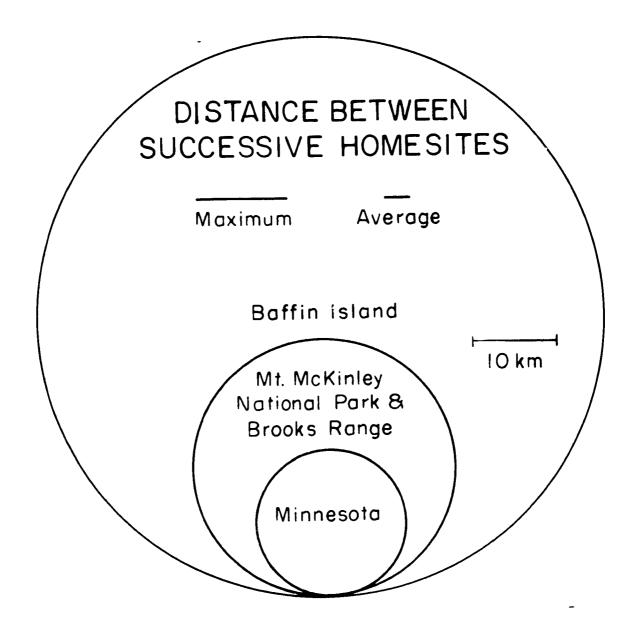


Figure 23. Distances between successive homesites relative to sizes of wolf summer home ranges. Home ranges are based on distances between active dens for Baffin Island, Mount McKinley National Park, and the Brooks Range (see Table 2); and on territory sizes for Minnesota (Mech 1974).

Table 5. - Duration of secondary homesite occupancy.

Locale	Occupancy (days)	Source
Isle Royale N. P.	11-48 (ave=26)	Peterson (1974)
Minnesota	25-59 (ave=34)	Van Ballenberghe et al. (1975)
Algonquin P. P.	6-30 (ave=17)	Joslin (1967)
Algonquin P. P.	<u>></u> 43	Rutter and Pimlott (1968)
Algonquin P. P.	2-11 (ave=5); 90	Voigt (1973)
Ontario	7, 13	Kolenosky and Johnston (1967)
British Columbia	∿21	Stanwell-Fletcher (1942)
Jasper N. P.	10-54 (ave=21)	Carbyn (1974b)
Baffin Island	16-45 (ave=30)	Clark (1971)
Mount McKinley N. P.	2, <u>≥</u> 27	Murie (1944)
Mount McKinley N. P.	. ∿45	Haber (1968)
Mount McKinley N. P	. 25	Present Study (1974)
Brooks Range	∿65	Quimby (1974)
Brooks Range	2, 17, 6±3	Present Study (1976)

response to disturbance by bears (Joslin 1967, Stephenson 1974); in response to a flooded or collapsed den (Stephenson 1974); in response to a den overcrowded by growing pups (Stebler 1951, Rutter and Pimlott 1968, Clark 1971); and for sanitation purposes due to accumulation of feces and debris (Young and Goldman 1944, Rutter and Pimlott 1968). Pups at the East Fork den in 1974 were moved on about 1 July to a larger den complex 0.3 km away. Pups at the Kongakut den in 1976 were whelped in a small, two-entrance den. Later in summer they were found 60 m away at a large, six-entrance den (Figure 7). These two observations support the overcrowding hypothesis. We were not able to determine why the pups in the Hulahula River valley were moved.

The locations of secondary homesites may be influenced by weather and insects (Voigt 1973, Carbyn 1974b) or food sources.

Rendezvous sites are often located near sources of human garbage (Murie 1944, Stenlund 1955, Voigt 1973, Van Ballenberghe et al. 1975) or carcasses of large prey animals (Murie 1944, Joslin 1967, Haber 1968, Voigt 1973, Peterson 1974, Van Ballenberghe et al. 1975). Temporary local abundance of items such as fish (Stanwell-Fletcher 1942, Bromley 1973, Bain 1974, Valkenburg pers. comm.) or small prey items (Rausch 1969, Kelsall 1968, Van Ballenberghe et al. 1975) may also influence homesite selection.

Re-use of homesites

Use of established whelping dens has been reported to occur in

as many as 4 consecutive years (Murie 1944, Stenlund 1955, Haber 1968, Clark 1971, Stephenson and Johnson 1972, Voigt 1973, Carbyn 1974b, Present study). Murie (1944) thought it probable that one den in Mount McKinley National Park was used in at least 5 consecutive years. Re-use of dens in non-consecutive years was commonly noted.

Rendezvous sites may be used in as many as 3 consecutive years (Voigt 1973, Carbyn 1974b, Peterson 1974). Voigt (1973) found that one rendezvous site was used at least five times, and four others at least three times, during a period of 9 years. Rendezvous sites may be occupied twice within the same year (Pimlott et al. 1969).

Tradition of use, death of some pack members, changes in prey availability, and marginal sites becoming less suitable may affect re-use of homesites. Flooding by beavers is another factor which limits re-use of rendezvous sites in forest regions (Joslin 1967, Voigt 1973). The effect of human disturbance on re-use of homesites is discussed in Part III.

Behavior of adult wolves when disturbed at homesites

Adult and yearling wolves responded in a variety of ways upon detecting humans near their pups (Appendix A). Human presence may have subtle effects which we are unable to recognize because of small samples from disturbed wolves and the lack of samples from undisturbed wolves. There are also many factors, e.g. prey availability, besides human presence which affect behavior, but which are usually not simultaneously assessed. Only gross, easily recognized behavior patterns associated with human disturbance are described below. For comparison, Appendix F contains observations in which wolves reacted to grizzly bears and, in one case, a red fox near their pups.

Show no alarm. Wolves showed no alarm in only one of the 51 reported cases (Appendix A, Case History 35).

<u>Watch intently.</u> In several cases wolves watched intently while humans approached the homesite (App. A, CH's 2b, 12b, 32c, 32e), while humans remained near the homesite (App. A, CH's 2h, 3, 13, 19a, 28, 31a, 41, 45, 49), and while humans were leaving the homesite area (App. A, CH's 2d, 12b). Wolves watched intently before and after they vocalized.

Observation leaps. In three cases wolves were observed jumping on their hind legs, apparently to gain a better view (App. A, CH's

10b, 17, 32e). Crisler (1958) described this behavior in a tame wolf and termed it an "observation leap". (See also App. F, CH 1.)

Approach humans without vocalizing. In some cases adult wolves approached humans without vocalizing, apparently to investigate (App. A, CH's 12b, 18, 19a, 31b, 48). In four cases wolves approached after humans howled. In these cases wolves approached to investigate the source of the vocalization and were probably not aware that humans had vocalized (App. A, CH's 2a, 4, 45, 50).

Barking and/or howling. The most characteristic behavior was barking and/or howling. Adult wolves remained near their pups to vocalize (App. A, CH's 2b, 2e, 2g, 2h, 3, 9, 13, 16, 19b, 32b, 32e, 33a, 34, 40, 44, 48, 49, 50); they approached humans before vocalizing (App. A, CH's 1, 19a, 26, 31b, 32c, 49); they moved a short distance (usually less than 0.4 km) from their pups before vocalizing (App. A, CH's 2b, 2c, 2d, 4, 5, 8, 18, 19a, 20a, 20b, 31a, 32a, 32c, 32d, 33c, 48); or they vocalized before approaching humans near their pups (App. A, CH's 6, 32c). In two cases wolves howled and then approached humans who had howled (App. A, CH's 25, 26). Wolves have also been reported to growl or emit gruff "woofs" (App. A, CH's 13, 19, 25, 26, 31a, 50).

Leave area or move into cover. In many cases adult wolves left the homesite area or moved into cover. They left after vocalizing (App. A, CH's 1, 2d, 31a, 32d, 33b) or without vocalizing (App. A, CH's 2a, 2f, 7, 8, 10b, 12a, 17, 20a, 30, 33d, 37, 38, 41).

Temporarily abandon pups at homesite. In one case two of five

pups were abandoned at a whelping den for 118 hours (App. A, CH 1). It appeared, however, that the pups were left behind because of their failure to follow the adults rather than because the adults intentionally abandoned them.

Abandonment of homesites. (See below.)

Abandonment of homesites

In one case pups were moved but brought back by the next day (App. A, CH 33d). In all other cases in which pups were moved, the homesite was abandoned for the season (App. A, CH's 1, 9, 10a, 11, 12a, 13, 24, 27, 29, 31b, 32c, 32e, 44, 48, 51). In three of these cases pups less than 20 days old were carried from the dens by their mothers (App. A, CH's 9, 29, 44). In the remaining cases pups were simply led from homesites by one or more adults.

Severity of disturbance. Table 6 lists the characteristics of cases of disturbance from Appendix A in which the outcome (abandonment or not) of single disturbances was known. Homesites abandoned within 2 days after human disturbance were considered abandoned because of the disturbance. I excluded case histories 18, 22, and 38 because in two cases the alpha-female was shot, and in the third the den entrance was blocked. Many of the values in Table 6 are not specifically stated in the case histories in Appendix A. Some values, therefore, are my interpretation of the circumstances. The purpose of the following analyses using data from Table 6 is to show that a refined analysis of the factors affecting abandonment is possible.

Table 6. - Characteristics of cases of disturbance in which the outcome (abandonment or not) of single disturbances was known.

Homesite Abandoned?	Approx. [®] Age of Pups (wks)	No. of Adult Wolves Present	Alpha ^b Wolves Present	Duration ^C of the Disturbance	No. of People	Distance from Pups to People (km)	Appendix A, Case History
yes	6	2	a, f	С	2	0.4	1
no	1-2	5	£	A	2	0.8	2a
no	S	1	£	A	1	1.0	2b
no	5	2	£	8	3	1.3	2b
no	7	2	-	A	1	1.0	2c
no	7	2	-	A	1	0.2	2d
no	8	5	£	A	1	0.1	2e
no	8-9	4	£	A	1	0.1	2 £
no	9-10	1	£	A	1	0.6	2g
no	11	>2	7	A	2	0.5	3a
no	5-6	1	f	A	1	<0.2	7
yes	1	>2	m,f	С	2	<0.4	9
yes	6	?	?	В	3	<0.2	10a
no	13	1	-	A	1	0.2	10ь
yes	5-6	?	?	A	2	<0.2	11
yes	4-5	>2		В	1	0.2	12 a
no	13	1	?	A	2	<0.4	12ь
yes	6-7	3	£	В	2	0.2	13
no.	8	?	?	В	1	0.0	14
no	6	7	7	A	1	<0.2	15
yes?	4	7	e,f	8	1	0.4	19
no?	9	4		B	2	<0.4	20
no	2	7	7	A	2	<0.1	24a
yes	2	7	7	В	2	0.0	24b
BO	7	2	7	A	2	<0.4	25
no	5	1	•	A	1	<0.4	26
yes	12	7	7	A	1	<0.1	27
no	1	2	£	A	1	<0.1	28
yes	1-2	4	7	В	>2	<0.4	29
no .	14	2	n, f	В	1	0.2	31a
yes	14	2	n,f	B	1	<0.4	315
20	1	2	n,f	A	1	0.0	32a
no	4	1		A	1	>0.8	32b
yes	8-9	3	£	A	1	<0.4	32c
yes	15	7	a,f	A	3	<0.1	32d
yes	20	7	u,f	A	1	0.2	32e
80	8-9	4	n,£	A	2	0.1	335
100	9	2	•	В	2	0.1	33e
80	12	3	£	A	2	<0.1	33d
no no	18	1	7	AT	2	<0.1	35
100	18	2	7	A	1	<0.1	37
no	< 3	†	†		1	0.0	43a
20	4-9	•	•	Ā	1	0.0	43b
20	1	1	£	 A	2	< 0.4	44a
yes	2-3.	1	ę	 A	2	< 0.4	44b

Table 6. - Continued.

Homesite Abandoned?	Approx. Age of Pups (wks)	No. of Adult Wolves Present	Alpha ^b Wolves Present	Duration ^C of the Disturbance	No. of People	Distance from Pups to People (km)	Appendix A, Case History
yes	7	2	n,f	С	≥2	> 0.8	45
yes	>9	1	•	A	2	1.5	46
yes	9	3	m,f	A	2	<0.1	48
по	13-14	2	£	A	3	0.2	49
yes	6	1	f	c	1	1.6	51

⁸ Based on assumed birth dates, see footnote at bottom of Table 18.

b mealpha-male; f=alpha-female.

C A=less than 1 hour; B=greater than 1 hour but less than 1 day; C=greater than 1 day.

Biologists and wildlife managers should in the future record the number of wolves present, their behavior, their social position, the number of pups, the date the disturbance occurred, the number of people, the time spent in the area, the distance from the wolves, the outcome of the disturbance, previous disturbances, and the historical extent of contact with humans.

Table 7 shows the percentage of homesites abandoned when a particular type of disturbance occurred. The resultant percentages are minimal since not all disturbed homesites were observed 2 full days after the disturbance. The type of disturbance is defined as a combination of the duration of disturbance, number of persons involved, and distance from the homesite at which the disturbance took place. The types of disturbance in Table 7 are listed from top to bottom in what would intuitively be considered increasing severity, that is, the first type listed (A, 1, >0.4) is the mildest disturbance, and the last type $(C, \geq 2, \leq 0.4)$ is the severest. It is apparent that as disturbances became more severe the percentage of homesites that were abandoned increased.

Age of pups. By comparing the expected percentage of cases in which homesites were abandoned, based on severity of human disturbance, with the observed percentage of abandonments, one can determine the probable influence that age of pups had on the percentage of homesites that were abandoned. Expected number of abandonments was calculated by multiplying the percentage of homesites abandoned for a type of disturbance by the number of cases at a type of disturbance in which

Table 7. - Percentage of homesites abandoned after a particular type of disturbance occurred, using data from Table 6.

TYPE OI	DISTUR	BANCE	Number		
Durationa	No. of People	Distance (km)	of Cases	Number Aban do ned	Percentage Abandoned
Α	1	>0.4	4	0	0
Α	1	<0.4	14	3	21
Α	<u>></u> 2	>0.4	3	1	33
Α	<u>>2</u>	<u><0</u> .4	12	4	33
В	1	>0.4	0	-	-
В	1	<u><</u> 0.4	6	3	50
В	<u>></u> 2	>0.4	1	0	0
В	<u>></u> 2	<u><0.4</u>	6	4	67
С	1	>0.4	1	1	100
С	1	<u><</u> 0.4	0	-	-
С	<u>></u> 2	>0.4	1	1	100
С	<u>>2</u>	<u><0.4</u>	2	2	100

a A=less than 1 hour; B=greater than 1 hour but less than 1 day; C=greater than 1 day.

the parameter (e.g. pups <4 weeks old) occurred. Due to small sample sizes this method of analysis is preliminary and has greatest value as a demonstrator. It is a method which attempts to hold the severity of human disturbance constant.

I divided the case histories into three groups: (1) those in which pups would be carried from homesites (pups 0 to 4 weeks old); (2) those in which pups were old enough to travel but were usually still at whelping dens (pups 4 to 9 weeks old); and (3) those in which pups would usually be at secondary homesites (pups older than 9 weeks). Table 8 shows the results. Comparing the expected percentage of abandonments, based on severity of disturbance, with the observed percentage of abandonments, it is apparent that age of pups had little influence on the percentage of homesites that were abandoned.

Based on information from Nunamiut Eskimos, Stephenson (1974:22) conjectured "that when the pups are old enough to travel some distance the bitch would be somewhat more inclined to take them from the natal den in response to a disturbance..." The information presented here indicates that age of pups was not important.

Number and social position of wolves. By comparing the expected percentage of abandonments, based on severity of disturbance, with the observed percentage of abandonments, wolves were more likely to abandon homesites when there were three or more adults at the homesite than when there were two or fewer adults present (Table 9)

In most cases one or more alpha-wolves were present when the

Table 8. - Influence of age of pups on homesite abandonment, using data from Table 6. Expected abandonments were calculated by multiplying the percentage abandoned for a type of disturbance by the sample size n, then dividing by 100.

TYPE	OF DISTUR	BANCE			0-4 week			>4-9 w	oeks .		>9 wee	ks
Duration	No. of Peopla	Distance (km)	Percentage Abandoned	n	Observed Abandonments	Expected Abandonments	n	Observed Abandonments	Expected Abandonments	n	Observed Abandonments	Expected Abandonments
A	1	>0.4	0	1	0	0	2	0	0	1	0	0
A	1	<0.4	21	2	0	.42	8	1	1.68	4	2	.84
A	<u>></u> 2	>0.4	33	1	0	.33				2	1	.67
A	≥2	<u><</u> 0.4	33	3	1	1	3	2	1	5	1	1.65
	1	>0.4	-									
	1	≤0.4	50	2	1	1	2	1	1	2	2	1
	≥2	>0.4	0				1	0	0			
9	<u>≥</u> 2	<u><</u> 0.4	67	2	2	1.34	4	2	2.68			
C	1	>0.4	100				1	1	1			
C	1	<u><</u> 0.4	-									
C	≥2	>0.4	100				1	1	1			
C	<u>≥</u> 2	<u><</u> 9.4	100	1	1	1	1	1	1			
			TOTALS	12	5	5.1	23	0	9.4	14	\$	4.2
		PERCENTAG	E ABANDONED		(5/12)=.42			(9/23)=.39	•		(5/14)=.36	
	EXPECTED	PERCENTAG	E ABANDONED		(5.1/12)=.43			(9.4/23)=.41	1		(4.2/14)=.30	

Apless than 1 hour; Begreater than 1 hour but less than 1 day; Cegreater than 1 day.

Table 9. - Influence of number of adult wolves present on homesite abandonment, using data from Table 6.
Expected abandonments were calculated by multiplying the percentage abandoned for a type of disturbance by the sample size n, then dividing by 100.

TYPE O	F DISTUR	BANCE			<two ad<="" th=""><th>ults</th><th></th><th>>two ad</th><th>ults</th></two>	ults		>two ad	ults
Duration	No. of People	Distance (km)	Percentage Abandoned	<u>tı</u>	Observed Abandonments	Expected Abandonments	n	Observed Abandonments	Expected Abandonments
A	1	>0.4	0	4	0	0			
A	1	<0,4	21	8	1	1.68	4	2	.84
A	<u>></u> 2	>0.4	33	1	1	.33	2	0	.67
A	<u>>2</u>	≤0.4	33	6	1	2	4	2	1.32
	1	>0.4	•						
•	1	<0.4	\$0	2	1	1	2	2	2
•	<u>></u> 2	>0.4	0	1	0	0			
•	≥2	<u><</u> 0.4	67	1	0	. 67	3	2	2
C	1	>0.4	100	1	1	1			
C	1	<u><</u> 0.4	-						
C	<u>></u> 2	>0.4	100	1	1	1			
C	<u>></u> 2	≤0.4	100	1	1	1	1	1	1
			TOTALS	26	7	8.7	16	9	6.8
		PERCENTAGE	ABANDONED		(7/26)=.2	7		(9/16)=.56	
	XPECTED	PERCENTAGE	ABANDONED		(8.7/26)=.3	3 .		(6.8/16)=.43	

A-less than 1 hour; B-greater than 1 hour but less than 1 day; C-greater than 1 day.

disturbance occurred. Because of the small sample size no real conclusion can be drawn with respect to whether the presence or absence of alpha-wolves was an important factor in abandonment of homesites (Table 10). Table 10 does indicate, however, that wolves were more likely to abandon homesites when both alpha-wolves were present than when one alpha-wolf was at the homesite. Because of the small sample size, the presence of alpha-males versus that of alpha-females cannot be compared.

Stephenson (1974), based on information from Nunamiut Eskimos, indicated that age, experience, and personality traits of adult wolves were important factors in the response of wolves to human presence. He indicated that the mother wolf was the key wolf.

Clark (pers. comm.) indicated that yearlings were the least reactive to human presence on Baffin Island, and that old alpha-wolves were the most likely to react strongly.

Information from the present study indicated that any adult (alpha or not) could leave the homesite following disturbance. It appeared, however, that the mother of the pups in the Hulahula River valley lingered near the homesite for longer periods before leaving (if she was going to leave; App. A, CH's 2e, 2g) than did other wolves (App. A, CH's 2a, 2c, 2d, 2f). Alpha-females probably show the most concern for their pups upon detecting humans.

Distances pups are moved

The distances pups were moved following human disturbance

	TYPE OF DISTURBANCE	PANCE			Alpha-wolf present	Tesent		No alph	No alphas present		Alpha-female present	e present
irat los	No. of Di	Distance (km)	Percentage Abandoned	a	Observed Abandonments	Observed Expected Abandonments Abandonments	=	Observed Abandonments	Observed Expected Abandonments Abandonments	c	Observed Abandonments	Observed Expected Abandonments Abandonments
<	-	*0.4	•	•	•	•	-	0	0	~	0	•
<	-	₹0.4	12	1	7	1.68	~	0	.42	40	-	1.1
<	ដ	¥0.4	33	-	•	.33	~	-	.33		0	.33
<	71	61 4.4	33	•	м	2.31				•	~	1.32
-	~	*0.4	•									
•	, ~	\$. •	20	*	•	2						
•	ង	*0.4	•	-	•	•				-	•	•
•	ង	\$.0j	29	7	-	1.68	~	•	.67	-	~	19:
v	-	^	100	-	-					-	-	~
u	-	10.4	ı									
ü	ង	≯ 0. 4	100	-	-	-						
v	ង	\$ 0	8	~	~	7						
			TOTALS	28	13	13	41	-	1.42	2	•	4.42
		PEACENTA	PERCENTACE ARANDONED		(13/29)=.45			(1/5)*.20	_		(4/15)=.27	

Acless than 1 hour; Degreater than 1 hour but less than 1 day; Cegreater than 1 day.

Table 10. - Continued.

TYPE (F DISTU	RANCE			Alpha-male	present		Both alphas	present
Duration ⁴	No. of People	Distance (km)	Percentage Abandoned		Observed Abandonments	Expected Abandonments	n	Observed Abandonments	Expected Abandonments
A	1	>0.4	0	1	0	0			
A	1	<u>≤</u> 0.4	21				2	1	.42
A	≥2	>0.4	33						
A	<u>2</u> 2	<u>≤</u> 0.4	33				3	2	1
	1	>0.4	•						
	1	≤0.4	50	1	1	.5	3	2	1.5
	≥2	>0.4	0						
	2.2	<u><</u> 0.4	67	1	0	.67			
C	1	>0.4	100						
C	1	<u>≤</u> 0.4	-						
C	≥2	>0.4	100				1	1	1
c	2,2	<u><</u> 0.4	100				2	2	2
			TOTALS	3	1	1.2	11	8	5.9
		PERCENTAGE	ABANDONED		(1/3)=.33			(8/11)=.73	
•	XPECTED	PERCENTAGE	ABANDONED		(1.2/3)=.40			(5.9/11)=.54	

A A-less than 1 hour; B-greater than 1 hour but less than 1 day; C-greater than 1 day.

(Table 11) were similar to those reported for wolves changing homesites for other reasons (Table 4). In eight of the ten reported cases adults moved pups from 1.6 to 3.2 km from the disturbance. One move was less than 1.6 km, and in the present study pups were moved more than 16.0 km from the whelping den on the Echooka River. Additional cases of homesite abandonment have been reported, but the distance pups were moved was unknown. Perhaps these litters were not found again because pups were moved relatively great distances. The distances that adult wolves move pups from homesites after human disturbance may provide some indication of the distance at which adult wolves feel their pups are safe from humans.

Behavior of pups upon detecting humans

The behavior of pups upon detecting humans was fairly predictable. In most cases they simply retreated into cover or the den after they sighted humans or after adults vocalized (Table 12). In captive wolves, "a growl, or an accelerated growl-bark from the mother would send the cubs back into their nest box. This warning signal always occurred when a strange person came near the enclosures" (Fox 1971:170). In two cases pups showed no concern despite barking and howling by adults nearby (App. A, CH's 2h, 31). Pups often approached humans who howled near homesites (App. A, CH's 5, 10, 19; App. B, CH 4). In the present study (App. A, CH 2g), pups trotted 0.7 km to the center of the homesite (Figure 22) after their mother began howling.

Table 11. - Distances adult wolves moved pups following human disturbance.

Locale	Distance (km)	Source	Appendix A, Case History
Yellowstone N. P.	1.6	Bailey (1930)	9
Algonquin P. P.	2.4	Joslin (1966)	24
Jasper N. P.	2.2	Carbyn (1974b)	10a
Jasper N. P.	1.8	Carbyn (1974b)	11
Jasper N. P.	1.8	Carbyn (1974b)	12a
Northwest Territories	<1.6	Kelsall (1960)	29
Baffin Island	1.6	Wayman (1967)	51
Mount McKinley N. P.	<u>≥</u> 3.2	Murie (1944)	31b
North Slope, Alaska	3.2	Stephenson (1974)	45
Brooks Range	>16.0	Present Study (1975)	1

Table 12. - Reaction of wolf pups upon detecting humans.

Behavior	Percentage of Cases in which Behavior was Observed	Case Histories
Retreat into den or cover	62	App. A, CH's 1, 2f, 2g, 5, 10b, 12b, 19, 20, 27, 32c, 33b, 37, 40, 41 App. B, CH's 1, 2, 3, 5
Leave area with adults	24	App. A, CH's 4, 8, 31b, 32d, 32e, 33d, 48
Watch intently; curious	17	App. A, CH's 5, 12b, 35, 41, 48
Show no concern	17	App. A, CH's 2h, 20, 31, 35, 41
Approach humans	14	App. A, CH's 19, 48, 50 App. B, CH 4
Vocalize		
Whine	3	App. A, CH 50
Short gruff barks	3	App. B, CH 1

Influence of pups on behavior of adult wolves

The proximity of pups, or perhaps of the homesite, influences wolves to react anxiously to the presence of humans. opportunity to test the hypothesis that it was the homesite and not the pups which caused wolves to react to human presence. On 14 July 1976 in the Hulahula River valley the pups were moved from the den to a rendezvous site 0.8 km away. By 17 July we were sure that only five of the eight adult wolves knew of the homesite change. At 1324 I observed a wolf approach the whelping den area, and remain there for several hours. I approached the den, and at approximately 1745 I stepped from cover in clear view of the wolf at a distance of about 50 m. The wolf stood and walked uphill to a small clearing in the brush below the den. It lay down and watched for a few minutes. The wolf did not appear anxious nor did it vocalize. It finally stood and trotted slowly away from me and the den in a direction opposite that of the rendezvous site. The wolf was small and slim, and urinated in the female squat position. In my estimation it was a yearling female.

The casual reaction of this wolf was not typical of that shown by disturbed wolves near pups. This wolf was probably not aware of the exact location of the pups but probably knew the pups were not present at the whelping den. Pups rarely fail to greet an adult arriving at a homesite; volcalizations by adults (Carbyn 1974b) may alert pups to their presence. On one occasion when I was within 100 m of the pups at the Hulahula den I heard frequent whining and growling

from the pups. The absence of these vocalizations would probably be conspicuous to an adult.

Murie (1944; App. A, CH 33a) reported an observation where an adult wolf barked at humans when a pup was being moved between homesites.

Crisler (1958) reported that a litter of pups was taken from a den in the wild and raised by two semi-wild, yearling wolves that were not the parents. Instead of vanishing, the yearlings stayed around and howled when two Eskimos, who had tormented the wolves previously, came to the Crislers' camp. The two yearlings kept alongside the Eskimos when they left; the male wolf uttered hoarse half-howls. Another case was reported by Rutter and Pimlott (1968) in which a captive wolf, normally subordinate to a pet dog, became the aggressor in the presence of wolf pups.

These observations indicate that pups are indeed the most influential component affecting the response of adult wolves detecting humans near homesites.

Disturbance of dens prior to whelping

Joslin (1966; App. A, CH 23) found two unused but freshly dug dens in an area he disturbed in early May in Algonquin Provincial Park. A similar case was reported by Stephenson and Johnson (1973; App. A, CH 47). Disturbance of den areas prior to whelping may greatly influence den selection since pregnant females can move to another location (Stephenson 1974).

Prolonged human presence

Several biologists during summer have observed wolves at close range over extended periods. Most attempted to be as unobtrusive as possible. Murie (1944) watched a den in Mount McKinley National Park from a distance of 0.8 km for 195 hours one summer, and for an undisclosed number of hours the following summer. His presence at this distance had no discernible impact on the denning wolves. At closer distances he was frequently barked and howled at. Haber (1968) described several incidents where he was detected by wolves that barked and howled when he attempted to observe them within 0.4 km in Mount McKinley National Park.

One biologist in the Northwest Territories observed a den for 40 hours between 13 June and 6 July from a distance of 1.2 km. The wolves generally tolerated his presence (Banfield 1954). Clark (1971) and his co-workers observed several dens on Baffin Island for 1,108 hours over a 4-year period from distances ranging from approximately 0.3 to 0.5 km (Clark pers. comm.). Their presence may have prompted the denning females to change den sites more frequently than would have been the case otherwise.

Both Joslin (1966, 1967) and Voigt (1973) were frequently approached and barked at by wolves in Algonquin Provincial Park when they howled within approximately 0.3 km of wolves at homesites. At greater distances they were usually not approached.

Peterson (1974) was able to observe a wolf rendezvous site in

Isle Royale National Park between 19 and 29 July. Observations were

made from a ridge 0.2 km from the rendezvous site, away from the main wolf trails. The wolves gave no indication that they were aware of his presence.

In Jasper National Park, Carbyn (1974b) gradually moved closer to homesites and increased the length of time spent in homesite areas. His base camp was 0.4 to 0.8 km from activity areas.

Observation distances were usually within 0.2 km. On two occasions his presence may have prompted wolves to abandon whelping dens. His presence at rendezvous sites was usually tolerated.

In 1974 we observed two dens 0.3 km apart used by one pack in Mount McKinley National Park from a distance of 0.8 to 1.0 km for 335 hours between 22 June and 26 July. We were not detected by wolves. In 1975 our presence 0.4 km from the Echooka den caused abandonment of the den. In 1976 the presence of our observation tents 1.2 to 1.6, and base camps 1.4 km, from the Hulahula homesites had no major impact on the behavior of the wolves.

In summary, wolves in open country were usually not disturbed by observers who were 0.8 km or more from homesites. At closer distances wolves reacted to the presence of observers. In forest regions observers not howling caused little or no disturbance while remaining within 0.4 km of homesites. Frequent howling near homesites by biologists may have resulted in more frequent homesite changes (Clark 1971, Peterson pers. comm.).

Response distances

The greatest distance from pups to humans at which human presence caused adult wolves to howl or bark was 2.4 km (Table 13). The greatest distance from pups to adult wolves at which adults howled or barked at humans was 2.0 km. In all but two cases wolves were within 0.8 km of pups.

Twenty cases were observed where adult wolves were from 0.8 to 2.4 km from pups when they detected humans a similar distance from pups (Table 14). In none of these cases did the adult wolves vocalize or significantly alter their behavior.

The sensory abilities of wolves are discussed in Part V.

Re-use of dens

Human disturbance has been reported to limit re-use of dens (Stenlund 1955; Kozlov 1964, in Joslin 1966; Joslin 1967). Other dens, however, were used the year after they were disturbed (Murie 1944, Clark 1971, Stephenson and Johnson 1972, Carbyn 1974b). The situation described by Carbyn was a den disturbed in 3 successive years but still used the 4th year. Each year, the den was abandoned soon after it was disturbed. As noted earlier, re-use of dens by undisturbed wolves is not highly predictable. Re-use may be affected by tradition of use, death of some pack members, changes in prey availability, and marginal sites becoming less suitable. Clark (1971: 96-97) made an interesting point:

...if suitable den sites are not available in the area in

Table 13. - Distances at which wolves howled or barked at humans near pups.

Locale	Distance from Humans to Pups (m)	Distance from Humans to Howling Wolves (m)	Distance from Pups to Howling Wolves (m)		Appendix A, Case History
Algonquin P. P.	few hundred	30-150	few hundred	Joslin (1966)	26
Algonquin P. P.	150	15-400	150-400	Therberge and Pimlott-(1969) 49
Baffin Island	nearby	400	400	Theberge (1975)	48a
Mount McKinley N. P.	180	800	<800	Murie (1944)	31a
Mount McKinley N. P.	180	few hundred	nearby	Murie (1944)	31b
Mount McKinley N. P.	0	140	400	Murie (1944)	32 a
Mount McKinley N. P.	<2400	7	1600	Murie (1944)	32b
Mount McKinley N. P.	400	90-180	400	Murie (1944)	32c
Mount McKinley N. P.	nearby-1600	few hundred	nearby	Hurie (1944)	328
Mount McKinley N. P.	150	140	nearby	Murie (1944)	32e
Mount McKinley N. P.	0	140	140	Murie (1944)	33a
Nount McKinley N. P.	100	180	200	Murie (1944)	33b
Mount McKinley N. P.	70	few hundred	few hundred	Murie (1944)	33c
Mount McKinley N. P.	30-800	15-700	0-few hundred	Haber (1968)	19a
Nount McKinley N. P.	•	few hundred	?	Haber (1968)	196
Mount McKinley N. P.	few hundred	few hundred	nearby	Haber (1968)	20a
Mount McKinley N. P.	Ť	few hundred	7	Haber (1968)	20ъ
Mount McKinley N. P.	25	400	400	Deen (pers. comm.)	3b
Mount McKinley N. P.	nearby-300	300	300	Tracy (pers. comm.)	App. D, CH 5
Mount McKinley N. P.	nearby	500	500	Tracy (pers. comm.)	8
Brooks Range	2400	400	2000	Stephenson (1974)	44b
Brooks Range	<800	few hundred	few hundred	Stephenson (1974)	Generalizatio
Brooks Range	450	100-200	300	Present Study (1975)	1
Brooks Range	1000	1000	50-75	Present Study (1976)	2b
Brooks Range	1300	1300	500	Present Study (1976)	'2b
Brooks Range	1000	600	500	Present Study (1976)	2c
Brooks Range	250-1400	250-1000	100-400	Present Study (1976)	24
Brooks Range	human scent ^a	100	<50	Present Study (1976)	2e
Brooks Range	600-800	600	<200	Present Study (1976)	2g
Brooks Range	400-100	400	<\$0	Present Study (1976)	Zh.
SUMMARY OF DATA	0-2400	15-1300	0-2000		

a Possible visual stimulus 1600 m away.

Table 14. - Molf-haman interactions away from pups.

No. of Molves	Distance from Molves to Pups (km)	Distance from Humans to Pups (km)	"Disturbance"	Behavior Prior to Detecting Humans	Behavior After Detecting Hamans	Source
-	2.4	3.2	human scent, and I human	leaving den	briefly curious, continued	Stephenson (1974)
-	0.6-1.2	0.5, 1.2	2 humans	leaving den	investigated, continued	Present Study (1975)
~	2.0	1.6	2 humans	returning to den	briefly curious, continued	Present Study (1976)
~	1.6	1.6	2 humans	leaving den	briefly curious, continued	Present Study (1976)
	1.4	1 :•	1 human	returning to den	loped toward den	Present Study (1976)
n	1.4	7:	busen tracks	leaving den	sniffed area, continued	Present Study (1976)
-	e. 0	1.6	1 human	leaving den	watched for several minutes, continued	Present Study (1976)
-	0.2(1)-0.9	1.2) human	leaving den	watched for several minutes, continued	Present Study (1976)
-	1.2	1.2	1 hvesn	leaving den	briefly curious, continued	Present Study (1976)
-	o. •	1.0	unoccupied tent	leaving den	briefly curious, continued	Present Study (1976)
-	1.0	1.0	unoccupied tent	returning to den	briefly curious, continued	Present Study (1976)
n	1.4	7:	base camp	leaving den	briefly curious, continued	Present Study (1976)
. ••	1.2	1.2	observation tent	leaving den	looked, continued	Present Study (1976)
-	1.4	7:	base camp	leaving den	investigated, continued	Present Study (1976)
-	:	1.4	I human and base camp	leaving den	watched for several minutes, continued	Present Study (1976)
-	9.9	0 .	l husen	at whelping den, cannot locate pups	briefly curious, left area	Present Study (1976)
-	2.4	2.4	1 human	on hunt	left area	Present Study (1976)
-	1.6	1.6	1 human	leaving rendezvous	briefly curious, continued	Present Study (1976)
•	1.6	1.6	1 human	leaving rendezvous	briefly curious, continued	Present Study (1976)
-	7.	1.6	observation tent	returning to rendezvous site	briefly curious, continued	Present Study (1976)

sufficient numbers to allow a choice of site to avoid proximity to humans, then the wolves would be pressured into either re-using or remaining at a den with a history of human disturbance, or selecting a suboptimal den site...

As noted earlier, whether homesites are in limited supply is not known.

Centers of human activity

In Mount McKinley National Park 11 of 12 dens known to be active since 1966 were located within 6.4 km of a road or campground. The average minimum distance to these centers of human activity for the 11 dens was 2.8 km (range=0.1-6.4 km), and seven were within 2.4 km. The average distance from a center of human activity for six dens known to be active in the Park since this study began in 1974 was 3.3 km (range=1.8-5.8 km), and three were within 2.4 km. Three dens that have not been used by wolves since the late 1950's were located within 1.0 km of a center of human activity (ave=0.6 km, range= 0.3-1.0 km). Comparable distances reported for active homesites by others include a den 2.8 km from a road (Stebler 1951); two dens 1.2 km from a trail, one of which was 2.8 and the other 3.2 km from a wilderness campground (Carbyn 1974b); a rendezvous site 0.4 km from an occupied cabin (Stanwell-Fletcher 1942); and a rendezvous site located 0.8 km from a highway (Rutter and Pimlott 1968).

Topography, vegetative cover, and amount and type of human activity in addition to distance probably influence the inclination of wolves to den near permanent centers of human activity. Carbyn (1974a:99) gathered some information on the possible impact of centers

of human activity on wolf denning activities in Jasper National Park:

Of the four deserted den sites actually examined, two are within 1/2 mile (0.8 km) from main highways, one is adjacent to railroad tracks, and another is immediately adjacent to an extensively used horse range and stables. All the human structures, except the railroad tracks, were either new facilities or greatly upgraded and more intensively used since the time when Wolves were known to have used these sites for denning activities.

To my knowledge the only reported instance in which wolves at a homesite reacted to a vehicle is that described in Appendix D, Case History 1. Tracy (pers. comm.; App. D, CH 5) described an interesting observation of an adult leading four pups across a main highway in Alaska. Other observations of interest are contained in Appendix D. It may be reasonable to expect that wolves avoid denning near roads though the road itself and vehicular traffic may not be the factors responsible. Human use of areas adjacent to roads may have the greatest impact.

The date that certain sections of the road are opened in Mount McKirley National Park (and, therefore, large numbers of humans have access to wolf denning areas) is probably important with respect to permanent abandonment of den sites near the road. The Park road runs east-west. In spring, as the snow melts, sections of the road are opened at later dates as one moves west. Those dens that were within 1.0 km of centers of human activity and not used since the 1950's were located near the east end of the road. Those within 1.0 km and used in recent years were located near the west end of the road which is usually opened in early June, well after parturition.

Alteration of wolf-prey relationships

The presence of humans may indirectly affect wolf denning activities by influencing wolf-prey relationships, and, therefore, the amount and quality of food brought to the pups. Normal summer wolf-prey relationships can be altered in several ways. First, wolves may avoid areas of human activity (Carbyn 1974a, Peterson 1974, Miller 1975, Singer 1975, Hoskinson and Mech 1976). This may reduce the number of prey available to wolves as well as limit the influence wolves have on the number and quality of prey animals in those areas.

Second, human presence may influence the chasing, killing, and utilization of prey. Several cases have been reported where wolves stopped chasing prey upon detecting humans (Cowan 1947; Banfield 1954; Tener 1954, 1965; Miller 1975). In Wood Buffalo National Park 11 wolves refused to kill a wounded bison in the presence of humans in a parked truck (Fuller 1966). On the other hand, Dixon (1938) described an incident where a wolf continued to chase a caribou despite repeated attempts by two shouting women to frighten the wolf. Murie (1944) and Carbyn (1974b) suggested that roads may be an advantage to wolves that are hunting by providing locations where prey can be ambushed. It is important to note that undisturbed wolves have a low success rate in killing prey (Mech 1970).

Wolves are easily frightened from carcasses, and in some cases they were reluctant to return to disturbed carcasses (Cowan 1947, Shelton 1966, Mech 1970, Kuyt 1972, Miller 1975). In other cases they approached disturbed carcasses but did not feed (Dunne 1939,

Joslin 1966, Carbyn 1974b, Magoun 1976, personal observations). In still others wolves returned and fed within a few hours after the carcass was disturbed (Joslin 1966, Gray 1970, Magoun 1976, personal observations). In this regard, undisturbed wolves sometimes utilized carcasses incompletely (Mech and Frenzel 1971, Wolfe and Allen 1973, Miller and Broughton 1974).

The third way in which normal wolf-prey relationships may be disrupted is through the utilization by wolves of artificial food sources such as garbage dumps (Murie 1944, Stenlund 1955, Voigt 1973, Van Ballenberghe et al. 1975, Grace 1976). Grace (1976:155-156) has speculated on what the effects a widespread dump-foraging habit among wolves might be:

...One result may be the impairment of health and a decreasing effectiveness of wolves as predators, reinforcing the dump habit. Alternatively, the extra food supply may increase wolf survival and thereby increase pressure on their prey....The only possible positive result of the habit is that it leads to wolves being commonly seen. Since the potential consequences of dump foraging are deleterious to wolves...it is reasonable to recommend that the habit be discouraged by incineration of garbage or the fencing off of dumps.

Wolves that habituate to the presence of humans probably do so because of the availability of artificial food sources (Anonymous 1975, Grace 1976), or the occurrence of substantial innocuous human activity within their territories. This seems to be the case for wolves in Mount McKinley National Park, in some areas of Minnesota (Van Ballenberghe et al. 1975), and along the haul road for the trans-Alaska oil pipeline (Anonymous 1975, Whitten pers. comm., Roby pers. comm.).

Aircraft disturbance

The response of wolves to aircraft is well documented (Burkholder 1959, Mech 1966, Shelton 1966, Jordan et al. 1967, Pimlott et al. 1969, Thomas 1969, Mech and Frenzel 1971, Peterson 1974, and others).

Responses varied between packs, and even between members of single packs. Some wolves ignored aircraft, others ran and jumped toward aircraft, while others fled. Previous experiences (frightening or innocuous) with aircraft influenced the response of wolves. Klein (1974:382) nicely summarized:

Wolves appeared least disturbed by low-flying aircraft of any of the large mammals observed. This is somewhat surprising in view of the fact that they were legally hunted from aircraft in the study areas [in Alaska] as late as November, 1969, and at that time, aerial hunters commented on the extreme alarm shown by wolves to aircraft. Currently, aircraft are common in the study areas, and wolves have apparently rapidly adapted to the discontinuance of the threat from this source.

Several authors indicated that wolves habituated to aircraft if they were repeatedly flown over at altitudes of 100 m or more. Flights at altitudes less than this seemed even to frighten wolves that were accustomed to aircraft (Jordan et al. 1967, Peterson 1974).

There has been little mention in the literature of wolves responding to aircraft flying near homesites in summer. During the course of this study, 47 observations were accumulated where wolves at homesites responded to aircraft (App. C, CH's 1-47). Two other case histories (App. C, CH's 49-50) were given to me by Dr. David Klein, who collected them from other observers for his study of aircraft disturbance (Klein 1974). The final three case histories

were taken from the literature (App. A, CH 45; App. C, CH's 48, 51). It should be noted that in all of these cases the wolves were probably somewhat accustomed to aircraft. Table 15 lists the various responses observed. In most cases the more severe reactions, i.e. abandon den, run from plane, or leave homesite area, occurred when aircraft flew relatively close to the wolves.

The existing information does not show aircraft disturbance near wolf homesites to be a serious problem. Frequent straight and level flights at altitudes of 100 m or more over wolf homesites in areas such as Mount McKinley National Park would probably have little impact on wolf populations. The potential exists, however, that wolves legally or illegally hunted or harassed from aircraft during winter may react strongly to aircraft passing over homesite areas in summer.

History of contact with humans

Previous history of contact with humans may affect the response patterns of wolves disturbed at homesites. As noted, wolves habituate readily to aircraft, and to substantial innocuous human acitivity particularly when artificial sources of food are available. Clark (1971:96) provided the most dramatic example:

...In 1967 the East Fork den bitch moved her litter 2.5 miles (4 km) to Nadluardjuk Summer Den, near which we were already established, and frequently approached our camp to search for scraps of food. In 1968 the Wopemado Den bitch who, I believe, was the same wolf, never approached our camp and always remained furthest from it whenever the wolves approached in a group. Her change in behaviour towards us probably arose from a foot she injured in a tagging operation we conducted several miles from the den area in 1968.

Table 15. - Reaction of wolves to aircraft disturbance near homesites.

Behavior	Percentage of Cases in which Behavior was Observed	Appendix C, Case Histories
Turn head in direction of aircraft, or stop previous activity to watch aircraft	50	1, 2, 3, 5, 7, 9, 10, 11, 12, 13, 18, 19, 21, 22, 23, 25, 27, 28, 30, 31, 32, 33, 35, 37, 39,
Stand and/or walk short distances; watch aircraft	33	4, 6, 8, 9, 10, 11, 15, 16, 17, 20, 26, 29, 30, 32, 34, 36, 48
Leave homesite area	10	8, 14, 15, 22, 24
No visible reaction	6	23, 38, 49
Run from aircraft	4	44, 48
How1	2	8
Abandon homesite	2	51
Miscellaneous		
Mother wolf exits den	2	1
Mother wolf runs to den	2	43
Pup behavior		
Watch aircraft	12	41, 42, 45, 46, 47, 50
No visible reaction	4	49; App. A, CH 45
Run from aircraft	2	48

An unanswered question is whether wolves will be less reactive to human presence at dens when habituated to human presence away from dens than when unhabituated or after having experienced frightening encounters with humans, e.g. trapping. A study of human disturbance at dens near the haul road of the trans-Alaska oil pipeline, where wolves are quite accustomed to humans, could provide an answer.

PART IV. WOLF PUP MORTALITY IN SUMMER

The most critical indicator of the seriousness of human disturbance on denning activities is probably the effect human disturbance has on pup survival. This section consolidates the available information on pup mortality and survival rate, and discusses the possible effects of human disturbance on pup survival.

Mortality factors

As indicated by Keith (1974:34):

Unfortunately,...the factors, ultimate and proximate which produce mortality during the first 5 months are almost wholly unknown. This is probably the single greatest enigma in wolf biology today.

Table 16 lists the reported causes of mortality of wolf pups in the wild and in captivity. In summer 1974 a member of the Park maintenance staff found a wolf pup just outside Mount McKinley National Park that had apprently died as a result of an encounter with a porcupine. About 50 quills were embedded in the carcass. The size of the pup indicated that it had died in fall 1973 (Lent pers. comm.). In contrast, on 16 July 1976 at the second rendezvous site near the Hulahula River all four pups intently watched, from a distance of about 2 m, a porcupine that slowly walked through the site. One adult wolf nearby appeared to ignore it. Neither the adult nor the pups followed the porcupine as it left the area.

Table 16. - Reported mortality factors affecting wolf pups in summer.

Mortality Factor	Found in Captive (c) or Wild (w) Pups	Source
IN UTERO		
Resorption	•	Rausch (1967)
Stillbirths	c	Kuyt (1972)
Abortion (rangiferine brucellosis)	c	Neiland (1975)
POST PARTUM		
Canine distemper	C,W	Murie (1944), Cowan (1947), Rausch (1953), Mech (1970), Choquette and Kuyt (1974)
Infectious canine hepatitis	C,W	Choquette and Kuyt (1974)
Rabies	w	Seton (1937), Rausch (1958)
Listeriosis	c	Rutter and Pimlott (1968)
Pneumonia	c	Kuyt (1972)
Malnutrition	*	Jordan et al. (1967), Kuyt (1972), Seal et al. (1975), Van Ballenberghe and Mech (1975)
Parasites	c	Kuyt (1972)
Drowning	c,w	Moolpy (1967), Clark (1971)
Other wolves	c,#(?)	Rabb et al. (1967), Kuyt (1972), Stephenson and Johnson (1972)
Golden eagles	w	Seton (1937), Stephenson and Johnson (1972)
Porcupine quills	w	Stephenson (1974), Present Study (1974)
Accidental death	w	Stephenson and Johnson (1972)
Humans	w	Numerous authors
PROBABLE MORTALITY FACTORS		
Abortion (due to stress)		
Sarcoptic mange		Cowen (1947), Carbyn (1974a)
lears .		Murie (1944), Joslin (1966), Carbyn (1974b), Present Study (1976)
FACTORS THAT MAY CONTRIBUTE TO MORTA	ALITY	
Cataracts	c	Woolpy (1967)
Displaced jaw	c	Woolpy (1967)
Broken bones, improper healing of bones, hyperostosis	W	Stephenson and Johnson (1973), Present Study (1974)
Rickets	c	Rutter and Pimlott (1968)
Behavioral differences	•	Peterson (1974), Present Study (1974, 1975)

On 2 July 1976 at the den on the Kongakut River I noticed that one of the pups was slower than the other six in leaving the den to greet their mother. It did not run to the group and join the melee, but sat and watched 15-20 m away. When the others moved off a short distance, this pup stumbled several times over what should have been easily negotiable tussocks while attempting to join them. When I returned to the area on 26 July, I saw only six pups, and found a pup skull covered with maggots approximately 20 m from the den (Figure 24). A pup, perhaps the lethargic one noticed earlier, had died and may have been consumed by its litter mates and/or by adult wolves. Mills (pers. comm.) saw seven pups at the den on 15 July which indicates that the pup had died no more than 10-11 days prior to my arrival. The cause of death was not known.

On 10 July 1974 one of three pups occupying the East Fork den developed a limp, favoring the left hind leg, after a particularly vigorous bout of play with the other two pups. By 22 July this pup sometimes hobbled along on three legs. The limp progressively worsened until 26 July when we lost contact with the pack. The pup was moved from the den at least 2 days after the others. Earlier that summer we noticed a behavioral difference between this pup and the other two. Following the arrival of an adult wolf to the den, this pup would leave the den to meet the arriving adult as did the other two, but this pup would soon return to the den leaving its two siblings to food beg, nurse, or play with the adults. This pup was probably not receiving as much food as its siblings. By 17 July



Figure 24. Skull of dead pup found at the Kongakut den in July 1976.

this pup was noticeably smaller than the other two. It is possible that nutritional bone disease (Hime 1968) was a factor in the development of the pup's limp, either by causing the bones to be susceptible to breakage or by preventing normal healing.

As noted in Table 16 bears are a probable predator of wolf pups. On 27 July 1976 I observed a grizzly bear partially enter the inactive Kongakut den (Figure 25), then walk over to the active den 60 m away. After attempting to dig out a ground squirrel 10 m from the active den, the bear walked by the den and entered a large stand of willows where at least one pup was situated. No adult wolves were near the den at the time. Approximately 1 min later the bear ran out of the willows to the river 200 m away. Appendix F contains additional observations of wolf-bear interactions near wolf homesites.

Nunamiut Eskimos have reported a few cases of golden eagles taking wolf pups (Stephenson and Johnson 1972). Several observations from the present study and one observation by Murie (1944) of eagles at wolf homesites provide some indication of the circumstances under which eagles take wolf pups (Appendix E). It is possible that other raptors and possibly even ravens take pups. Predation in this case is, however, a "two-way street". In 1975 along a wolf trail 0.3 km from the den on the Echooka River I found the remains of a snowy owl (Nyctea scandiaca) that may have been killed by wolves (Figure 26). In 1976 many feathers from an immature golden eagle were found below the den on the Hulahula River. Talons, possibly from this eagle, were found 10 m from the den entrance. Kuyt (1972)



Figure 25. Grizzly bear partly in the inactive Kongakut den in July 1976.



Figure 26. Remains of a snowy owl found near the Echooka den (arrow) in 1975.

found the remains of a young gyrfalcon (Falco rusticolus) near a wolf den in the Northwest Territories. It is possible that raptors are attracted to den areas because of food remains usually present (Kuyt 1972), and not because of the presence of vulnerable wolf pups. Clark (1971) thought that the cryptic coloration of young pups was a protective adaptation against predation.

Another factor which could cause mortality of young is the selection by females of marginal dens in which to whelp pups. As noted in Part I, pups have been whelped in excavations in snow (Kelsall 1960), on surface beds at the base of spruce trees (Soper 1942), and in very shallow "pit dens" (Stephenson 1974:17). Stephenson hypothesized that either inexperienced females, or less proficient diggers, or females caught away from one of the prepared dens at the time of parturition were responsible for these types of "dens". Coyotes have been reported to whelp pups in thickets or under brush piles (Gier 1968). Perhaps these seemingly marginal dens are all that is necessary to successfully whelp and rear pups. No one has demonstrated that pup survival is lower at these sites.

Survival of pups

Loss of pups in utero

Rausch (1967) indicated that 89 percent of the ova shed in Alaskan wolves were implanted - a loss of 11 percent. Pimlott et al.

(1969) indicated that most counts of corpora albicantia were between five and seven (no mean was given), and that females had an average of 4.9 placental scars. This gives an implantation rate of approximately 82 percent - a loss of 18 percent. Gipson et al. (1975) found an ovulation rate of 6.2 eggs per female in coyotes, and, from placental scars and embryos, he found that an average of 4.5 eggs were implanted - a loss of 27 percent.

For wolves the average in utero litter size seems to be about six pups (Table 17). It is not clear how this value varies between populations at different latitudes, between those under different degrees of exploitation by humans, or between those on different nutritional planes.

Placental scars are commonly used to estimate in utero litter sizes for canids (Hamlett 1938, Layne and McKeon 1956, Layne 1958, Wood 1958, Rausch 1967, Gier 1968, Macpherson 1969, Pimlott et al. 1969, Gipson et al. 1975, Nellis and Keith 1976, and others). It has not been demonstrated in canids, however, that placental scars accurately represent the number of pups born live. Because it would be difficult to separate placental scars representing full term pups from those representing aborted, resorbed, or stillborn pups (Wood 1958, Layne 1958), placental scar counts probably give values somewhat higher than the actual number of young that are born live.

Rausch (1967) reported two instances of embryo resorption in wolves, one in each of two litters. His is, however, the only report of resorption in wolves. Gier (1968) reported a resorption

Table 17. - Reported in utero litter sizes for wolves.

Locale	Number of Litters	Average Litter Size	Information Based On	Source
Algonquin P. P.	10	4.9	Placental scars	Pimlott et al. (1969)
Northwest Territories	18	5.8	Fetuses	Kuyt (1972)
Alaska	33	5.5	Fetuses	Kelly (1954)
Alaska	175	6.5 ^a	Fetuses	Rausch (1967)
Alaska	69	5.3 ^b	Fetuses	Rausch (1967)
Alaska	534	6.7 ^a	Placental scars	Rausch (1967)

a From animals 3 years or older.

b From animals 2 years old.

rate of approximately 20 percent in Kansas coyotes. Gipson et al. (1975) reported a resorption rate of 8 percent in a sample of 30 coyote embryos from Arkansas.

Abortion has been reported in captive wolves as a result of experimental infection with rangiferine brucellosis (Neiland 1975), but it has not been reported for free-ranging wolves. Gipson (1976) reported two cases of abortion in coyotes following abnormal stress; one female was caught in a trap and another was brought into the laboratory. The age of the fetuses was approximately 40 and 31 days respectively. Stenlund (1955) reported that a trapper found six wolf pups suckling from the dead body of their mother who was caught in a snare. Stenlund did not report a date for this observation. Undoubtedly the pups were near full term when the female was snared.

It is not clear how physiological, nutritional, or psychological stress affect rates of abortion and resorption. The age of the fetuses when stress occurs may be important. There may be a tendency for young fetuses to be resorbed and older fetuses aborted. It is possible that the fetuses of only one, or part of one, uterine horn are aborted. Fetuses that die near parturition may be stillborn.

Neonatal mortality

Mortality during the first 2-3 weeks of life (prior to the time pups begin to leave dens to explore, play, and eat, and are observable) is essentially unknown for wolf pups. In a discussion of neonatal mortality in the dog, Fox (1963:1221) concluded that

nutrition and maintenance of body temperature were the two primary needs of the neonate. Disturbance in either of these factors caused early death in some neonates. "In very large litters [size not specified], underweight pups usually died between 1 and 4 days of age." Another factor that caused death in the first few days of life was neglect of the litter by inexperienced (usually primiparous) mothers. Scott and Fuller (1965) found an avergae neonatal mortality rate of about 15 percent for pure-breed dogs. The Basenji, a breed which had been recently obtained from African villages, suffered only 3.5 percent neonatal mortality.

It is not clear what the magnitude of neonatal mortality is for wolves under usual conditions. A reasonable figure may be 10-15 percent. Neonatal mortality could be calculated by comparing the number of placental scars in mother wolves collected late in summer, with the number of pups whelped by the same mothers and observed soon after they leave the den when about 3 weeks old. Superficial examination of the uterus of a wolf taken on 18 May in southeast Alaska indicated that she had given birth to seven pups (Garceau 1960). The next day seven pups were found in a den near where the female was shot. Gipson et al. (1975) found a litter of six coyote pups approximately 3 weeks old. The mother was trapped, and seven placental scars were present, suggesting that one pup had died at birth or shortly thereafter.

Information on neonatal mortality is not easy to obtain.

Logistically it is difficult to locate active dens and count pups

early in summer, and it may be even more difficult to collect the mother late in summer. Some researchers have been reluctant to count pups early in summer in forest regions for fear that disturbance of dens may possibly reduce pup survival (Mech, submitted). The effect of human disturbance on pup survival is discussed later. The factors causing early death in wild wolf pups may be almost impossible to determine.

Summer survival rates

Pup mortality was rare in the present study and in others where litters were observed over long periods (Table 18). The average litter size and age when pups were first observed was 5.0 pups and 34.7 days respectively. The average litter size and age when they were last observed was 4.7 pups and 94.9 days respectively. This indicates a mortality rate of about -0.006 pups/litter/day. If this mortality rate is applied to the summer period (pups 21-150 days old), the summer survival is 85 percent. This is probably as high a summer survival as can be expected.

Table 19 reports summer survival rates for wolf pups, calculated from the present study and others. It is important to note that the values calculated according to the method of Mech (1970), which was based on autumn age structure of the population, average litter size, adult sex ratios, and percentage of adult females that bred in the population, will generally be equal to or lower than values calculated from observations of litters in summer or autumn, and

Table 18. - Reported pup survivel in litters observed during summer.

Locale	Period of Coverage	Initiel Age of Pups (days)	Initiel Litter Size	Final Age of Pups (days)	Final Litter Size	Source
Minnesota [®]	3 June-1 Oct.7	44	4	164	4	Van Ballenberghe et al. (1975)
Minnesota	15 June?-1 Oct.?	25	S	163	2	Van Ballenberghe et al. (1975)
Algonquin P. P. ^b	30 May-15 Sept.	20	S	129	5	Joslin (1966)
Jasper N. P. ^C	27 Aug30 Aug.	119	S	123	S	Carbyn (1974b)
Jasper N. P.	9 June-25 July	4 Q	6	87	6	Carbyn (1974b)
Jasper N. P.	30 May-1 Aug.	29	3	93	3	Carbyn (1974b)
Northwest Territories	i 23 June?-6 July	23	4	38	4	Sanfield (1954)
Baffin Island ^e	1 July?-1 Sept.?	25	5	87	s	Clark (1971)
Baffin Island	20 June?-10 Sept.	15	6	97	3	Clark (1971)
Baffin Island	20 June?-10 Sept.	15	S	97	S	Clark (1971)
Baffin Island	20 June?-6 Aug.	15	s	62	S	Clerk (1971)
Baffin Island	20 June?-11 Aug.	15	3	67	3	Clerk (1971)
Mount McKinley N. P.	15 May-28 Sept.	5	s	142	s	Marie (1944)
Mount McKinley N. P.	21 June-5 Aug.	42	4	88	4	Nurie (1944)
Mount McKinley N. P.	30 June-5 Aug.	51	6	88	6	Murie (1944)
Mount McKinley N. P.	4 June-19 Aug.	25	4	102	3	Haber (1968)
Mount McKinley N. P.	22 June-24 July	43	3	76	3	Present Study (1974)
Brooks Range ^g	3 Aug16 Oct.	75	11	150	11	Quimby (1974)
Brooks Range	28 June-8 July	39	6	49	6	Stephenson (1974)
Brooks Range	30 June-2 July	41	5	44	s	Present Study (1975)
Brooks Range	8 June-2 Aug.	19	4	74	4	Present Study (1976)
Brooks Range	28 June-26 July	39	7	68	6	Present Study (1976)
	AVERAGES:	34.7	5.05	94.9	4.68	

MORTALITY RATE: (4.68-5.05)/(94.9-34.7) = -0.006 pups/litter/day

a Assumed a 20 April birth data for pups in Minnesote.

b Assumed a 10 May birth date for pups in Algonquin P. P.

^C Assumed a 1 May birth date for pups in Jasper N. P.

d Assumed a 1 June birth date for pups in the Northwest Territories.

^{*} Assumed a 5 June birth date for pups on Beffin Island.

f Assumed a 10 May birth date for pups in Mount McKinley N. P.

g Assumed a 20 May birth data for pups in the Brooks Range.

Table 19. Reported pup survival and mortality rates.

	NGE .	SURVIVAL (in p	ercent)		
From	To	Population Natural Control		MORTALITY RATE (pups/litter/day)	Source
Birth	5 to 10 months	6-13 ^a			Kelsall (1968)
Birth	5 to 10 mo. hs	10-20 ^a	85 ⁴		Fuller (1955), Fuller and Novakowski (1955)
Birth	5 to 10 months	43 ^a	28-56 ^a		Pimlott et al. (1969)
Birth	5 to 10 months		45-52 ⁸		Rausch (1967)
Birth	6 months		44-57 ^ħ	-0.0190.014	Van Ballenberghe et al. (1975
In utero	6 weeks		34-74 ^C	-0.0900.036	Kuyt (1972)
Birth	3 months	42-53 ^d		-0.0390.031	Mech (submitted)
Birth.	8 months	24-62 ^e		-0.0220.011	Mech (submitted)
3 months	8 months	58 [£]		-0.009	Mech (submitted)
3 weeks	5 months	85 ^g		-0.006	Present Study (Table 18)
Birth	5 months	73 ^h		-0.011	Present Study (Table 18)
Birth	3 weeks	86 ^h		-0.041	Present Study (Table 18)

a From Mech (1970:58-64, 354-360). Based on autumn age structure of population, average litter size, adult sex ratios, and percentage of adult females that bred.

b Lower value calculated according to the method of Hech (1970). Upper value based on average litter of six pups and on a known survival of 17 pups in five packs.

^C Eighteen pregnant females averaged 5.8 fetuses. Lower value from caribou-free area - four litters averaged 2.0 pups. Upper value from caribou inhabited area - seven litters averaged 4.3 pups.

d Lower value calculated by assuming each pack had at least one female who conceived six pups. Upper value excludes those packs that "did not den". Based on maximum number of pups observed in packs in summer, which can be assumed to be the minimum number of pups produced by the packs.

Cower value calculated by assuming each pack had at least one female who conceived six pups and by comparing previous spring pack sizes with winter pack sizes to obtain minimum production per pack. Upper value excludes those packs that "did not den" and is based on "maximum pups surviving" in Mech's Table 4 (Mech, submitted).

Based on maximum number of pups observed in packs in summer, which can be assumed to be the minimum number of pups produced by the packs, and on the minimum production per pack calculated from previous spring pack sizes and winter pack sizes.

⁵ See text. Mortality rate of -0.006 pups/litter/day was calculated from Table 18. This mortality rate was applied to an average summer period (pups 21-150 days old).

h Assumes an average litter size of six pups at birth.

average litter sizes in utero or at birth. Those calculated according to Mech (1970) reflect loss of litters during pregnancy and shortly after parturition. The other values reflect the survival of pups whose litters survived to the time they were observed. One possible source of error in comparing litter sizes in late summer with an average litter size at parturition is that some litters may be combined late in summer (Murie 1944, Clark 1971), thus lowering the apparent mortality rate. This may be the case with the litter of 11 reported by Quimby (1974), and the litter of 15 reported by Summerfield (1974).

Availability of food seems to be a major factor in determining late summer litter size. Kuyt (1972) attributed the 40 percent loss from the potential 5.8 pups per litter to the absence of the primary prey, caribou, in the denning area. Mech (submitted) attributed the low litter sizes found in northeastern Minnesota in recent years to a drastic decline in white-tailed deer (Odocoileus virginianus).

Pups that survive the first 20 or so days of life in areas where prey is abundant may under most circumstances suffer little mortality in summer (Table 18). The higher mortality rates probably occur in utero, soon after parturition, or in winter. In areas where prey is unavailable, high mortality seems to occur in utero and/or in summer. The mortality rates calculated from Mech (submitted) in Table 19 indicate that the rate decreases as the pups get older. Van Ballenberghe and Mech (1975:57) found "that by early October most

of the underweight pups had already died, leaving only individuals in relatively good condition."

Clark (1971) found that the number of adults providing food to pups was probably important for pup survival. In one year, two females in the same pack had pups. Food was brought to the alpha-female's pups by their mother and five other pack members. The pups that were whelped and cared for by the subordinate female were not in as good condition as those of the alpha-female. Six wolves can and probably do, under normal conditions, provide more food to pups than one wolf.

Effects of human disturbance on pup survival

Pup mortality as a result of human disturbance has never been reported. The discussion that follows is concerned with potential factors that may affect survival. The most important factors are probably related to nutrition and selection of homesites. A minor factor may be accidental death when pups are moved between homesites.

Effects on nutrition

A serious potential effect of human disturbance is that disturbance could lead to malnutrition of pups, and if compounded by other factors, such as disease or parasitism, lead to the death of pups. Van Ballenberghe and Mech (1975) found that pups of low relative weight at summer's end were not recruited into the population

as yearlings. Neglect of litters during the first few days of life caused death in some neonate dogs (Fox 1963). Presumably neglect of wolf litters for any reason including human disturbance could lead to the death of young pups. Important factors are abandonment of pups, and disruption of normal feeding regimes because wolves left or lingered at homesites.

Human disturbance may increase the probability of pup abandonment (e.g. App. A, CH 1). Behavioral differences seemed to account for some of the susceptibility of wolf pups to temporary abandonment during homesite changes (see page 87; App. A, CH 1; Peterson 1974). Abandoned pups tended to be smaller than their siblings, perhaps because of competition for regurgitated meat. Seal et al. (1975) found that male pups had a significantly higher intake of protein than females in an area of reduced prey densities. Abandonment may reinforce such disparities in nutritional state. An argument can be made, however, that human disturbance would not be a significant factor in cases of this type because temporarily abandoned pups would tend to be the ones that would not survive anyway.

Human disturbance in some cases caused adults to leave homesites or conversely to linger near homesites. These responses could lead to malnutrition of pups by disrupting normal feeding patterns. There are several problems with this simplistic argument. Table 20 shows that arrivals of adults, usually followed by regurgitation of meat to pups, prior to and after incidents of human disturbance at the

Table 20. - Arrivals of adult wolves to homesites on the Hulahula River prior to and after incidents of human disturbance.

Date	Hours of Observa- tion 5 Days Prior	No. of Arrivals 5 Days Prior	Arrivals per Day	Hours of Observa- tion 5 Days After	No. of Arrivals 5 Days After	Arrivals per Day
6/26	115	12	2.5	100	15	3.6
7/06	114	14	3.0	71	10	3.4
7/08	100	11	2.6	92	15	3.9
7/16	120	19	3.8	120	21	4.2
7/20	120	22	4.4	120	21	4.2
ТОТА	LS 569	78	3.3	503	82	3.9
Date	Hours of Observa- tion 2 Days Prior	No. of Arrivals 2 Days Prior	Arrivals per Day	Hours of Observa- tion 2 Days After	No. of Arrivals 2 Days After	Arrivals per Day
Date 6/26	Observa- tion 2	Arrivals 2 Days	per	Observa- tion 2	Arrivals 2 Days	per
	Observa- tion 2 Days Prior	Arrivals 2 Days Prior	per Day	Observa- tion 2 Days After	Arrivals 2 Days After	per Day
6/26	Observa- tion 2 Days Prior	Arrivals 2 Days Prior 4	per Day 2.0	Observa- tion 2 Days After	Arrivals 2 Days After 8	per Day 6.0
6/26 7/06	Observa- tion 2 Days Prior 48	Arrivals 2 Days Prior 4	per Day 2.0 2.0	Observa- tion 2 Days After 32 28	Arrivals 2 Days After 8	per Day 6.0 6.0
6/26 7/06 7/08	Observa- tion 2 Days Prior 48 48 28	Arrivals 2 Days Prior 4 4	per Day 2.0 2.0 5.1	Observa- tion 2 Days After 32 28 20	Arrivals 2 Days After 8 7	per Day 6.0 6.0 3.6

homesites on the Hulahula River were not significantly different, using a t-test on paired observations. This can possibly be explained in several ways. First, Table 20 shows a trend toward more arrivals by adults after disturbance than before disturbance. The wolves arriving after a disturbance may be those who would have arrived anyway plus those who were disturbed and left the den. Differences in number of arrivals before versus after disturbance, in Table 20, were not significant, possibly because the latter incidents of disturbance were influenced by prior incidents of disturbance. Wolves leaving dens because of human presence may hunt; thus, disturbance may increase the amount of food brought to pups.

Second, in most cases only two or three of the eight pack members were present when the disturbance occurred. Thus, only a small percentage of the adults became aware of the disturbance. This may mask differences in arrival and departure patterns among individual wolves. One may argue that disruption of feeding regimes would be a serious factor for small packs. It has generally been found that one or more adults usually remain with the pups at all times (Murie 1944, Haber 1968, Clark 1971). Upon closer examination, it becomes evident that relatively large packs (greater than five adults) were involved in those studies. In the present study we accounted for the presence of one or more of three adults at the East Fork dens between 20 and 27 percent of the observation time; of one or more of at least three adults at the Echooka den 50 percent;

and of one or more of the eight adults using the Hulahula den 96 percent of the observation time. It appears that whether a pack can afford "babysitter" wolves is a function of pack size. Other data (Chapman, unpublished) indicated that at both the East Fork and Hulahula dens adults tended to arrive in the evening and depart in the morning, and that usually more adults were present at the den during the night than during the day. This is important since most hiking by humans occurs during the day and not at night. This factor, considered with the importance of pack size in whether an adult will be present, indicates that the probability that adult wolves will detect humans near their pups is low for small packs.

Third, if any significant differences in feeding regimes were reported as a response to human disturbance, one must then be sure that prey availability did not change significantly between periods before and after disturbance. When migratory prey such as caribou are involved, this could be the most significant influence on feeding regimes, regardless of human disturbance.

It is possible that frequent disturbances could lead to disruption of feeding regimes. Infrequent incidents of disturbance would probably not influence feeding regimes significantly and differences may be masked by other factors.

Effects on homesite selection

Earlier it was shown that for arctic and subarctic regions, where home range size is relatively large, the availability of prey

probably influenced den selection. Both Kuyt (1972) and Stephenson and Johnson (1973) found that wolf pups in areas devoid of caribou were considerably lighter than pups in areas where caribou were abundant. Kuyt (1972) found that litter sizes were smaller in areas without caribou, which indicated a higher mortality rate.

As noted earlier, centers of human activity may affect homesite selection. Also, there were several cases where wolves probably did not use dens, and others where wolves probably abandoned homesites, because of human disturbance. Abandonment of a homesite as a result of human disturbance may mean that prey will be less available to adult wolves, and consequently to pups, at the new homesite. There are a few problems with this argument. First, wolves that are prompted to move as a result of human disturbance may move to a homesite where prey are more available. In 1975 the pups at the Echooka den were moved over 16.0 km following human disturbance. In my estimation caribou were much more plentiful in the area they moved to than in the area near the whelping den. Second, Figure 23 shows the maximum and average distances pups were moved to homesites relative to the sizes of summer home ranges. I question whether the magnitude of these moves is sufficient to seriously alter the availability of prey.

Another factor is that human disturbance prior to or near parturition may cause females to whelp pups in physiographically marginal dens, thereby possibly lowering pup survival. As noted

earlier, pup mortality at such dens has not been reported.

Accidental death

In situations where wolves abandon homesites, adults under stress could possibly attempt to lead pups across rivers. It is important to note that in the case of drowning described by Clark (1971) the wolf that attempted to lead the pups across the river was not the mother of the pups, but was probably the alpha-female who was the mother of another litter. There may have been socially based pressures for her to amalgamate the two litters. In the case described by Murie (1944; App. A, CH 33a) it is not clear what influence human presence had on the pups entering the water. The probability that pups will die accidentally following human disturbance is undoubtedly low.

PART V. MANAGEMENT OF WOLF HOMESITES

Assessing the status of known dens

An important part of any management plan to protect denning wolves is to assess accurately the status of known wolf dens soon after pups are whelped. In Mount McKinley National Park the known dens have been periodically checked from the air in May and early June using Piper Supercub aircraft. Some of these dens were observed for several hours from the ground as a further check. Mistakes, however, have been made.

My experience has been that aerial checks are unreliable. In 1975 signs of activity were not observed at the Echooka den despite numerous passes made over the den on 22 May, and 2 and 27 June. A ground check on 29 June revealed that it was indeed being used by wolves. In 1976, on the other hand, low passes over the Echooka den on 28 May revealed a set of wolf tracks in the snow leading to the den. A ground check on 1 June revealed that it was not being used. Since wolves sometimes clean out several dens prior to whelping, wolf sign at a den may not be a good indicator of its activity status.

The most reliable means of determining the status of a wolf den is to observe it from the ground. The den should be observed continuously for at least 24 hours or until wolves are seen, since one often sees no activity for several hours at dens known to be active (especially when pups are young and/or the number of adults

in the pack is small). In 1976, three field assistants and I, in pairs, were flown to known den sites in the Brooks Range beginning in late May. Each site was observed for a 3 day period. The status of each den was usually accurately determined within the first 24 hours of observation.

If the objective of the management plan is to minimize human disturbance at wolf dens, careful checking of dens from the ground at distances of 0.8 km or more will probably avoid disturbance.

Sensory abilities of wolves

The ability of wolves to detect other animals is pertinent to a discussion of management of wolf homesites. Wolves are generally regarded as having excellent senses of vision, scent, and hearing. This section consolidates the available information on their sensory acuity.

<u>Vision</u>. The greatest distance reported at which wolves visually detected other animals is only 1.6 km (Table 21, part A). Wolves, however, can probably visually detect other animals at greater distances. Clark (1971) stressed the importance of movement in visual detection and identification of other animals. The following discussion of dog vision probably pertains as well to wolves:

In experiments in form perception dogs seem to be baffled when neither themselves nor the object is moving. Form perception improves when the object moves, and is still better when the dog is also moving....According to our human eyes, many animals appear to wear camouflage, so that they blend into a landscape, but we cannot be sure that dogs' eyes record, or fail to record, this same camouflage.

Table 21. - Reported cases in which wolves detected other animals at distances of 0.4 km or more.

No. of Wolves	Animal(Detecte	•	Source
A. DETEC	CTION BY VI		
1	1 human	1.6	Wayman (1967)
1	carib	ou 0.4	Haber (1968)
13	3 wolve	s 1.2	Jordan (1969)
1	1 carib	ou 0.8	Clark (1971)
3	56 carib	ou 0.8	Clark (1971)
1	25 carib	ou 0.8	Clark (1971)
1	10 carib	ou 0.9	Clark (1971)
	carib	ou 1.6	Clark (1971)
8	human	s 0.8	Peterson (1974)
3	4 wolve	s 1.3	Peterson (1974)
	human	s 1.6	Peterson (pers. comm.)
1	1 deer	0.6	Mech (pers. comm.)
1	sheep	0.8	Present Study (1976)
1	1 human	1.0	Present Study (1976)
1	1 human	1.0	Present Study (1976)
1	1 human	1.2	Present Study (1976)
2	1 human	1.3	Present Study (1976)
1	3 human	s 1.3	Present Study (1976)
6	5 carib	ou 1.6	Present Study (1976)
B. DETE	CTION BY SO	ENT	
10	2 moose	0.4	Mech (1966)
10	2 moose	0.4	Mech (1966)
11	2 moose	0.4	Mech (1966)
16	2 moose	>0.4	Mech (1966)
10	3 moose	0.6	Mech (1966)
8	l deer	0.4	Mech (1970)
5	5-6 sheep	0.5	Present Study (1976)

Studies of the lens in the dogs' eye indicate that the point of focus is at a point just in front of the retina. This would indicate that the picture conveyed to the brain will be out of focus, and therefore less sharp than would be the case in human vision. By comparison to man a dog has little capacity to focus its eyes. It may not need so sharp a picture; movement is a more important factor. [Dangerfield et al. 1971:428]

Hearing. For wolves the importance of hearing in detection of other animals is not known. The following discussion of hearing in dogs is probably pertinent to wolves:

It is generally believed that dogs can hear sounds from a much greater distance than human beings. Experiments have been conducted both in the laboratory and in the field. Dogs and their owners were tested at varying distances when hunting horns were used. The dogs would alert to a blast from the horn when their owners could not hear it, even though the owner was deliberately listening for the sound and the dog was not....

The ability of dogs to locate sound is superior to that of man. The dog cocks his ears, then may turn his head to face the origin of the sound....When dogs are placed in the centre of a circle and then tested with sounds coming from various points in the perimeter, they can locate the source within five degrees. This may be because the sound waves reach the two ears at different times....
[Dangerfield et al. 1971:229-230]

Scenting. In forest regions scenting is probably the most common and important method of detecting prey (Mech 1970, Peterson 1974). The greatest distance reported at which wolves scented other animals is only 0.6 km (Table 21, part B).

General. The greatest distance reported at which wolves detected other animals is 2.4 km (Mech 1966), though method of detection was unknown and the incident was in part interpreted from tracks. The greatest distance at which wolves were reported to detect humans near a homesite, visually or by scent, was less

than 1.5 km (Stephenson and Ahgook 1975).

For animals to be scented they must usually be upwind of wolves. Vision and hearing are effective over a wider area. Wolves can probably identify an animal more accurately by scent than by vision (Banfield 1954, Pruitt 1965, Kelsall 1968). Hearing is probably unreliable for identifying animals except when characteristic vocalizations or other sounds are involved, such as the clicking of caribou hooves. Information from two or more senses may result in more rapid identification of an animal.

Wolves do not always detect animals within sensing range. I have observed several instances where wolves failed to detect humans, and also a grizzly bear, within 0.4 km. Mech (1966) found that 29 of 85 groups of moose went undetected despite the fact that some were within 150 m. Many animals are simply discovered by chance at extremely close range (Mech 1970, personal observations). Topography, cover, weather conditions, and the behavior of both wolves and other animals influence the probability of an animal being detected by wolves.

Closed areas

As noted earlier, the mere presence of humans seems to be sufficient to disturb wolves at homesites. Also noted was the fact that wolves are limited in their ability to detect humans, and that distance from the pups of both the humans and adult wolves plays a major role in how wolves react. This suggests that human use of

areas near wolf homesites should be restricted during the denning period to avoid disturbance.

Wolves may prepare dens as much as 4-5 weeks prior to whelping. Disturbance of den areas at this time may greatly influence den selection since pregnant females can move to another location. This argues for limiting human use of areas near established dens approximately 4-5 weeks prior to whelping. In Mount McKinley National Park it would seem wise to establish closed areas by 1 April around dens traditionally active. Most closed areas around active wolf dens in Mount McKinley National Park should remain closed until 1 August unless circumstances dictate that they be opened at earlier or later dates. Effective management of closed areas through summer will be difficult because duration of occupancy of secondary homesites is quite variable, and their prospective location is unpredictable. If it proves possible to implement closed areas around secondary homesites, the area should remain closed for as long as pups are at the site. No closed areas need be established after 1 October because wolves will no longer be using homesites.

There are five factors which are important in determining the size of closed areas around wolf downs. First, wolves have not been reported to detect other animals or humans by vision or by scent beyond 1.6 km. Second, most reported movements of pups following human disturbance have been from 1.6 to 3.2 km from the disturbance. Third, in most cases howling by wolves in response to human presence near pups occurred when the humans were within 1.4 km of pups.

Fourth, wolves 0.8 km or more from their pups usually have not altered their behavior significantly upon detecting humans similar distances from pups. Finally, wolves have regularly denned within 2.4 km of established centers of human activity in Mount McKinley National Park and in other regions.

Based on these considerations, it would be unlikely for wolves to become disturbed if human activity were excluded within a 2.4 km radius of active dens. I consider this to be a minimum "safe" distance in tundra regions. A circle with this radius circumscribes an 18.1 km ² area. In forest regions where visibility is restricted smaller closed areas may be adequate to protect active wolf dens. Conclusions reached by Stephenson (1974:25), based on his knowledge and that of the Nunamiut Eskimos, are pertinent to this discussion and are quoted here:

...for wolves that are generally shy of humans, such as those around Anaktuvuk, human presence...more than about two miles from the den for a limited period of time does not cause any significant alteration in the behavior of wolves....At distances less than this, prolonged presence may cause abandonment of the den...

The guidelines discussed for the protection of whelping dens can be followed for secondary homesites. As discussed above, the duration of occupancy is variable and somesites short, and movements between homesites can be substantial. In some cases secondary homesites may be used in non-consecutive years or in 2 or more consecutive years. It is usually very difficult, however, to predict where wolves will move. In cases where the first move from the whelping den is 2.4 km or less, the closed area around the whelping

den may offer some protection.

If everyone was to observe the boundaries of a closed area, an area of the recommended size would be sufficient to protect wolves at homesites. Unfortunately, there are individuals who will attempt to photograph or observe wolves regardless of closed areas. The policy at Mount McKinley National Park is not to publicize the exact locations of wolf homesites. A vigilant observer, however, should be able to locate most dens in open country within a few days even if he remains outside a radius of 2.4 km. One solution to this problem is to make the closed areas asymmetrical by extending the boundaries to include larger areas that offer good hiking routes and exceptionally good visibility such as gravel bars and ridges. This would make it more difficult for a person to locate a den in a closed area. Another solution which is replete with public relations problems is to leave the reason for the closed areas unannounced. These precautions would probably not be necessary in forest regions since visibility is restricted.

Is an area of approximately 18 km² manageable? In Mount McKinley National Park, closed areas around active wolf dens are currently based on backcountry-unit boundaries. Six dens active since 1974 were located in temporary closed areas ranging between 72 and 99 km² in area. These closed areas are approximately four to five times the minimum size recommended in this report (Figure 27). The current closed areas are also of irregular shape, and therefore do not pinpoint dens. Since the boundaries of the backcountry-units

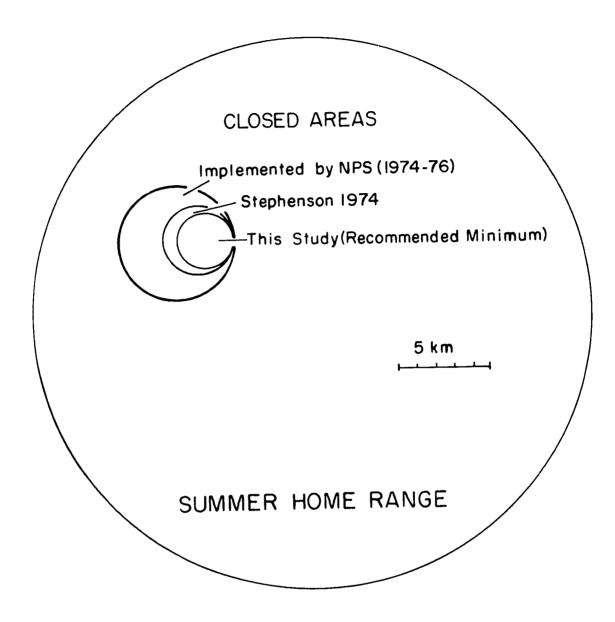


Figure 27. Sizes of recommended minimum closed areas relative to the average size of summer home range of wolf packs in Mount McKinley National Park. Size of home range is based on distance between active dens (see Table 2).

are usually ridge-tops or rivers, and since overnight users of these units are assigned an area on a permit basis, such visitors can easily be directed away from backcountry-units containing active wolf dens. Special signs are posted to deter day-hikers from entering active den areas (Figure 28). It is difficult, however, to prevent some day-hikers from inadvertently entering closed areas. The closed areas around wolf homesites established under current policies in Mount McKinley National Park appear to be manageable and are of a size more than sufficient to protect denning wolves. A closed area 21 km² in size is successfully managed to protect grizzly bears in the Park, but human access to the area is permanently restricted. It is not known if temporary closed areas of approximately 18 km² in size will prove manageable.

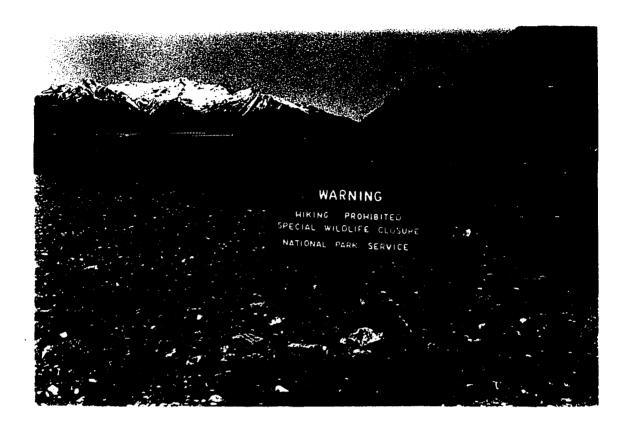


Figure 28. Special sign erected near a major hiking route in Mount McKinley National Park to deter day-hikers from entering a wolf den area.

SUMMARY AND CONCLUSIONS

Wolves reacted in several ways upon detecting humans near their pups. The most characteristic behaviors were barking and howling, leaving the area, or abandoning the homesite. Severity of the disturbance seemed to be the most critical factor influencing abandonment of homesites. As another response, wolves abandoned pups. This was noted, however, in only one of 51 cases, and appeared to be a result of the behavior of the abandoned pups.

Pup mortality as a result of human disturbance has not been reported. In fact, mortality of pups older than about 3 weeks was rare during summer under most circumstances. The most important mortality factor with respect to survival of pups was malnutrition.

Abandonment of pups could lead to decreased nutritional intake. One could argue that abandoned pups would be the least likely to survive anyway, since they tend to be less aggressive and smaller than their siblings.

Human disturbance could disrupt the feeding regime of pups by causing adult wolves to leave or linger near the homesite. Such an effect of disturbance has not been documented. Infrequent disturbances would probably have a negligible effect on feeding regimes.

Following human disturbance, wolves may abandon homesites and move pups to a new homesite 3 km distant on the average. It was shown that homesite selection was probably related to prey availability in arctic and subarctic regions where home ranges were

large, and prey migratory or clumped. Movements from these selected sites as a result of human disturbance could change prey availability. Wolves sometimes moved their pups closer to prey or other food sources. It is not known whether the magnitude of the moves associated with human disturbance is sufficient to seriously alter prey availability.

A minor factor was that some pups could perish from accidental causes such as drowning when moved between homesites.

Evidence indicated that wolf dens within 1.0 km of established centers of human activity were usually permanently abandoned by wolves. Wolf dens within 2.4 km of roads or campgrounds, however, were frequently used by wolves in Mount McKinley National Park and in other areas. Again, this human influence on homesite selection could possibly affect the nutritional plane of pups. It is not known whether the differences in location are significant with respect to prey availability between permanently abandoned dens and dens that are frequently used by wolves.

Some biologists have noted that wolves avoid areas of human activity. Human presence was shown in some cases to affect the chasing, killing, and utilization of prey. The presence of artificial sources of food such as garbage dumps, however, usually attracted wolves, and in some cases wolves selected homesites near garbage dumps. Avoidance of areas of human activity did not seem to exist where artificial sources of food were present or where substantial innocuous human activity occurred.

The conclusion drawn from these observations was that human disturbance of wolves at levels characteristic of National Parks probably does not have a significant impact on survival of wolf pups, nor does it seriously affect the ecological relationships between wolves and their prey.

The seriousness of human disturbance, however, is ultimately a human judgement and, as such, any alteration of the normal activities of wolves in summer may be judged by some to be undesirable. The management plan developed in this study was based on sensory abilities of wolves, distances (adults to humans, adults to pups, humans to pups) at which wolves reacted to human presence, distances pups were moved following human disturbance, and distances from human activity centers that wolves normally denned. The conclusion drawn was that restricting human activity within a 2.4 km radius of homesites is a sufficient minimum to adequately protect wolves. The recommended minimum size of closed areas around active wolf homesites is four to five times smaller than those currently implemented by the management staff at Mount McKinley National Park.

APPENDICES

The appendices consist of material edited from field notes, personal communications, and edited, direct quotes from the literature. Refer to "Study Areas" and Methods and Materials" for photographs and schematic maps of the den areas observed in the present study. The section "Secondary homesites" contains photographs and descriptions of the rendezvous sites that were observed. Times for this study, Ritchie (pers. comm.), and Tracy (pers. comm.) are reported in Alaska Standard Time.

APPENDIX A. - Case histories of human disturbance at wolf homesites.

App. A, Case History 1 (Present study 1975)

27 June. Pilot Audi and I made two low passes over the Echooka den in a Piper Supercub aircraft. We flew down river and landed on the gravel bar approximately 6.4 km from the den. As I emerged from the plane, I spotted a white wolf moving on the bluff above the river about 0.8 km to the south. It looked at us and after about 15 sec trotted off to the west. We unloaded the plane, took off, and made three passes at about 60 m over the area where we suspected the wolf had gone. We located it on the third pass and then made an extremely low pass (less than 20 m) over the wolf. Remains of a caribou were nearby. The wolf was sitting with muzzle raised looking toward the plane as we flew by. I had no way of determining whether it vocalized. We flew to the gravel bar and landed.

On 29 June the den was observed from 1314 to 1700 hr. A white wolf (probably the same individual seen on 27 June) was seen near the den. She headed down river on a hunt but apparently caught Sinnott's scent. Sinnott at this time was approximately 0.4 km from the den; I was 0.8 km from the den. She investigated but did not approach closer than about 150 m from Sinnott. Sinnott remained motionless and partially hidden behind a ridge across the river. As the wolf continued under the bluff where I was observing, I stood and saw her running slowly away. She ran about 0.3 km, stopped, turned, and looked toward me, then trotted rapidly away. She did not vocalize at any time. She had dark lactation marks along her abdomen.

The next day (30 June) we set out to observe the wolves at this den continuously until they left. We arrived at 0950 and for the next 182 hours and 53 min we continuously observed the area. Between 1130 and 1230 on 30 June we set up our dark blue observation tent approximately 0.4 km from the den and about 45 m above it. Activities outside the tent were minimized and were usually performed when no adult wolves were in the vicinity of the den.

When we arrived on 30 June we immediately saw the white female wolf (the Bomb). Shortly, we spotted a gray female (Teenangel). Upon the arrival of Teenangel several pups popped out of the den. Bomb left the area around 1100 and came upon our trail. investigated for about 10 min but continued down river. a large, dark gray male (Big-Daddy) approached Teenangel. Teenangel cowered. The five pups begged for food by nipping and pawing at Big-Daddy's muzzle. He obliged by regurgitating a fist-sized chunk of meat which one pup grabbed and ran off with. At 1425, after hassling with the pups, Big-Daddy walked to the gravel bar and lay down. Teenangel was still near the den with the pups. At 1434 Big-Daddy began walking, then loping, up river, and was out of view below the ridge by 1441. At 1450 Big-Daddy began barking and howling at us from perhaps 100-200 m. Teenangel, upon hearing the first howl, stood and appeared not to know what was happening. The pups had immediately run back to the den and were out of sight. The last bark-howl was heard at 1453. Big-Daddy was neither seen nor heard from again. At 1500 Teenangel walked onto the gravel bar directly toward us and was soon lost to view. The pups played and explored the area near the den off and on throughout the remainder of the day.

At 2311 on 30 June Teenangel appeared near the creek approximately 300 m west of the den heading away from the den. She was hunting small prey: microtines, birds, etc. A grizzly bear was also spotted approximately 1.5 km west of the den. These two animals saw each other at 2333. They chased one another for several minutes. Teenangel finally trotted back to the den (see Appendix F, Case History 5). At 0038 on 1 July she left the area apparently to hunt and headed toward the lake south of the den. Teenangel arrived back at the den at 0357. All five pups greeted her, and she regurgitated twice.

Teenangel went off on another hunt at 0403 toward the creek northwest of the den. Four of the pups followed her to the creek. Teenangel lay in the willows along the creek, and at 0417 she nabbed a duck and began trotting back toward the den with the duck

between her jaws. (We were unable to identify the duck to species.) She stopped once to look in the direction of the four pups near her. She apparently was not sure whether to bring the duck to these four pups or to bring it back to the den. She arrived at the den and dropped the duck for the fifth pup who wagged its tail vigorously and began chewing the duck. Teenangel picked it up again and dropped it. The pup this time carried it off in its jaws. Teenangel remained where she had last dropped the duck and appeared to lick the ground. The pup cached the duck behind a willow and ran back to Teenangel. Teenangel then trotted in the direction of the duck but the pup dashed back to ITS bird. The other pups soon ran back to the den.

At 0425 Teenangel went back to the same spot along the creek. Between 0425 and 0429 I observed her shaking several times to rid her fur of water. It appeared that she was waiting on the bank prior to jumping in to get the ducks. This time she was unsuccessful. Teenangel finally headed up the creek, hunting. All five pups were near the den playing with the duck. Teenangel arrived back at the den at 0550, but at 0607 she headed southwest on a hunt and was lost to view. We again saw her at 1127 trotting toward the den. She arrived at 1135. At 1315 she headed off to the northwest, apparently to hunt again. She was last seen at 1342. Teenangel returned at 1743 and regurgitated to the pups. At approximately 2121 she headed west to the creek and then proceeded to the lake south of the den, hunting, and was constantly in view. At 0012 on 2 July Teenangel began to trot toward the den. She arrived at 0017 and regurgitated to the pups. She soon trotted to the creek west of the den. All five pups followed her to the creek but they eventually returned to the den. Teenangel returned to the den at 0218, but she did not regurgitate. She immediately went to the creek again to hunt. She arrived at the den at 0310 and regurgitated. By 0315 Teenangel was at the creek again and was lost to view. At 0502 the Bomb approached the den from the north. She regurgitated for the pups and allowed them to

nurse. A raven flew low over the six wolves, and the Bomb ran about 10-15 m apparently chasing after the raven. The run was a bouncy sort of run as though she wanted to jump and grab the raven. The pups again begged for food, and she regurgitated a second time at 0504.

At 1125 Teenangel appeared near the den. Both female wolves were near the den at this time. At 1300 Sinnott left the tent; and as he did so the Bomb stood, looked toward us, and perked her ears. She may have caught a glimpse of Sinnott, but I was not positive. At 1305 the Bomb walked east onto the gravel bar, frequently looking our I lost sight of her as she went below the ridge at 1311. Teenangel was resting behind a patch of willows near the den. At 1458 Teenangel became active and played with the pups. Then she rested for the next 3 hours. At 1758 the Bomb was seen southwest of the creek approaching the den. She arrived at the den in a few minutes. Teenangel was also active around the den at this time. Just before the Bomb was spotted I had left the tent to get some water. I came back to the tent; and as I reached the entrance Teenangel looked toward us, then the Bomb did also. Both wolves stood, Teenangel first. Both Sinnott and I believed that I was out of sight behind the tent before the wolves looked our way. Perhaps Teenangel saw me out of the corner of her eye.

For the next several minutes the two females led the pups northwest away from the den. At 1839 the Bomb and Teenangel and at least two pups were last seen 1.6 km northwest of the den.

Teenangel appeared to initiate the move and was consistently 2 or 3 m ahead of the Bomb. Both females frequently looked in our direction while leading the pups. They frequently stopped, turned around and waited for the pups to catch up. This is in contrast to the typical behavior at other times when they would snarl and/or snap at the pups and trot rapidly from them after they regurgitated for the pups. Perhaps two of the pups thought that this was again going to be the case for at 2226 two pups were seen wrestling 5 m north of the den.

An important point is that earlier, following the arrival of an adult,

one or two of the pups would often remain near the den while siblings continued to chase after and food beg from the adult. Perhaps the two pups that were abandoned and the two that were not as aggressive were the same individuals. For the next 118 hours 7 min these two pups remained alone at the den.

Figure 29 shows that the pups began to howl approximately 29 hours after they were abandoned, probably as a result of their abandonment. The number of howls heard each day after abandonment increased until the fifth day. Incidents of play decreased during this period:

Day	1	13	incidents
Day	2	12	incidents
Day	3	3	incidents
Day	4	3	incidents
Day	. 5	2	incidents

We could not hear howls during periods of high wind, hard rain, or when we had our camp stove on. Also, play may have occurred when the pups were out of view. Despite these drawbacks, I believe the trends are realistic.

We could, however, often see the pups howling, and it appeared that howling was correlated with a lack of wind and/or an abundance of mosquitos. When mosquitos were bad we often observed the pups walking into or through small dwarf birch bushes. The high density of stems probably helped knock the bugs off. The pups would also paw their faces and sometimes rub their heads on the ground to rid themselves of bugs.

On 7 July at 2033 Teenangel was seen at the den. She began looking for the pups by sniffing the ground and trotting rapidly. She found them at 2043, 200 m from the den. To say the least, the two pups were exuberant. Teenangel did not regurgitate for the pups. After several minutes of trying to avoid the pups she began walking slowly toward the creek west of the den. The two pups by this time were less excited but continued to stay close by her. Teenangel

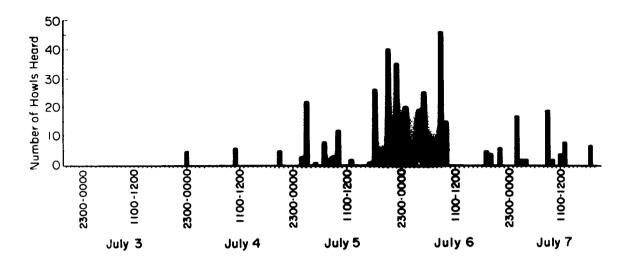


Figure 29. Number of pup howls heard during period of abandonment at the Echooka den in 1975.

frequently stopped and looked back at the pups. At 2059 the three entered the willows of the creek and were lost to view. Several pup howls were heard over the next couple of hours. At 0043 (8 July) the last howl was heard. It seemed to come from a considerable distance down the Echooka River. A ground check of the den a few hours later revealed that there were no wolves present.

App. A, Case History 2 (Present study 1976, Hulahula River)

CH 2a (Ritchie pers. comm.)

[1 June] "1830 hr - Climbed knoll north of Hulahula [lake] to watch wolves with Reilly. Two were sleeping in front of a mound below the hillside. A third wolf was approaching from the north. It stopped, pounced and fed on something small.

"1845 hr - The third wolf stopped about 100 m away and rested.

1900 hr - Reilly got restless and howled. The two nearest wolves perked up and stretched. A fourth wolf came around the mound into view. The first three wolves approached rapidly, then a fifth wolf came from behind the mound. The first three, with rapid gaits, approached our observation knoll. Reilly and I crept over the knoll to the east side and came head on into the first three wolves. They saw us, hesitated, and burst south between our two camps. One returned to the 'den', the remaining two kept a steady pace to the river. With some hesitation they crossed. They were playful but continued moving up a large fork of the Hulahula River.

"1930 hr - When the first wolf returned to the den the two there were very ecstatic and playful, although they received no attention from the returning wolf. Both were wagging their tails, bounding about, but only one approached to muzzle distance. The returning wolf went out of sight behind a large rock. The other two lay down on the hillside. No other activity was observed and we left at 2200 hr."

[We arrived in the area on 4 June and found the den on 5 June near where Ritchie's observation occurred.]

CH 2b (Present study)

On 26 June at 0449 I walked from the river toward the disturbance tent located approximately 1.0 km from the den. Pearl (the mother) watched from near the den and moved so as to get a clear view of my actions. Pearl lay down at 0454. At 0458 I arrived at the tent and proceeded to take it down. Pearl began to bark and howl and did so until I started to return to the river (about 2 min). Pearl then rested for 1.7 hours. Since the wolves had reoccupied the whelping den, Ray and I decided to take down the tent located about 1.3 km from the den used to observe the first rendezvous site, and put it up on the knoll to observe the den. Cathy had been observing from this tent. At 1107 Pearl watched us from the den area and she began walking north from the den. She lay down about 500 m above and north of the den. Cathy remained where the tent had been, and observed. Pearl continued to look toward Cathy. At 1137 Ray and I arrived at the observation knoll and put the tent up. Pearl then stood, walked about 25 m, sat, howled once, then trotted north stopping to look at Cathy who was plainly visible on the tundra. Another wolf that had been at the den also trotted north but did not pay attention to any of us. At 1155 both Pearl and the other wolf met each other. They continued north walking and trotting, and frequently looking toward Cathy. Both wolves were out of sight approximately 1.8 km from the den at 1324.

CH 2c (Present study)

On 6 July I had approached the den to take pictures of Pearl and another wolf from atop a small knoll. At 1253 Pearl left the den area and traveled north. I soon left the top of the knoll and walked south. At 1313 as I went behind a ridge approximately 1.0 km from the den, and was no longer visible to any wolves, a gray wolf began to bark and howl harshly many times during the next 8 min. I did not see this wolf but was able to determine that it was howling from a creek approximately 500 m from the den and approximately 600 m from my location. Pearl was approximately 1.6 km from the den when

the howling started. She apparently did not hear the howls as her behavior did not change. The wolf that I had taken pictures of trotted to the howling and barking wolf, and also howled a few times. Both wolves trotted around and seemed nervous and frequently looked toward the ridge I had gone behind. At approximately 1335 one wolf was out of sight, and the other frequently looked around, sat, lay down, stood, and walked around. At 1400 this wolf left the den area to the southeast apparently to hunt.

CH 2d (Present study)

On 8 July I approached the knoll near the den to photograph the wolves. Unbeknownst to me two wolves had walked south from the den. At 1414 Cathy saw a gray wolf running to the south. It stopped, trotted 5 m further south, sat, and began to harshly bark and howl at me. Both wolves were approximately 100 m, and I about 200 m, from the den. I was approximately 250 m from the two adults. I immediately turned and walked south directly away from the wolves. Both wolves vocalized and moved further south until 1424. Both wolves lay down approximately 400 m from the den and watched me as I walked from the area. One wolf was lost to view at 1429. At 1440, when I was approximately 1.4 km from the den, I turned and walked west. This caused one wolf to bark and howl again several times during the next 5 min. This wolf then left the area to the southeast apparently to hunt. No other wolves were seen near the den for the remainder of the day.

CH 2e (Present study)

On 16 July a hiker had been on a small ridge near the second rendezvous site for most of the day attempting to photograph the wolves. Pearl and four other adults were with the pups. At 1504 the wolves sensed the person's presence approximately 100 m from them. Pearl investigated briefly. The hiker left the area to the west at 1506. At 1535 Pearl barked and howled over a 7 min period while looking to the northwest. The other four adults appeared to pay her no attention. While Pearl was vocalizing I was walking on the tundra

in full view of the wolves approximately 1.6 km northwest of the wolves. It is possible that I was a visual stimulus to Pearl who had already detected human presence (probably by scent) near her pups. At 1650 the four adults walked from the rendezvous site apparently to hunt. Pearl howled again at 1555 and at 1600. Pearl then lay down with her head up and looked around constantly during the next 1.75 hours. At 1745 Pearl stood, walked, trotted, and loped away from the den in the trail of the other four adults.

CH 2f (Present study)

On 20 July I approached the rendezvous site to photograph Pearl, three gray wolves, and the pups. I was slightly above the wolves and approximately 125 m from them. At 1819 one gray stood and oriented toward me. Immediately the other two grays and Pearl stood and also oriented toward me. The three grays left the area rapidly (fast walking and trotting), frequently looking toward me. Pearl left with these three but she stopped approximately 100 m from the pups, lay down, and watched the entire area. One pup had run out from the rock as the wolves left. It appeared confused and returned to the rock. Pearl eventually walked back toward the rock, interacted with the pups a short while, walked around, and lay down, but continued to be observant until 2045. I left the area around 1840. No vocalizations were heard. The wind direction was variable and wind velocity varied between 0 and 8 kmph. My interpretation of this incident is that the first wolf detected my presence and the other three wolves reacted to that wolf. Pearl did not bark or howl and only watched the area probably because she was not quite sure what was happening.

CH 2g (Present study)

On 27 July at 1410 Ray left the observation tent to observe Pearl and the pups located about 600 m from him. As Ray walked around the tent, Pearl began barking and howling while lying on her belly and elbows. All four pups trotted 0.7 km uphill toward the rock at the rendezvous site and arrived there at 1425. Ray entered

the tent at 1415, but Pearl did not stop howling until 1425. Pearl then stood and walked approximately 75 m further from the pups, turned and walked behind a small ridge. Pearl was again seen at 1512 walking and trotting from the rendezvous site apparently to hunt.

CH 2h (Present study)

The pups were moved 2.4 km on 31 July to another rendezvous site. While hiking in the area on 2 August, in an effort to find the pups, Cathy and I inadvertently disturbed the pups and two adults. Ray was observing from a location high above the wolves. Αt 1545 Ray saw one gray wolf leading the pups east approximately 500-600 m from Cathy and I. Five minutes earlier Cathy and I had spotted another adult with a full belly returning to the rendezvous site. This wolf saw us and as it continued it frequently stopped to briefly watch us. It crossed the river and came back toward us. As it turned out this wolf met the wolf with the pups at 1609. At 1555 the wolf with the pups ran east, sat and howled, barked twice, then barked and howled. Cathy and I were not aware of this since we were near the river and were unable to hear these vocalizations. When Cathy and I stopped walking (approximately 0.4 km from the pups), this adult ran back toward the pups, looked at us, then trotted 25 m east and sat watching us. The pups were not paying any attention to this wolf. At 1600 this wolf trotted west, sat, and howled. At 1601 the pups began walking west. adult trotted east, sat, and howled. The pups not knowing we were near them continued to walk and play as they approached us. The pups approached as close as 100 m then eventually went back toward the adults who were no longer visible. We soon left the area. Due to bad weather we were not able to check this site again until 8 August. No wolves were seen.

App. A, Case History 3 (Dean pers. comm.)

CH 3a

Between 1945 and 2030 hour on 27 July, 1957, Fred Dean and Harry Merriam watched a wolf den on Moose Creek from a distance of approximately 500 m. An adult male(?) wolf watched them from a distance of about 250 m. This wolf was also located about 500 m from the den. Other wolves howled from near the den.

СН 3ъ

The next day at 0600 they briefly searched for and found the den. They saw one pup leave the den; Merriam was within 25 m of this animal which saw him. An adult (possibly the same one seen the previous day) barked at the intruders from a ridge to the northeast about 400 m from the den. (These pups had been seen on the creek bar several days earlier by a small group of hikers who did not find the den. Dean did not know how long this other group had spent in the area or the details of their encounter. This incident occurred in Mount McKinley National Park.)

App. A, Case History 4 (Johnson pers. comm.)

"On September 15, 1972, Bill Ruth and I were moose hunting about one mile into the Yanert Valley [near Mount McKinley, Alaska]. It was 8:00 A.M., snowing lightly and the temperature was around 28°[F]. We had been watching for moose from a high knoll along Dennis Kogl's sled trail for about an hour when Bill saw the wolves.

"There were twelve wolves: eleven tawny and one black. The black wolf appeared to us the obvious leader. There also seemed to be at least five pups. From our high vantage point we observed the pack quite well for about thirty minutes. Their activities included chasing snowshoe hares, resting and play.

"After a time, the black wolf gathered the others and the pack began to move up the valley. On previous occasions Bill and I had howled at wolves and had them answer back. So we decided to try this again before the pack was out of sight. Though our efforts left much to be desired, they certainly had an effect on the wolves.

"The entire pack stopped immediately and for several seconds

stood listening then they all surrounded the black wolf, as if asking what should be done. This lasted perhaps a minute, but soon a decision was reached and the whole pack came racing up the hill towards us. Bill grabbed his camera and we both looked for a place to hide and watch from. We were too slow, as we started for a clump of dense spruce, wolves began to emerge all around us. Some were as close as thirty feet. Having seen us, the wolves immediately vanished. They answered our howls for another half hour but never approached closer than a quarter mile."

App. A, Case History 5 (Johnson pers. comm.)

"On August 25, 1974, I was moose hunting on the lower slopes of Carlo Mountain, about one mile Southeast of Deniki Lakes [near Mount McKinley, Alaska]. It was a very windy, overcast evening and the temperature was about $40^{\circ}[F]$.

"I had been watching a small valley for about thirty minutes, but as it was beginning to get dark, I started to leave. I noticed something off to my side about 60 yards away...Closer observation showed a large tawny wolf sitting on top of a boulder. The wolf was looking intently at something below me so I elected to stalk closer and got to within thirty or forty yards. I concealed myself under a large spruce and observed the wolf for about twenty minutes.

During that time, it kept looking intently below and finally I noticed two black wolves also lying down about seventy yards below me. I watched for several minutes through binoculars and they all appeared to be adults.

"It was getting darker and I finally decided to make something happen. I took a deep breath and howled to the best of my ability. Their reactions were immediate. The tawny wolf leapt to its feet, stared intently in my direction for a moment and then vanished. The two black wolves also quickly disappeared.

"I howled again and this time at least a dozen voices answered from the undergrowth all around me. We all howled for two or three

minutes and then all at once the wolves stopped. I continued but got no response.

"I got up to look around and at that same moment, five coal black wolf pups came bouncing out of the brush directly at me. I froze and the pups seemed puzzled. They started to run off and then returned, two approaching to within twenty feet. After a moment, apprehension overcame curiosity and they left. As I left, darkness descended and the wolves continued to howl as I made my way back to the car a mile away."

App. A, Case History 6 (Peterson pers. comm.)

"This summer [1975, in Isle Royale National Park] we approached a wolf den in a wooded area, and stopped one-quarter mile from the den in a gusty cross-wind that was blowing perpendicular to the line from us to the wolves. The wolves did detect us, had a group howl, then only two adults came directly to us. They left after determining exactly where we were by smell through the thick undergrowth, without ever seeing us."

App. A, Case History 7 (Ritchie pers. comm.)

[Kongakut River, northeastern Alaska. 27 June 1976. 2145-2155.]
"I was on a high ridge-like bank with lots of wolf sign, bedding spots (sandy areas), south of the creek. Then as if arranged a large gray wolf loped away from me along the willow bar on the Kongakut.

After 0.8 km it stopped and circled back out of view west into the creek I had just come from. I think it was possibly a female - looked like she had distended teats."

[This occurred near the den that two field assistants observed in early June, and that I observed in late June-early July and in late July.]

App. A, Case History 8 (Tracy pers. comm.)

[On 1 September 1972, Tracy, Peterson, and Mako, a large male

Husky, were in Mount McKinley National Park camped on the west side of the Sanctuary River with the camp mostly hidden by brush.]

"At 0600 a dark, tawny (brown) adult wolf appeared out of the brush only 10 m from camp. It stood and stared several seconds, then ran down the bar to the south. In the next 1.5 hr two black adults were observed. One appeared from the north about 100 m above our camp on a hillside. It looked at the camp, moved away another 100 m then continued at a walk-trot to the south along the side of Double Mountain....Between 0700 and 0900 wolves were heard howling to the south several times. At 0900 we climbed the side of Double Mountain to the southwest of our camp. At 0930 we observed the wolf pack in an open grassy meadow surrounded by willow brush. When the animals were lying they could not be seen. We approached to a patch of willows about 400 m from the pack and observed them from there until about 1300. Fourteen wolves were present, including at least 8 pups and at least 5 adults. The dark tawny seen earlier in the day was not present....Between 0930 to 1300 the wolves slept most of the time. A couple of pups played together for about 10 min. Once the light tawny got up from under a bush where he had been resting and walked into the clearing - several pups greeted the adult wagging and begging. Another time several animals sat up and howled together. Between 1200-1300 all the animals were lying and not visible. At 1300 we slowly made our way from bush to bush right down to the edge of the clearing. We all huddled behind one willow and watched. One black adult was lying only 5-7 m from our position. lay there, raising its head occasionally for two hours, then got up, walked around a little and lay down again further away. We watched until about 1700. The animals mostly slept, getting up frequently to defecate and occasionally to walk around a bit. Two pups got up and played together several times. During the afternoon two of the black adults and one pup spotted us at separate times when they were walking around. The pup entered the brush and reappeared at the far edge of the clearing late in the afternoon. One adult trotted into

the brush and was not seen again. The other adult stared at us 2-3 minutes and then trotted up the side of Double Mountain and was lost from view and not seen again. The light tawny adult, although not obviously taking note of us, did wander into the brush at the far side of the clearing and was not seen again. No warning sounds were made. Around 1700 several of the wolves became restless and wandered around the clearing as if ready to move on. Quite suddenly all the wolves were aware of our presence so we stood up in view and began taking pictures. The two remaining adults looked for a few seconds and then ran up the side of Double Mountain, sat on a knoll about 500 m away and howled to the pups. The pups continued to sit, stand, and stare, approach, and back off. After 15 minutes all the pups, singly and in pairs had followed the adults. My dog, Mako, was with me the entire time, and although he was excited he was on a leash and kept still and quiet."

[Tracy's camp was about 1.6 km from the rendezvous site.]

App A., Case History 9 (Bailey 1930:136-137)

- "...One found by Stevenson and Black, on the rough slope near Hellroaring Creek on March 26 [1916], was watched for some days in an effort to shoot the old wolves, which finally became suspicious and carried the pups away to another location farther up the side of the mountain.
- "...On April 14 this family of wolves was located about a mile from the first den in a natural cave among some loose rocks. Back about eight feet from the entrance of the cave seven wolf pups, estimated to be three weeks old, were secured....The old wolves were very shy and kept well out of sight while the den was being watched, but were frequently heard howling and answering each other from different points, and the old male was several times seen guarding the den from a point high above..."

App. A, Case History 10

CH 10a (Carbyn 1974b:58)

"On 10 June, 1970, three men on horseback rode to a den site to take photographs. The wolves left the den site."

[The wolves moved to a rendezvous site 2.2 km away.]

CH 10b (Carbyn 1974b:56)

"...On another occasion, 25 July [1970], an adult and three pups became alarmed when they were suddenly confronted by the observer at about 800 ft (250 m) in a recently occupied rendezvous site. The adult jumped a number of times on its hind legs, much in the same fashion as a circus dog, presumably to get a better view. Both the adults and the pups then disappeared into cover, but the pack did not abandon the rendezvous site."

App. A, Case History 11 (Carbyn 1974b:58)

"On 8 June, 1971, two riders inadvertently rode through a denning area. This was followed by a desertion of the den."

[The wolves moved to a rendezvous site 1.8 km away.]

App. A, Case History 12

CH 12a (Carbyn 1974b:58)

"On 31 May, 1972, I observed the wolves for 10 hours from a distance of about 150 paces. Throughout this interval the wolves at the den showed no alarm towards the observer; however, a wolf returning to the den fled immediately upon encountering the human. At about 1800 hrs the alpha male moved to the den entrance, called the pups, and left the area with the pups at its heels. The wolves were subsequently (4 June) encountered at a rendezvous site [1.8 km away]."

CH 12b (Carbyn 1974b:56, 58)

"...A particularly detailed observation of the reaction of wolves to a large group of riders was made on 1 August, 1972 when people were riding along the edge of a rendezvous site. One pup fled for cover while one adult and two pups watched intently but remained

hidden until the riders had passed. The disturbance lasted three minutes. Shortly afterwards two riders passed through the area and were conspicuous by their loud whistling. These riders had passed within about 0.25 miles (0.4 km) and the adult wolf moved into cover towards the intruders, presumably to investigate. After eight minutes the adult returned to the pups."

[This site was not abandoned.]

App. A, Case History 13 (Carbyn 1974b:58-59)

"On 15 June, 1973, two observers watched the wolves for 12 hours at 150 paces from the whelping den. Only once did the wolves show any alarm. At 1424 hrs two wolves were lying 50 paces from the observers, watching them intently. At 1428 hrs the adult bitch, a nursing female, therefore presumably the alpha female left, travelling in a direction away from the den where the pups were located. The second wolf continued to watch, fixing its eyes for two minutes on the observers. It then gave several low guttural 'woof' calls and wagged its tail from side to side. This could clearly be interpreted as a combination alarm/threat gesture. The wolf then left in the same direction as the bitch. Subsequently, both the pups and a third adult were almost continually in sight and there were no signs of alarm. The bitch returned at 1643 hrs. A continuous sequence of howls (approximately 60 in total) was heard at a distance from the den. This howling aroused the wolves located at the den. The significance of this howling was difficult to interpret although several possible explanations can be offered. At 2031 hrs the nursing bitch appeared at the den entrance, gave several 'whimpers' and drew the pups out of the den. The bitch then led the pups away much in the same fashion as was observed the year before when the alpha male led the pups away. Wolves were not seen, subsequently, at the whelping den in that season."

App. A, Case History 14 (Cowan 1947;155)

[Banff National Park.]

"Mr. Page dug out this den in the last week of June and found four black pups in it. Two of these were destroyed, one eluded capture, and one was held captive until July 10, on which date we tagged and released it at the den site. The female and remaining cub were seen on the day we released the captive and there is little doubt that the family was successfully reunited."

App. A, Case History 15 (Cowan 1947:154-155)

"...About June 7, 1945, Frank Wells found a den...on Buffalo Prairie, Jasper Park. The young, apparently four in number, were active but still in the den. When the area was again visited, on June 15, the pups had left the den and were found to be hidden among the huge boulders of an adjacent rock-slide....Two were seen on this date and two others heard whining deeper in the slide."

App. A, Case History 16 (Crisler 1958:224)

[Three men at den. One crawled in and removed the pups.] "Two wolves, the parents no doubt, bounded around crying."

App. A, Case History 17 (Garceau 1960:459-460)

[August 3.]

"...During our examination of the area, I saw a dark grey wolf standing about 50 yards from me on a grass flat adjacent to a timbered point, Lensink joined me and as he did so the wolf saw us and took several steps away from the edge of the timber. Another wolf, smaller and lighter colored, came from behind the timbered point. It saw us almost immediately and rose on its hind legs momentarily to get a better look before bounding back around the point from where it had come. It was followed by the first wolf seen....Since we were unsuccessful in our attempts to locate a den we referred to the location as the 'rearing area'....20 days later...Presumably the

wolves had not returned as a result of our previous disturbance."

App. A, Case History 18 (Garceau 1960:460-461)

"On May 18, 1959,....At approximately 4:30 p.m. I arrived in the arm below where the two wolves were seen the year before by Lensink and myself [100-200 m from the den]. Here I kneeled behind an old tree that had fallen outward from the timber onto the grass flats.... I had not had the binoculars to my eyes for more than a minute before I heard, and then saw to my left, five grey wolves running across the mud flats toward me. I stood up, shouted, and waved my arm and the leading wolf stopped for a moment just below the slight slope at the edge of the grass flat. Two wolves passed about 15 yards to my left and the wolf farthest behind continued toward me. A fifth wolf behind and to the left of the lead wolf stopped. The lead wolf started up the slope toward me...

"...At the time I was wearing hip boots and a green, knee-length rain parka complete with hood. The wolves, lying around the den, undoubtedly saw me kneeling beside the downed tree and mistook me for an animal such as a black bear....I returned to the boat for about an hour....In my absence the three remaining wolves had reunited and they howled during the time I took measurements of the two dead wolves....The first wolf killed was a one year old male....The second wolf killed was a female. Superficial examination of her uterus indicated that she had recently given birth to seven pups.

"On the afternoon of the following day I returned with Graham, located the den, and found five male and two female pups...

"...I believe that the pups we found on 19 May, 1959, were born in April."

App. A, Case History 19

CH 19a (Haber 1968:104-109)

"An unusual incident at the Savage den on June 7, 1967 may further illustrate the tendency of adults, particularly the dominant male, to

display alarm or 'concern' in the face of a threat to the young....I decided to seek a better vantage point from some large rocks on the ridge crest, approximately 400 yards east of the den and slightly above it...

"...At 9:20 AM the parent black male either spotted me or detected my scent, and began looking intently in my direction as I remained crouched close to the ground. Immediately, with what seemed to be 'calm concern,' he began a steady, deliberate trot toward my position, and kept coming - with no apparent fear or hesitation - until 10 to 20 feet away. As he approached I knelt with the movie camera, filming the activity. When he arrived at my position (10 to 20 feet away), he stood quietly, looking at me directly in the eyes and periodically glancing back toward the den. When out of film I raised my head (still kneeling) and began to talk to him in a normal tone of voice. He continued watching me - silently - with the characteristic impersonal attentiveness of the wolf, as I talked. At no time did he display any hint of a threat...

"After three or four minutes of this he urinated once, retreated about 10 to 20 feet, and lay down broadside to me, facing mostly back toward the den. At this point the parent tan female also began trotting toward me from the den; however, she seemed to be more shy than the parent black, as she only approached to within 50 feet, and then retreated and sat down 100 to 200 feet away. I began talking again, in a normal tone of voice, but this seemed to disturb neither of the two wolves. After about 10 more minutes of this both began walking calmly back to the den, without turning to look back at me. When they arrived at the den they summoned the two dark pups (the other was apparently sleeping inside the den) and led them to a point along the ridge approximately 200 to 300 yards west of the den. Here both parents lay down and watched the pups (but not me) as the latter romped about the area playing and hunting mice. Within about 15 minutes, as the pups continued to play, both adults had lowered their heads on outstretched paws and appeared to be sleeping. Meanwhile,

and throughout all of the activity thus far, the other five adults and one pup continued to sleep soundly at the den. At this point I was left with the impression that the parent black had investigated not knowing initially whether I was a threat or a potential meal. Upon 'checking me out' from close range he seemed to determine that I was neither.

"At 10:30 AM the largest black (dominant wolf of the pack) awoke and with tail upraised and displaying obvious excitement, proceeded to run to and arouse each of the other six adults. Very quickly all then assembled around him and with tails wagging and excitement apparently building, engaged in the nose-push ceremony with him for about one minute. At this point I began to look for a moose or caribou in the area, as it appeared the wolves were about to set out on a hunt. When instead all seven adults and the tawny-brown pup, with the largest black in the lead, began running at top speed toward me, I became somewhat apprehensive. The largest black was obviously very riled, as his hackle and tail were raised and at about 200 feet away and still running I could hear his disturbing growls and low gruff barks. As he led the others his eyes never left me, while I remained crouched behind the camera. At about 100 feet the pup and six adults following the largest black fanned out and formed a semicircle on my west side, where most stood but some sat - all silently watching both me and the largest black male. The largest black, still barking, growling, and displaying a generally aggressive attitude, continued toward me. When at about 50 feet he hesitated briefly and then proceeded around me (never taking his eyes from me) until gaining a snow patch on a knoll approximately 50 feet away on my east side. Here, as the others silently held their positions on the opposite side, he began running back and forth on the snow patch, growling, barking, howling, and several times urinating. By this time, since I was in some doubt as to the intentions of the wolves and wanted to insure that they recognized me as something other than an ordinary prey animal, I had stood up

and began yelling and waving my arms. Although this action failed to stimulate any obvious fear in them, it nevertheless became apparent that they were now more confused than belligerent; one of the smaller tan females even began to wag her tail. After another two or three minutes of this the largest black - still barking at me - ran back around to the others and led them off at a run toward the den. Here the tawny-brown pup appeared to enter the den with the other two, and the seven adults ran a few hundred yards further to the west, stopped, and proceeded to howl in unison for about five minutes.

"At this point I departed to an area of thick willows approximately one half mile north of the den and continued watching. At about 11:AM, one-by-one, the wolves began walking back to the den. In a short while most had returned and had lain down, although they continued looking toward the east where I had been. Apparently they regained complete composure, as normal routines were resumed for the balance of this day and the next two, at which time all departed to an unknown location."

CH 19b (Haber 1968:53-54)

"...On July 5 the smallest male of the pack, a black, howled at a companion and I for 25 minutes from a hill a few hundred yards away, obviously disturbed at our presence...[At Savage den which was disturbed then vacated in early June]...on August 19 all seven adults and three pups were observed within two miles of the den site."

[A rendezvous site may have been close to the den.]

App. A, Case History 20

CH 20a (Haber 1968:84-85)

"...On July 12, 8:15 PM four adults and three pups were present at the Surprise Pass den, but it is possible that other adults normally with this family may have been off hunting elsewhere at the time. Only three pups...were observed in the two and one quarter hours K. Smith and I spent watching the site. Shortly after we arrived the adults spotted us and three ran up onto and then over a

nearby ridge and disappeared. The fourth, a large black and white male, remained nearby for the entire two hours, howling and barking at us. At first, even after the adults had run off, the pups were unconcerned at our presence, and two of them, a black and the tan, continued playing a few yards from the den. A short time later, however, apparently responding to a series of barks and howls from the black and white male, the two entered the den. A few minutes later the third pup, a black, which had been further away from the den in a patch of willows, also ran to the den. For the next two hours all three remained inside. Although the pups appeared able to run well at this time, no attempt was made by them to follow the adults; and, judging from the actions of the black and white male, it appeared that the adults encouraged the pups to remain in the den rather than follow."

CH 20b (Haber 1968:92-93)

"...We observed him to display the same type of behavior on August 29, 1967, north of Wolfpup Flats along Stony Creek. Very fresh tracks nearby indicated that pups as well as other adults were present in an area of thick willows, and when we began searching the area the black and white male proceeded to run up onto a high hill only a few hundred yards away - putting himself plainly in view - where he then sat down and barked and howled at us until we left. His vocalization was of an extremely excited nature, almost exactly as it was in the July 12 observation....After he had carried on in this manner for about 15 minutes we heard another wolf howl twice from the opposite side of the river (a few hundred yards away), possibly in the area...[where]...the other adults and pups...[were]..."

App. A, Case History 21 (Haber 1968;110)

"...A wolf hunter from Fairbanks describes a similar incident where after he and his partner had taken wolf pups from a den along the north boundary of McKinley Park, several adults followed them at close range for several miles. On the first evening in camp with the

captured pups, the adults remained nearby and during the night when the former managed to escape from a makeshift cage, the adults led them off. Tracks showed that the adults had ventured right up to the cage and apparently encouraged and/or aided the pups in their attempt to break free."

App. A, Case History 22 (Harper 1956:52)

[June 12.]

"...The dens were about 18 feet apart, at the edge of a spruce thicket; one of them extended beneath a thick snowbank....The entrances had been blocked up by Charles on the previous day, and there was no evidence of attempts on the part of the parent Wolves to dig out the problematical cubs..."

App. A, Case History 23 (Joslin 1966:27)

[May 19.]

"...That same evening gruff wolf howls...were heard from the west side of Omemei Lake. This wolf responded from Omemei Lake on numerous nights, sometimes in the company of a second wolf, and then was heard no more. I had disturbed the area around Omemei Lake on several occasions, and thus was not surprised that the wolf moved.... Two dens were also found in the Omemei Lake area, neither of which appeared to have been used, though both had been freshly dug."

App. A, Case History 24 (Joslin 1966:22)

"On May 30 Mr. George B. Kolenosky, a research biologist with the Department of Lands and Forests, and I examined the Source Lake den and found it occupied by wolves. We caused no disturbance, other than perhaps our scent. We returned the following day and removed five pups, tagged them and put them back. The pups were approximately two weeks old. By the next day the den had been abandoned,"

[The pups were moved approximately 2.4 km.]

App. A, Case History 25 (Joslin 1966:49)

"On one occasion my assistant and I were approached to within 12 feet by two wolves, one of which whimpered and growled. We were sitting in a beached canoe, and had spent most of the night howling back and forth with the wolves at the lower Raven Lake rendezvous when the incident occurred. They trotted back and forth to either end of the canoe, and peered out at us over the surrounding leather-leaf bushes. The early morning mist was rising off the lake, and drawing with it the air away from the shore, thus our scent could not be detected. One of the wolves whimpered perhaps a dozen times, pausing only when it stopped to observe. Twice it growled softly. At one point it walked out two or three feet from shore and waved its head around, sniffing the air, presumably attempting to detect our scent. They gradually lost interest, and after approximately twenty minutes they left."

App. A, Case History 26 (Joslin 1966:53)

"The following narrative records the circumstances in which I was 'challenged.' The incident happened to me on the night of June 13, while I was howling back and forth with the Fools Lake pack which was a few hundred yards away. From the direction of the pack I heard a single wolf come trotting noisely towards me through the underbrush. It came to within about a hundred feet and commenced to bark and growl. For a time it moved back and forth over a space of about 20 feet. As mentioned above, its barking had a definite pattern. It consisted of two, occasionally one, sharp barks followed by a more drawn-out bark which ended in a series of softer, lower pitched barks....It was repeated 37 times over a period of 27 minutes. Following each series of barks there was a pause of approximately 50 seconds. Frequent growling occurred during this pause. By the time the wolf had stopped I had moved away about 150 yards through the forest."

App. A, Case History 27 (Joslin 1966:18-19)

"On the afternoon of August 5, while attempting to make tape-recordings of the pups in the upper Owl Lake group, I came so close to them that I forced them to move off one of their beds. The main activity area, if there was one, was probably very close, but since I did not wish to disturb the pups further I retreated. The pack responded several times that evening in the vicinity of the site, but then was never heard from again. It is possible that my intrusion had caused them to move."

App. A, Case History 28 (Kelsall 1960:69-70)

"...The first den was found...by Thomas on June 8, 1957. While he was watching a male wolf at a distance of about 200 yards, suspecting that there was a den in the vicinity, a female wolf rushed past him at a close range and went about 100 yards before stopping. On the following day the field crew went back to the den. Both wolves watched from a distance of 150-300 yards during the two hours the men were in the vicinity....The pups were very young and none had its eyes open. They were about 12 inches long from nose to tip of tail and were fat and chubby. There were three male pups and one female, judged to be three to four days old."

App. A, Case History 29 (Kelsall 1960:70)

"A second den was located on June 12, 1957,...At 3:15 in the afternoon a white wolf was noted loping along carrying a chunk of meat. It disappeared in the vicinity of a sand-gravel dune where the den was found later in the day. The field men returned to the den site on June 14 and discovered that the pups had been moved. The original site was on a low hill in a dry river bottom where the den consisted of four shallow holes 2 1/2 feet deep dug into the sand....On looking around the men saw four wolves sitting on a hillside and nearby a den with a mound of freshly-dug earth. A fifth wolf suddenly appeared out of the den, and there the men

found three pups in a shallow hole about two feet by two feet, dug into the side of a sandy gravel hill. The pups were still very young and had their eyes closed..."

App. A, Case History 30 (Mech and Frenzel 1971:22)

"On April 17, a den west of Big Moose Lake known to have been used at least intermittently for 13 years was seen from the air to have fresh activity of some kind in the snow in front of it, and on April 24 we saw a wolf at the mound. A few days later, two local human residents unaware of our interests approached this den and looked in. An adult wolf, presumably the bitch, leaped over their heads and fled the area. The men dug up the den and removed six pups whose eyes had not yet opened."

App. A, Case History 31

CH 31a (Murie 1944:19-20)

"... August 14, near the head of Savage River.... I first had a glimpse of the head of an adult black wolf on the edge of an extensive growth of willows bordering the bar. After watching me a few moments the animal disappeared, but by climbing a slope, I obtained a view of it running off, a half mile away. ...about 3 hours later...I heard low growling in the willows just ahead of me. I knew it was a wolf or grizzly, but in either case I did not wish to disturb it, so I backed away cautiously, moved slowly toward a ridge nearby, and then climbed a short distance up the slope. Down river I heard a wolf howl, and a little later from the slope where I was screened by willows I saw a black wolf running. A half mile away it stopped to bark so I was sure the pups were near me. Presently a black pup passed an opening in the willows near the place where I had heard the growling and a short distance away on the bar other pups were discovered feeding on the remains of a large bull caribou....Later another black adult joined the first one. Both barked, sometimes a series of barks, terminating in a long howl. The parents moved up a knoll across the narrow valley and watched. At 5 p.m. I departed, without disturbing the pups, which for 3 hours had been oblivious of my presence about 200 yards from them."

CH 31b (Murie 1944:20-21)

[August 15, near the head of Savage River.]

"The following day I hiked the 9 miles up the bar in hopes of getting moving pictures. Carefully I made my way to where I had watched the pups feeding on the caribou and arrived there at about 10:30 a.m. After watching a half hour I saw a black wolf galloping down a tributary on the other side of the valley. It was coming toward a knoll on which I saw another black wolf. The latter was lying about 30 feet above a narrow bar covered with willows 7 or 8 feet tall. After lying there for 15 minutes, frequently looking around, it moved out of sight. Soon the wolves howled in chorus.

"I waited until 1:30 p.m. hoping the wolves would return to the carcass. At that time rapidly moving heavy clouds were rising above the horizon so I decided to approach the wolves for a picture before the sun disappeared. As I neared the mouth of the side stream where I had seen them a pup scurried across the gravel from one clump of willows to another. Two other pups scurried across openings. Continuing slowly through the willow-covered bar, I saw two adults and two pups running away in the distance. For a better view I climbed the knoll where the wolf had been lying. I continued climbing and presently saw the two adults returning toward me at a gallop. One was a large gray animal. They barked at me, then moved down to where the pups had been. Later I saw two black adults galloping downstream a half mile below me. The pups had dispersed; one of them I heard howling later 2 miles downstream."

App. A, Case History 32

CH 32a (Murie 1944:22-23)

[May 15, at East Fork den.]

"When I approached this den the black male wolf was resting 70

yards away. He ran off about a quarter of a mile or less and howled and barked at intervals. As I stood 4 yards from the entrance, the female furtively pushed her head out of the burrow, then withdrew it, but in a moment came out with a rush, galloped most of the way down the slope, and stopped to bark at me. Then she galloped toward the male hidden in a ravine, and both parents howled and barked until I left.

"From the den I heard the soft whimpering of the pups. It seemed I had already intruded too far, enough to cause the wolves to move. As I could not make matters much worse, I wriggled into the burrow...

"After my intrusion it seemed certain that the family would move, so the following morning I walked toward the den to take up their trail before the snow melted. But from a distance I saw the black male curled up on the point 15 yards from the entrance, so it was apparent that they had not moved away after all. In fact, they remained at the den until the young were old enough to move off with the adults at the normal time."

CH 32b (Murie 1961:286)

"On June 5, 1940, at 5:45 p.m., I saw the black-mantled male as I was going towards the den lookout. He was lying on a knoll, howling, a mile from the den. To avoid disturbing the wolves, I retraced my steps. For five minutes after I reached the road the wolf continued howling at short intervals, and then he trotted briskly toward Sable Mountain."

CH 32c (Murie 1944:34-35)

"...July 9....The gray female and both black wolves were with the pups and saw me when I came in view around the point on which the den is located. They sat on their haunches watching me approach. There had been no chance to make a stalk so I continued forward, hoping that the wolves would stay close enough to the pups to permit me to take some pictures. After watching me advance for about 200 yards the three adults ran up the long open slope, stopping at intervals

to bark and howl. The black male, after angling up the slope, galloped along the hill in my direction, keeping his elevation above me and frequently stopping to bark. I continued forward and passed the three wolves which were now barking at me from directly up the slope. The gray female joined the black male, but the black female moved higher up. When I was almost opposite and within about a quarter of a mile of the pups (they had taken refuge in a burrow 10 feet long and open at both ends) the black male galloped down the slope to the bar, followed closely by the gray female. came out on my trail and headed directly into the wind toward me at a gallop. The female took the lead and with noses to the ground they came on at a rapid, brisk trot. I set up the movie camera and saw them in the finder, running silently and swiftly. Their purposefulness and intent manner worried me some, and I began to wonder if they would turn aside. They were accustomed to seeing people, so lacked the timidity of most wolves. I wondered if the two grays and the other black might not join the two coming toward me....By that time the wolves were about 100 yards away and, circling to one side, they commenced to bark. The female passed me and the male remained on the other side. Both continued howling and barking, about 200 yards away. After exposing my film I walked down the bar. The female remained opposite the pups, howling at intervals, and the male kept abreast of me for a half mile as I went down the bar to camp. The black female remained on the slope, howling. When I returned to the spot an hour and a half later with more film, the wolves had all departed. The pups were not seen again until August 22, when they were found about 5 miles away..."

CH 32d (Murie 1944:36-37)

[August 23, on the flat below Polychrome Pass.]

"...with two companions. ...seven adults in the band.

"We stalked the wolves, coming first to the large gray one on the bench. He rose 50 yards or so ahead of us and loped away toward the others on the flat and aroused them. They ran off from in front of us, all headed southward, I hurried over the flat to get a picture of a black pup which was standing uncertainly watching the others run. While I was photographing the pup the mantled male got up behind me a short distance and ran close past me between me and my companions. He must have been sound asleep to be aroused so tardily. Five of the adults and some of the pups stopped on a knoll about a mile away. The parents hung back, barking at us, probably solicitous over some of the pups which had been left some distance behind. When I walked toward them they barked and howled and those on the knoll howled in the usual mournful chorus. Soon the parents hurried to join the others. The pups in the rear must have caught up with the band by this time..."

CH 32e (Murie 1944:38-39)

"The wolf family was seen at Polychrome Pass on September 22, 23, and 24. But on September 28 it had moved to a point on Teklanika River 20 miles away.

"My attention was first attracted by the yellow pup which disappeared in a fringe of trees. Later I heard the howling of several wolves and saw the yellow pup trot in the direction of the sound and join the four black pups. Soon they all galloped out of sight. I advanced cautiously and came upon the five pups, their parents, and grandpa, 140 yards from me. I exposed some motion-picture film, then dropped out of view to change film. I was thus occupied they all howled and there was considerable barking which resembled the yapping of coyotes. When I again peered over the rise all but the black male were moving away with much tail wagging and milling around. The black male saw me and trotted after the others, and all disappeared around the base of a low ridge. On my way back to the road I met the other four adults heading toward the spot where the wolves had howled. Apparently they had heard the noise too. The mantled male was quite surprised when he saw me 150 yards away and made several high jumps with head turned toward me. They all stopped to watch me, then slowly trotted on around

the ridge after the others. This was about 9:30 a.m.; at 3 p.m. I found all the wolves resting near the base of a long slope about a mile away. They saw me approach in the distance and moved up the slope a short way from where they watched me. The following day I saw the band 4 miles to the north but I was unable to stalk them."

App. A, Case History 33

CH 33a (Murie 1944:39-40)

"On June 30 two hikers saw the black female coming up East Fork River followed by a pup which, in crossing the river, was carried downstream some distance and treated a little roughly by the fast water. The hikers were able to run it down and catch it by the tail. They said that the mother barked at them from a point about 150 yards away. When they released the pup the mother continued up the river toward the den occupied by the gray female."

CH 33b (Murie 1944:40-41)

"On the morning of July 9 I approached the wolf den with a companion and managed, without being discovered, to gain a clump of willows on the bank 100 yards south of the den and at about the same elevation. The black female was later seen a few yards above the den. I do not know that she was aware of our presence, but she trotted to the den and nimbly entered one of the three burrows. A little later a black pup emerged from some brush and waddled up to a burrow. In the afternoon the large gray mate of the black female came trotting down the den knoll. He sniffed at a pup, which then followed him. A moment after arriving at the burrows he suddenly became alert and looked intently toward us. Apparently he had heard the motion picture camera. He took a step forward and stood with muscles tense, peering searchingly at us. Then he loped up the slope out of view above us. The pups continued to move about near the den, unaware of any danger. The male soon appeared on the bar below us, about 200 yards away, and for several minutes howled and barked. While he howled at us the very tip of his tail twitched back and forth, as it does on a cat when it is waiting to pounce on a mouse. When he retreated we walked up the bar toward the rendezvous where we had seen the other pair with their pups. The male we had disturbed went ahead of us to this pair and as we neared them they all ran up the slope and out of sight. Several pups were seen and we found two of them in a clump of willows and spent some time trying to approach them for pictures, but they finally moved off and kept a respectable distance between us."

CH 33c (Murie 1944:41-42)

"On July 12 the pups of both families were together among the willows at the rendezvous. We approached slowly, taking advantage of the scattered willow clumps along the way. When about 75 yards from the willow clump where we knew the pups to be, we saw the head of the black male near the willows. After looking in our direction he put his head down but raised it again almost at once. A second time he seemed assured but his uneasiness persisted and again he looked at us. I started my motion picture camera. He stood up to look and listen, then trotted diagonally toward us, examining us intently as he trotted nearer. Then he became certain of what we were and galloped out on the bar and began to howl and bark. gray male was approaching in the distance, carrying what appeared to be a ground squirrel. A little later we failed to see the gray male but he no doubt was not far off. We frightened a number of pups from a clump of willows in which they had well-beaten trails and many beds in the tall grass. They disappeared in the brush along the bank, all except one which ran out on the bar toward the black male. During the hour or so that we were at the rendezvous, the black male howled and barked. He followed us up the bar when we searched for the pups.

"In spite of our intrusions the two wolf families remained at the rendezvous..."

CH 33d (Murie 1944:42)

"...On July 31 a companion and I, with much crawling, managed

to gain a gully adjacent to the flat where the wolves rested and played. We watched for some time from the creek which was bordered by tall willow brush. At about 1 p.m...the gray female appeared on the creek bank 25 feet away, passed behind some willows, and reappeared 15 feet away. She then saw us and bounded away. All the wolves were alarmed and 3 adults and 10 pups scattered over the bar. The general retreat was southward, but the pups crisscrossed so much that the bar seemed covered with wolves.

"The following day the two families were again at the rendezvous, and 4 days later when the study was terminated and I left the park the wolves were still there."

App. A, Case History 34 (Parmelee 1964:7-9)

[Late September, Ellesmere Island.]

"It was during our third trip to the musk-ox carcass that I chose to go after the male wolf which, unlike its mate, was reluctant to come to us....Moments later, we stood looking at four wolf pups! All four bounded off clumsily, following in the tracks of the father wolf, who was attempting to lead them away...

"After a mile-hard chase, one lagged behind, surely tiring. It suddenly turned and lunged at my leg but bit the steel of my shotgun instead. With two broken teeth and a new spurt of energy off it raced again, I in hot pursuit...

"The male wolf leading but two pups now had greatly outdistanced us... .They were seen no more.

"Pursuit of my wolf pup continued unabated. Up and down one slope after another it went until its undulating flight ran out atop a broad ridge. And just when I had the pup at bay the she-wolf appeared. She was running hard for us, her tongue flashing black as she came.

"...The big wolf skidded to a full stop and whined pitifully.

Ambling around the pup and me, she whimpered and emitted strange ululations. There were no fierce snarls - not even one good growl.

"With a burst of hidden energy the wolfling raced off with its mother, but the ensuing chase proved a short one...

"...The she-wolf lost spirit, too, the moment I grasped her youngster. With three great jumps she cleared the gully wall and stood above us. Slowly she raised her head skyward and howled - low melancholy howls more chilling than the polar air. Then she was gone...

"The lively weight of two wolf pups was more than we could manage, so we left one with the mother wolf who had just returned to the gully. She examined her young carefully and accepted it...

"...Thus we started off on the long trek back to camp in the twilight...

"By the time we were half way to camp it was pitch dark, I was hungry and sore and not thinking about much of anything else when Stu discreetly told me to glance backwards. Following close in my footsteps was the big she-wolf, her nose touching the ptarmigans as they swayed back and forth. Incredible as it surely is, we several times had to drive that wolf off with snowballs for fear that we would lose our specimens!

"The wolf followed us right into camp....According to Stu the next morning, the mother wolf had remained just outside the tent most of the night."

App. A, Case History 35 (Peters 1974:37-38)

[August 22.]

"0700. Pup appears on far end of ridge, about 40 m away. Stands broadside to us, lowers head, stares at me and Mech...Disappears over edge of ridge, and about a minute later another pup appears at the same place where the first one appeared...We got occasional glimpses of both pups for about 15 minutes, then an adult...appears where we first saw the pups. Adult lowers head, stares at us for about 5 seconds. Pups appear in front of adult, thrust noses at corners of its mouth. The adult stands briefly, then steps away from

pups towards us, takes a couple of steps in our direction, staring with head lowered almost to ground. Adult then moves just over the edge of the ridge, walks quickly in a tight circle, drops down behind Pups play on slope, chasing each other from rock to rock, occasionally competing for position atop largest boulders. One approached to within 10 m tail down, ears up, the other staying about 15 m away. Camera noises startle them, they walk away, looking back frequently, and soon they wander off down the slope....This adult was probably highly fatigued, since it went behind the log, presumably to sleep, in our presence. Even in great fatigue the adult allowed a rudimentary greeting ceremony, which probably assured it that the pups were all right. Pups were both curious and fearful, but did not leave, either because of attachment to the rendezvous site or to the adult, or both. They may have been willing to approach us because of the presence of the adult, or because they had not yet learned to fear strange stimuli. The adult examined us carefully before dropping behind the log -- could this wolf have realized that if we hadn't hurt the pups already, we probably weren't going to?"

App. A, Case History 36 (Peters 1974:188-189)

"During August of 1972, I visited the Jackpine pack's rendezvous site almost every night for two weeks, accompanying Fred Harrington, who was recording howls...

"On one occasion, we were able to determine, on the basis of howls, tracks, and a sighting, that an adult approached the rendezvous site from one direction, made a large loop around us, and then approached the rendezvous site from the other side. We heard no howls during his detour..."

App A, Case History 37 (Rutter and Pimlott 1968:69-72)

"On September 13 I decided to walk in to the rendezvous to see if I could see any of the wolves. I left the highway at 3:15 and

went around the end of Eos Lake....It was a fine, sunny day...

"About three hundred yards from the end of the lake I was crossing a grassy opening and trying to identify several trails which seemed to lead down to the creek when a movement ahead caught my eye, and I looked up to see an adult wolf standing on a moss-covered mound of rock only a hundred feet away.... There were two pups, one on each side, less than one-third the size of the adult.... They were jumping up towards the adult's mouth as though expecting food. None of them seemed to be paying any attention to me, but the old wolf knew I was there, all right, and about fifteen seconds after I had seen them the pups vanished down the other side of the rock, although I saw or heard no kind of warning. The adult stood there for nearly a half minute after the pups left, looking about very casually but never directly at me, then it also disappeared. My interpretation was that the pups had been playing around the rock when the adult became aware of my approach and came to send them away. It was the movement when it came out on the rock that caught my eye.

"I walked ahead to the rock where the wolves had been and looked around...

"I went on to where the creek goes down through a small canyon into the valley and sat down to wait for something to turn up. I had been there only a few minutes when another adult wolf, somewhat smaller and darker than the first, appeared on the other side of the creek, loping along in my direction as though heading for the place where the other wolves had been seen. I sat quite still, but at about fifty yards it saw me, stopped and stared intently for several seconds, then bounded away up the slope to the east and out of sight. It appeared to see rather than smell me, but it was downwind and may have got both sensations at the same time. I wandered around a bit more but saw no further signs of life, but the next night, September 14, the wolves answered our howls from the same spot, so they were not much alarmed by my intrusion."

App. A, Case History 38 (Seton 1937:273)

"...I had trailed the wolf about a mile when, suddenly, the dog began to growl and show signs of uneasiness, and at this I began to look closely for the wolf, and suddenly I came upon the den. It was situated in a rough pile of rocks, facing south.

"It was now about noon. I stood there quietly for a moment, and then, to my great surprise, the old wolf came out of the den. She had not seen me yet, and not being over 15 feet from her, I killed her with a shot....The male, hearing the shot, jumped up about 50 yards away, but the ground was so rough that I got only one shot at him. We worked all the afternoon at the den, but did not get to the pups; but the next day we went back and got 5 young ones."

App. A, Case History 39 (Seton 1937:309)

"In the northern Cattle ranges, the young are born while yet there is snow on the ground, and it has proved quite easy to back-track the old Wolves, discover the den, destroy the brood, and later the old ones, for they continue to hover about till shot..."

App. A, Case History 40 (Seton 1937:342)

"Thomas Simpson (1843, p. 275-76) while exploring the Arctic coast east of the Copper-mine, on July 25, 1838, encountered wolves at the mouth of a small stream near Hepburn Island, and thus refers to the incident: 'The banks of this river seemed quite a nest of wolves; and we pursued two females, followed by half a score of well-grown young. The mothers scampered up the highest rocks where they called loudly to their offspring; and the latter, unable to save themselves by flight, baffled our search by hiding themselves among the willows which fringe the stream. The leader of the whole gang - a huge, ferocious old fellow - stood his ground, and was shot by McKay.' "

App. A, Case History 41 (Stanwell-Fletcher 1942:143, 146-147)

[At a rendezvous site located approximately 0.4 km from their cabin, Stanwell-Fletcher was able to observe members of a pack of 10-12 wolves at extremely close range (in some cases as close as 5 m) every morning for 3 weeks while keeping absolutely still in a skiff. Most of his observations were of wolves attempting to catch fish.]

- "...The wolf eventually saw my skiff, 30 feet away and, after a moment of statue-like stillness, he loped slowly and gracefully off, across the river into the willows, where he apparently stopped...
- "...The skiff was moving at the moment, and the wolf saw it at once. For a second he stood still, then lowered his head eight inches, while the hairs on his shoulders rose stiffly. A moment later he loped away...
- "...On the fourth morning...then at the sound of the movie camera [the wolf] stopped dead still. Again the head lowered and the ruff stood stiff. The camera stopped, and what was to become a frequent game began: the single movement of a cramped finger would send the wolf away...

"It was a moment later that she saw me or heard the camera, and for a long time we watched each other. Her beautiful golden eyes widened. The only other touches of color in the coal black body were her white and gray whiskers and muzzle. Long minutes passed, then she turned slowly, forded the river, stood where the bait had been, and once more looked at me.

"...The third one was a young male, well fed and strong. His belly bulged uncomfortably, and he moved slowly, though with an air of abandon. Approaching to within 30 feet of the camera, he saw the boat and stopped, leapt back a dozen yards, and then sat down to watch. After a few minutes he came on again, head lowered, ears pricked forward. Once more he sat down and for a few minutes peered this way and that, with head low, then high, staring at the boat with great interest. Then I said 'Hello!' The young wolf bounded into

the air. For a while he played hide-and-seek with me, in and out of the willows, once interrupting the game for a good long scratch. Then he vanished into the bushes and began to circle the boat. Three times his head showed out of the willows at different places. Later, I thought I saw the same pup twice. On the last occasion I was almost chagrined at his complete disregard of my presence...

"I believe that most of the wolves seen at close quarters were aware of my presence. Since no wolf was shot or harmed in any way by us or others in this area, it seemed probable that they realized there was no danger. Had one of them been harmed, the others would doubtless never have allowed themselves to be seen and watched..."

App. A, Case History 42 (Stebler 1951:139)

"... As an example, on April 29, 1950, the den of the Hubbert wolves was located. There was still sufficient snow on the ground to require the use of snowshoes. Travel on snow which is alternately thawing and freezing is rather noisy, and this is particularly noticeable in wilderness areas away from the hum-drum of human activity. The wolf mother was in the den with her eight pups, when the den was found. Surely she must have heard the den hunters approach. The den was in a rather long, hollow pine log. To reach the pups, which could be heard well toward the center of the log, it was necessary to chop a hole through the log shell near its center. When a hole had been opened, one of the hunters...peered into it to see where the pups were. While he was trying to spot the pups in the dimly lighted interior of the log, he noticed the head of an adult wolf slowly raise into view. While this wolf watched him, he shot and killed it. It is difficult to say whether or not this was a manifestation of solicitation on the part of the wolf mother for her pups. But it does seem reasonable to interpret this behavior as such, however, for it would seem that this wolf had an opportunity to flee as the den hunters approached."

App. A, Case History 43 (Stephenson 1974:21)

"Harry Reynolds of the Alaska Department of Fish and Game relayed information that he had obtained from Elmer Debock of the Canadian Wildlife Service, Edmonton. In the summer of 1973 Debock entered a den east of the Mackenzie River, N.W.T. and handled and tagged an entire litter of pups. About two weeks later he found the wolves still present at the den and again entered the den to determine the status of the litter. Later checks revealed that the wolves remained at the den until the normal time."

App. A, Case History 44

CH 44a (Stephenson 1974:23)

"An experience we had with denning wolves in 1972 might be of interest as an example of the response one might expect from a female wolf that is extremely wary of humans. The den in question was located 12 air miles from Anaktuvuk Pass and the parturient female had lost the lower part of one hind leg, almost certainly in a trap.

"The den area was located in a general way on 24 May, but observation during the next day failed to show any activity. The area was then visited by Bob Ahgook and myself and we inadvertently disturbed the female who had been resting about 300 yards from the den. From her appearance Bob judged that she had either just had or was just about to have her pups. We withdrew to our camp one and one-half miles away and attempted to observe the den area as much as possible for the next several days, with minimal activity in the camp area..."

CH 44b (Stephenson 1974:23-24)

"We saw the wolves on only a few occasions due to topographic features which allowed only a limited view of the den area. On 2 June, a yearling wolf which was seen only on this occasion barked and howled at the camp for about one hour at a distance of about one-fourth mile. For a few days prior to June 7, no activity was

seen and we assumed that the pups had been moved. We again visited the den on June 7, to explore the area before leaving, and found the female still there. We withdrew immediately and again began observing the den area. Later that day, about ten hours after having disturbed the female for the second time, we saw both parent wolves at the den and watched the female carry one pup away. We did not see other pups moved, but since the one pup was moved shortly after we began observation that evening, it is very possible that an unknown number of others had been moved prior to that time. At any rate, the litter was moved after we had camped one and one-half miles from the den for 13 days and visited the den area proper on the first and last days of that period, when only the female wolf was present."

App. A, Case History 45 (Stephenson 1974:24-25)

"During the summer of 1974 I had another encounter with denning wolves which resulted in the female moving her pups. On June 28, I set up camp two miles south of an active den located north of Sagwon on the coastal plain. Noise from the turbine helicopter used to reach the den area elicited no response from four pups seen near the den entrances. An adult male, adult female, yearling male and six pups were observed at the den during the ensuing 10 days. On the evening of June 29, the adult male traveled south from the den and when about one-half mile away noticed the tent. The wolf proceeded to a point approximately 300 yards downwind of the camp, behind a low rise, then disappeared to the east. Although very curious and alert, the wolf did not evidence alarm at discovering the camp. This was the only response to the camp observed until July 7; during this time the wind blew predominantly from the north and the wolves hunted primarily north, east, and west of the den. On July 7, following several days of cold, snowy weather, the female wolf apparently first became aware of the camp. During the evening the weather had cleared and the two adult wolves, and occasionally. the pups, were heard howling over the course of about two hours. For

no particular reason I finally answered with one howl and watched as both adults stopped howling, looking intently toward the camp for a few minutes. The female then moved to within one mile of the camp and alternately watched the camp and slept for over an hour before returning to the den where she frequently looked intently toward the camp and appeared anxious, investigating the den area intensively. Six hours after returning to the den she was observed traveling east with three pups following her. However, she and the pups returned to the den, where the remaining three pups waited, after having gone one mile. They remained at the den for an additional 24 hours. The following morning the female and all six pups were observed as they traveled east for two miles, using the same route as on the previous day. Although the female and pups moved out of sight and appeared to be heading toward the Shaviovik River three miles east of the den an aerial search the following day revealed that the six pups had been left at what appeared to be an old wolf den in a pingo two miles east of the original den. The female and pups had crossed this pingo without even pausing on the previous day.

"Judging from her decisive reaction, the adult female was probably not previously aware of human presence near the den. Things that might account for her rapid movement of the litter include: 1) previously having been hunted, 2) the combination of a foreign 'wolf howl' and human presence, 3) the fact that the camp was located in full view of the den, and 4) the fact that the pups could travel readily at the time of the disturbance. This incident constitutes one of the most drastic reactions of a denning female to human intrusion of which I am aware and probably illustrates one extreme in the range of reaction to human presence."

App. A, Case History 46 (Stephenson and Ahgook 1975;289)

"...On one occasion, two Nunamiut watched a yearling wolf rush to a rendezvous site and lead a litter of pups away upon discovering the hunters about 1.5 km from the pups."

App. A, Case History 47 (Stephenson and Johnson 1973:10)

"A den that had been cleaned out, apparently in readiness for parturition, was discovered on 17 May, 1971 in Kollutarak valley and tracks of two wolves were seen in the vicinity. A few days prior to the discovery of the den two Nunamiut hunters reported that two wolves had howled and barked at them for more than an hour as they traveled on the river ice nearby. The wolves were high on a mountain 1 mile north of the den site and the Nunamiut stated that the presence of humans in the vicinity of the prospective den had been the cause of the howling and barking. The den was not used, perhaps because of human interference...another den was probably used."

App. A, Case History 48

CH 48a (Theberge 1975:136-137)

"Gaylen saw the wolf first, spotting it while scanning the hills from our boat....Before we were able to land, it disappeared from the top of a rocky ridge a mile away. By the time we reached the hill, the wolf reappeared and came loping straight towards us. It veered off, then stopped....It turned and galloped out of sight.

"...As I considered our next move, the animal reappeared about a quarter of a mile away, joined by two more wolves.

"The three stood facing us...and howling in chorus. So reluctant were they to leave that we were certain their den must be nearby. We found four pups at the base of a rock wall, only a few yards away. Several minutes passed before they realized that their well-concealed home had been discovered. Then, overwhelmed by curiosity, they climbed the rocks to get a better view of us. The wind had dropped, and we stood motionless....The boldest pup came closer and closer. Then, suddenly, inquisitiveness gave way to fear and it bolted in panic, triggering alarm in the others. Perhaps their fear resulted from some slight movement, or the click of my camera shutter. Possibly the pup was reacting to a

new experience and would have run from its first acquaintance with a lemming or an Arctic hare. In a flash the adult wolves raced after the pups which, by the time they were overtaken, were far out on the plain.

"The den was actually a tunnel into the wall, with two entrances, one higher than the other. In front of it was a well-trampled sedge meadow and a small pond. The wolves had lived there for at least two weeks, judging by the bones and droppings scattered around."

CH 48b (Theberge 1975:157-138, 141)

"The next day Gaylen brought me back to the den, which was eight miles from our base camp. I had decided to camp there for a few days, to see if the wolves would accept my presence and go about their normal activities...

"When we first appeared near the den, fortune was still in my favour. My field notebook for Tuesday, August 3, reads:

'While we were eating lunch on a ridge within sight of the den, I heard a faint howling. Down on the plain below were the three adult wolves and two of the pups. They were trotting southeast, towards the den....The lead wolf suddenly saw us; we were silhouetted against the sky. They all immediately swung in our direction, the lead animals making a semicircle around us at about seventy-five yards while the others moved up the ridge farther back, trotting a few steps, stopping to look at us, trotting again. They all circled back to the plain, deciding we were not worth further concern, and, strung out in a line, continued towards the den. When almost there, the lead wolf stopped, and in a cluster together, they howled - pups too - short treble howls, weakened by the wind.

'At the den, two adults stood together in the wet grass, while the other walked along the wall of rock, exploring the crevices. The pups followed. Then, in a curious display, they all came together, nose to nose, and milled around each other for about fifteen seconds. As they broke their huddle, they started back along the plain, retracing their route, strung out again, but this time moving faster.

The pups lagged behind. Occasionally the adults stopped to let the pups catch up. As they passed us, they paused to look up, but only momentarily. Soon they were far out on the plain and out of sight.'

"...But the wolves came back to their den only occasionally. They appeared, now and then, at the base camp and ate a few free meals of caribou meat before we discovered them and raised our stores well out of their reach. The pups had moved, and we never saw them again. Occasionally, wolf prints showed up around my scent posts, along with white hair where the animals had rolled on the scent."

App. A, Case History 49

(Theberge and Pimlott 1969:122-123)

- "...four adult timber wolves...and three pups observed for 16 days in August, 1962, in Algonquin Provincial Park, Ontario.
- "...Observations were made in the open, often within sight of the wolves, at a distance of 500 feet. The wolves rarely paid any attention to the observers, however once, Pimlott was approached by a single wolf to within 75 feet."

(Rutter and Pimlott 1968:20-21)

"...my wife...my daughter...and I were observing a family of wolves in the Annie Bay Burn in the Park. It was late afternoon, but still daylight, when the female became aware that we were watching them from the open face of a small hill. She became alert but showed no evidence of alarm. For several minutes the observing was mutual - wolf watching people, people watching wolf. Finally, she seemed satisfied and began to move slowly around the resting site and, a few minutes later, along a game trail that followed the edge of the bog which separated us. After moving slowly away along the trail for about two hundred yards, she left it and began to pick her way across to our side of the bog. She was still gradually moving farther away from us. In a minute or two she reached

our side and disappeared into a strip of forest that had escaped the fire. We then turned our attention back to the resting site to watch for the remainder of the wolf family.

"In a few minutes the male wolf appeared, and our attention focused on him; at the same instant we were startled by a harsh challenging bark from the edge of the trees only 50 feet behind us. The doglike barking challenge was repeated over and over again. We forgot all about the rest of the wolf family in our momentary consternation. The barking wolf, which was probably the female we had seen earlier, remained just out of our sight in the trees - but so very close....Only then did we remember to look for the male wolf, but in vain; he had disappeared.

"The barking challenge continued, but by then we had regained our aplomb and were busy recording and, occasionally, howling back to see what her response would be. After a time she began to move slowly away, continuing to bark the same deliberate sequence all the while. As the distance increased, the barking changed to howling, but still in the unusual sequence of the earlier barking. When she reached the top of the hill, a quarter of a mile or so away from us, the barking ceased..."

[There were 11 minutes of barking.]

App. A, Case History 50 (Voigt 1973:17-18)

"...Wolves hearing imitation howls or howls of other wolves reacted in various ways. On 12 occasions near homesites, wolves approached without howling after the author had howled. Two pups approached to within 5 m of the author on two occasions. Near the den of the Source Lake pack lone adult wolves approached on five occasions. On one occasion three adults of the Fool's Lake pack approached to within 10 m of the author. Thirty minutes later, a single adult approached to within 3 m after the author gave a series of imitation howls...

"Barking occurred on nine occasions; on seven of these wolves

were less than 300 m from the author. In one case, an adult barked continuously for 1 min near a group of pups which continued to howl. On five occasions, howling by groups of wolves was abruptly terminated by two sharp barks. An adult wolf barked and growled 15 m from the author when the author was heard near homesites on two other occasions. Combined bark-howls were heard in nine instances from wolves at homesites. Whining was heard from pups (five cases) which were approaching other wolves or the author. Adult wolves howling in groups were also heard whining between howls (12 cases)."

App. A, Case History 51 (Wayman 1967:59-60)

"...I decided to give them a couple of days before returning, but the next night a heavy fog offered cover too good to ignore. I was within a mile of the den when the fog briefly lifted and I saw the wolf bitch leading the cubs [five approximately 6 weeks old] away from the den. She disliked the idea of a strange neighbor so close, and she was moving bag and baggage, using the fog the same as I...

"I went back to Seth's Ridge where, to my delight, I discovered that in the fog the wolves had moved their home to the deserted den only a mile away. While the wolves never completely accepted their strange neighbor, I was at least grudgingly tolerated...

"One parent always stayed near the den while the others hunted with the rest of the pack..."

APPENDIX B. - Case histories of human disturbance affecting pup behavior at wolf homesites.

App. B, Case History 1 (Present study 1976)

26 July. I arrived at the Kongakut den around 1300 hr. I walked quietly to the active den and saw the ears of one pup approximately 1 m away. I backed up and whined. The pup jumped up and faced me. Five others ran toward me from the willows. All were surprised when they realized I was not a wolf. They all vocalized with short gruff "woofs", and scampered into the den 10 m away. I approached the den and peered in. Their heads sometimes appeared briefly at the entrance. This continued for about 30 seconds. For the next several minutes I could hear them moving inside the den. I soon left the area and returned to my observation post across the river. I saw two pups at 1730. Previous to this sighting I was fairly certain that the pups had not been out of the den since I had disturbed them.

I returned to the den for a short while on both 27 and 28 July. One pup was seen on each occasion, and it retreated into willows upon seeing me. On 29 July I again saw one pup before observations were terminated. I do not know if any other pups were present these last 3 days, or if they had been moved from the den and the one pup abandoned. I did not see any adult wolves in 41 hours of observation during the 4 days.

App. B, Case History 2 (Clark 1971;89)

"...At the age of nine weeks the pups of the 1966 litter disappeared into their den to remain until a human intruder had gone..."

App. B, Case History 3 (Clark 1971:89-90)

"...When these pups were almost 11 weeks old, the adults attempted to lead them across the Amaroktalik River. Only one pup

followed the adults across the river. The others refused and eventually slept huddled together by a boulder at the river's edge while the adults continued to howl to them from beyond the opposite shore. At this time two of our party were making their way downriver under the shorebank out of sight of the adults, unaware that the pups were lying directly across the river. One of the pups spotted us and stood up to watch. It then loped up the bank and across the tundra, heading for the den and closely followed by the others."

App. B, Case History 4 (Joslin 1966;51)

"On another occasion...when I was trying to make tape-recordings of two pups belonging to the Source Lake pack, I crept to within a hundred yards of their site and howled. A single pup replied with a couple of howls, then came running towards me. Twice it whined as it came through the underbrush. I suspect the pup interpreted my howling as that of one of the adults arriving back at the site. When the pup saw me, it did not appear to relate me to the source of the howling. It tried to find sufficient cover to by-pass the small clearing I was standing in, however, when it was not successful it returned to the site after a minute or two."

App. B, Case History 5 (Ognev 1931:146)

"...In the beginning of June 1891 a forester found a wolf den....Five young wolf cubs, no larger than cats, played near the entrance to the den. On the appearance of the man, two ran into the den, and three remained nearby."

See also Appendix A, Case Histories 1, 2f, 2g, 2h, 4, 5, 8, 10b, 12b, 19, 20, 27, 31a, 31b, 32c, 32d, 32e, 33b, 33d, 35, 37, 40, 41, 48, 50.

APPENDIX C. - Case histories of aircraft disturbance near wolf homesites.

It should be noted that two gravel bar landing strips accommodating a Cessna-180 and a Piper Supercub aircraft were located approximately 3.6 and 2.2 km, respectively, from the whelping den on the Hulahula River (case histories 1-37).

The behavior of wolves reacting or not reacting to aircraft was recorded only when we heard or saw aircraft. It is possible that the wolves reacted to aircraft that we did not hear. Because we were interested in the behavior of the wolves, it was not always practical to determine the altitude or type of aircraft that flew near the wolves. Unless otherwise noted most aircraft were light, fixed-wing aircraft.

App. C, Case History 1 (Present study, Hulahula River 1976)

8 June. One wolf was walking from the den area; the mother was in the den. 1300 - a plane (Supercub) flew over the area. The wolf sat and watched it pass. 1303 - the mother came out of the den and watched the plane, walked 5 m, and lay down in a small group of willows. The other wolf continued walking from the den area. 1308 - the wolf sat and watched the plane fly by again. 1309 - the wolf lay down and watched the plane. 1311 - the wolf walked from the den area again. The mother remained in the willows and watched. 1315 - the wolf sniffed the ground then watched the plane fly by again. It continued to leave the den area. The mother continued to rest.

App. C, Case History 2 (Present study, Hulahula River 1976)

9 June. The mother was resting near the den. 1818 - a plane (Supercub) flew along the river. The mother briefly watched the plane. She continued to rest.

App. C, Case History 3 (Present study, Hulahula River 1976)

11 June. The mother was resting near the den. 0655 - the mother looked up as a plane flew high overhead. She lay down and continued to rest.

App. C, Case History 4 (Present study, Hulahula River 1976)

11 June. One wolf was resting near the den. 1905 - the wolf stood, apparently alarmed by a Cessna-180 that flew over. The wolf walked uphill and occasionally looked in the direction of the plane. The wolf lay down approximately 150 m above the den and continued to rest.

App. C, Case History 5 (Present study, Hulahula River 1976)

15 June. The mother was nursing the pups near the den. 0910 - she looked in the direction of a small plane, but continued to nurse the pups.

App. C, Case History 6 (Present study, Hulahula River 1976)

15 June. A wolf was resting near the den. 1544 - the wolf stood as a plane flew over. The wolf walked approximately 7 m, lay down, and continued to rest.

App. C, Case History / (Present study, Hulahula River 1976)

16 June. The mother was resting near the den. 1143 - a Jet flew over, and she raised her head to look around briefly. She continued to rest.

App. C, Case History 8 (Present study, Hulahula River 1976)

16 June. The mother and another wolf were resting near the den. 1307 - a plane (Cessna 185?) with floats flew low over the area. The mother looked up, then stood facing toward the plane. The plane circled our base camp 1.4 km from the den. The mother continued to look in the direction of the plane. The other wolf

began walking. It stopped, sat, and appeared to howl. The mother walked 10 m. Both wolves walked away from the den. The wolf lay down and eventually returned to the den. The mother continued to walk from the den area, and was out of sight 200 m from the den.

App. C, Case History 9 (Present study, Hulahula River 1976)

16 June. The mother was lying near the den with the pups.
1603 - the mother looked in the direction of the plane. She stood, walked 20 m, and lay down. The plane landed at 180 strip. 1610 - the plane took off. The mother looked in that direction, but remained lying down. Two other wolves also resting near the den looked toward the plane.

App. C, Case History 10 (Present study, Hulahula River 1976)

16 June. The mother and another wolf were lying with the pups near the den. 1913 - the wolf stood and looked toward a plane flying up the valley. This wolf trotted to the den, sat, and watched the pups. The mother looked toward the plane.

App. C, Case History 11 (Present study, Hulahula River 1976)

16 June. The mother and another wolf were resting near the den. 1925 - both wolves looked toward the plane. The wolf stood and walked past the den. The pups followed. The wolf lay down approximately 6 m from the den and watched the plane. Both adults continued to rest.

App. C, Case History 12 (Present study, Hulahula River 1976)

16 June. The mother and another wolf were resting near the den. 1941 - a plane took off from 180 strip. Both wolves looked toward the plane. The mother licked the pups briefly and both adults put their heads down. They ignored the plane as it flew up the river, but as the plane circled back both wolves looked up. The mother then ignored it, but the other wolf continued to look

toward the plane. Both wolves continued to rest.

App. C, Case History 13 (Present study, Hulahula River 1976)

19 June. A wolf was resting near the den. 1537 - a plane flew down river. The wolf looked up a couple of times but continued to rest.

App. C, Case History 14 (Present study, Hulahula River 1976)

19 June. Five wolves were resting near the den. 1942 - all five stood and began walking from the den area as a plane circled the area and landed at the 180 strip. When approximately 150 m from the den, two of the wolves lay down, and the other three wandered around. 1958 - the plane took off from the strip; all the wolves stood and watched. Plane came toward them, circled, and headed down river. The wolves continued to watch the plane while they walked from the den area. They detected several sheep to the north and chased them.

App. C, Case History 15 (Present study, Hulahula River 1976)

20 June. A wolf had just walked from the den area and lay down. 1351 - a Jet flew over. The wolf sat and looked up toward it and continued to walk from the den area.

App. C, Case History 16 (Present study, Hulahula River 1976)

23 June. A wolf was resting near the den. 1157 - a plane was heard. 1201 - the wolf stood, then lay down again. 1202 - the wolf looked toward the 180 strip and stood. The plane landed at the strip. The wolf walked from the den area. 1204 - the wolf lay down, stood, continued walking and continued to look toward the strip. 1207 - When 200 m from the den the wolf lay down. 1231 - the plane took off. There was no visible response from the wolf.

App. C, Case History 17 (Present study, Hulahula River 1976)

23 June. A wolf was resting near the den. 1401 - a plane flew near the 180 strip. The wolf looked up and stood. The plane landed at the strip. 1403 - the wolf walked a short distance, stopped, looked around, walked again, then lay down, and continued to rest.

App. C, Case History 18 (Present study, Hulahula River 1976)

24 June. The mother was walking from the den area. 0751 - she stopped, defecated, and looked toward a Jet flying over. She continued to walk from the den area.

App. C, Case History 19 (Present study, Hulahula River 1976)

26 June. A wolf was resting near the den. 2037 - the wolf turned its head toward a plane flying up river. 2039 - the wolf continued to rest.

App. C, Case History 20 (Present study, Hulahula River 1976)

28 June. Three wolves were resting near the den. 1453 - a plane flew near them and landed at the Supercub strip. All three sat and looked toward the plane. All three stood, walked off a short distance, and lay down. Two wolves lay completely down, one continued to look toward the Supercub strip for approximately 30 minutes. 1543 - two wolves left the area in a direction opposite that of the strip. 1554 - the plane took off. The wolf that was resting near the den looked up briefly, but did not look toward the plane as it flew by the observation tent. 1558 - the wolf stood, and walked away from the den a short distance.

App. C, Case History 21 (Present study, Hulahula River 1976)

29 June. A wolf was resting near the den. 0948 - a Jet flew over. The wolf poked its head above the brush to look up. 0950 - the wolf stood, stretched, and walked to den area and interacted

with the pups.

App. C, Case History 22 (Present study, Hulahula River 1976)

2 July. A wolf was resting near the den. 2135 - a plane flew over. The wolf looked toward the plane and watched it land. The wolf stood and left the den area in a direction opposite that of the strip. It frequently looked back toward the strip. 2210 - another wolf at the den watched as the plane took off.

App. C, Case History 23 (Present study, Hulahula River 1976)

3 July. Two wolves were resting near the den. 1047 - a Jet flew over. One wolf did not react, the other lifted its head and looked up toward the Jet. Both continued to rest.

App. C, Case History 24 (Present study, Hulahula River 1976)

6 July. A wolf was leaving the den area, but was now resting. 1410 - the wolf stood and continued walking from the den area as a high flying plane flew down river. The wolf looked toward the plane. The wolf continued to leave the area.

App. C, Case History 25 (Present study, Hulahula River 1976)

7 July. The mother and another wolf were resting near the den. 1742 - a light plane flew up river. 1743 - the wolf raised its head and looked around for approximately 30 seconds. 1745 - the mother raised her head for a few seconds. Both wolves continued to rest.

App. C, Case History 26 (Present study, Hulahula River 1976)

12 July. A wolf was resting near the den. 2147 - a Supercub circled the observation tent. The wolf watched the plane, stood, lay down, and continued to rest.

App. C, Case History 27 (Present study, Hulahula River 1976)

13 July. A wolf was resting near the den. 0137 - a small plane was heard in the distance. The wolf looked toward the plane, but soon lay its head down and continued to rest.

App. C, Case History 28 (Present study, Hulahula River 1976)

14 July. A wolf was resting near the den. 2002 - a plane was heard in the distance. The wolf looked up briefly. 2006 - the wolf stood, walked a few meters, then lay down. 2022 - the plane took off from 180 strip. 2024 - the wolf raised its head, then continued to rest.

App. C, Case History 29 (Present study, Hulahula River 1976)

16 July. A wolf was grooming itself near the rendezvous site.

0708 - a plane flew over. The wolf sat and looked toward it. 0709 - the wolf stood and trotted to another location and lay down.

App. C, Case History 30 (Present study, Hulahula River 1976)

16 July. Two wolves were resting near the rendezvous site.

0759 - a plane was heard. Both wolves looked around and toward the plane. 0800 - one wolf stood to watch the plane and walked toward the pups.

App. C, Case History 31 (Present study, Hulahula River 1976)

16 July. A wolf was resting near the rendezvous site. 0905 - the wolf raised its head and briefly looked in the direction of a plane in the distance. The wolf continued to rest.

App. C, Case History 32 (Present study, Hulahula River 1976)

17 July. The mother and another wolf were resting near the rendezvous site. 1427 - a plane (Helio-Courier) flew up river.

Both wolves looked up for several seconds. 1430 - the plane circled back. The mother stood and walked several meters. She looked

briefly toward the plane when it was overhead. The mother wolf looked up and watched the plane. 1431 - the mother lay down and continued to rest.

App. C, Case History 33 (Present study, Hulahula River 1976)

17 July. Three wolves were resting near the rendezvous site.
1717 - a plane flew high and circled directly overhead. All three wolves looked up. The plane circled back. The wolves looked up again. All three continued to rest.

App. C, Case History 34 (Present study, Hulahula River 1976)

18 July. Two wolves were resting near the rendezvous site. 1245 - a plane flew over. One wolf sat and scratched, lay down, stood, walked 15 m, and looked toward the plane. The other wolf walked around. 1253 - Both lay down and continued to rest.

App. C, Case History 35 (Present study, Hulahula River 1976)

18 July. One wolf was resting near the rendezvous site. 1337 - a wolf looked up briefly as a plane circled in the distance. The wolf continued to rest.

App. C, Case History 36 (Present study, Hulahula River 1976)

25 July. No wolves were in view. 2131 - a plane landed at the Supercub strip. 2134 - a wolf walked into view and looked around. 2136 - the wolf lay down.

App. C, Case History 37 (Present study, Hulahula River 1976)

27 July. A wolf was resting near the rendezvous site. 1921 - a large, very noisy plane flew low overhead. The wolf looked around, but was looking around before the plane was heard. The wolf continued to rest.

App. C, Case History 38 (Present study, East Fork River 1974)

22 June. An adult male wolf was resting near the den. 1125 - he did not respond to a high flying light plane.

App. C, Case History 39 (Present study, East Fork River 1974)

22 June. An adult male was resting near the den. 1221 - he responded to a high flying light plane by turning his head toward the plane. The wolf continued to rest.

App. C, Case History 40 (Present study, East Fork River 1974)

8 July. The mother wolf was resting near the den. 2026 - as a light plane flew over, she raised her head and looked toward the plane for several seconds. She continued to rest.

App. C, Case History 41 (Present study, East Fork River 1974)

13 July. 0612 - as I flew over the den in a Piper Cherokee-Six at an altitude of about 75 m, three pups apparently came out of the brush near the den to watch the plane.

App. C, Case History 42 (Present study, East Fork River 1974)

14 July. 0926 - as a small plane flew over the den at an altitude of approximately 75 m, two pups briefly became visible near the den. Perhaps they were watching the plane. Both soon entered a patch of willows.

App. C, Case History 43 (Present study, Kongakut River 1976)

9 June. The mother was resting approximately 200 m from the den. 1430 - the mother ran toward the den as a Cessna-180 flew low over the den.

App. C, Case History 44 (Present study, Kongakut River 1976)

28 June. 1655 - as we approached the den in a Supercub at an altitude of about 100 m, the mother was seen running from the den.

She stopped approximately 100 m from the den as we circled the area.

App. C, Case History 45 (Present study, Kongakut River 1976)

25 July. 2305 - while we circled the den in Supercub at an altitude of about 50 m, at least two pups came out of the den apparently to watch the plane.

App. C, Case History 46 (Present study, Echooka River 1975)

2 July. Four pups were resting near the den. 1741 - an F-27 could be heard in the distance. All four pups sat up and perked their ears in the direction of the noise. They soon lay down again.

App. C, Case History 47 (Present study, Echooka River 1975)

5 July. Two pups were resting near the den. 1511-1513 - both pups raised their heads to look toward the plane. One sat up but soon lay down again. Both pups continued to rest.

App. C, Case History 48 (Haber 1968;104)

"...during aerial reconnaissance on September 8, 1967,...Nine wolves, apparently from both the Surprise Pass and lower Toklat families, were together at a fresh kill along Stony Creek, nine miles north of the park road. When we circled overhead six pups which had been out in the middle of the open gravel bar with three adults ran immediately for the cover of the spruces several hundred yards away along the river bank. The two smaller black adults also ran, but the largest black - a male - began walking slowly in the opposite direction from the rest, looking up at the aircraft and remaining in plain view on the open river bar. After another minute or so, as we continued to circle, he sat down on the bar and with apparent composure continued looking up at the plane and following our movements. In our judgment this may have been an attempt by him to decoy us from the others as they sought cover in the spruces. It is, however, also possible that this wolf was simply less afraid than the

others, and the decoy effect was coincidental."

App. C, Case History 49 (Klein pers. comm.)

On 28 June 1973 at 1600 hr observers in a Cessna-185 aircraft at an altitude of approximately 50 m flew over two adult wolves (one lying and one sitting) and one or more pups (playing with the adults) near a den on the Kongakut River, northeast Alaska. There was no visible reaction to the aircraft. This den had previously been flown over on at least five other occasions.

App. C, Case History 50 (Klein pers. comm.)

On 27 July 1973 at 1030 hr observers in an FH-1100 helicopter at an altitude of approximately 35 m flew over four wolf pups that were lying at a rendezvous site on the Marsh Fork of the Canning River, northeast Alaska. The pups watched the helicopter pass over them, but they showed no apparent alarm. This homesite was frequently flown over by helicopters at low altitudes.

App. C, Case History 51 (Stephenson 1974:22)

"In 1966 BLM surveyors discovered a wolf den near Olnes (near the Elliott Highway north of Fairbanks) and flew over and around the den with a helicopter on several occasions to better observe the wolves [early June]. Fish and Game personnel visited the area about two weeks after the den was discovered and found that the wolves had vacated the den [late June]..."

See also Appendix A, Case History 45.

APPENDIX D. - Case histories of vehicle disturbance at wolf homesites.

App. D, Case History 1 (Present study 1974)

10 July. The mother wolf and a young female were resting near the East Fork den. At 0626 both adults became alert. The mother sat, then stood. The other female soon stood also. I could hear and see a Wildlife Tour Bus and a small van on the road near the East Fork Bridge (approximately 2.0 km from the den). Both wolves were looking in that direction. At 0627 both wolves lay down. The wolves probably became alert when the Bus shifted gears to climb Polychrome Mountain. At 0634 the mother wolf again became alert as another Bus began the climb up Polychrome Mountain. Both wolves continued to rest.

App. D, Case History 2 (Mech 1970:151)

"...On May 8, 1967, at 6:45 pm, having just stopped my truck on a narrow dirt road, I saw a silver-black wolf rounding a bend about two hundred yards away. It trotted briskly toward me with its head down, appearing intent on reaching a particular destination [den?]. When it was about 150 yards away from me, the wolf noticed the truck, crossed the narrow road, and headed into the woods, I saw then that the animal was carrying something in its mouth. I drove to the point where the wolf had disappeared, and I walked toward where I had first seen it. When I returned to the truck, I saw the wolf emerge from the woods about 150 yards behind the vehicle and continued on down the road, having deviated only to bypass the truck."

App. D, Case History 3 (National Park Service 1932)

"On the 14th of September,...a gravel truck driver, who was returning from Stoney [sic] Creek to Headquarters was rounding a curve in the road about one mile west of the Teklanika Bridge when he saw three wolves in the road ahead. There had been a fresh snow

of three or four inches and the wolves seemed reluctant to leave the well beaten trail for the hard traveling in the brush, so they proceeded to turn tail and start down the road with [the driver] ...giving chase. He succeeded in running over all three, two he killed outright and the third went limping off on three legs. All of them were half grown pups and that solves the mystery of why they used such poor judgement."

App. D, Case History 4 (National Park Service 1938)

"On October 26...[a] Surveyor for the Alaska Road Commission, and his helper...were returning to McKinley Park Station in a Ford pickup. At Mile 37 they noticed an animal in the road. At first... [he] started to stop the car and prepared to take a picture of it. Then upon getting closer he saw that it was a wolf pup. Remaining in the car he speeded up. The pup refused to leave the road and was run over. A hind leg was broken, but the wolf managed to run into a ditch on the side of the road. Each man grabbed an ax, ran to the wolf and both struck him on the head about the same moment, killing him instantly....This incident illustrates a peculiarity of wolf pups that they will frequently remain in the road instead of leaving it as the wiser and more experienced wolves do. Although this wolf was a young pup he weighed over a hundred pounds."

App D, Case History 5 (Tracy pers. comm.)

[On August 22, 1973, around 1700 hr about 8 km north of Healy on the Anchorage-Fairbanks Highway, Tracy and two companions observed five wolves, all black, one adult and four pups, by the road.]

"Apparently the adult had just crossed the road, west to east. Upon our approach the pups scattered in the brush west of the road. We stopped and over several minutes the pups crossed the road. The adult had entered a patch of spruce about 300 m south of the road and began howling. At least two of the pups were observed entering the same patch of spruce 10-15 minutes after the adult.

One pup also howled while still separated from the adult."

[Perhaps the wolf was leading the pups between homesites.]

APPENDIX E. - Observations of golden eagle-wolf interactions at wolf homesites.

App. E, Case History 1 (Present study 1975)

At 0954 on 3 July at the Echooka den, both temporarily abandoned pups were in sight near the den. One pup was sitting approximately 5 m south of the den; the other was chewing on an object (bone?) 10 m from the den. The sitting pup stood, trotted 2 m east, then ran madly for the den. The other pup jumped up from the object it was chewing. He looked toward the den, then looked around. When he looked east, he too ran for the den. An immature golden eagle was soon seen 10 m east of the den about 5 m above the ground. It made a turn over the den, flew east about 80 m, and landed, facing the den. About half a minute later it took off and flew over the den and further west in circles. By 0957 the eagle was 0.8 km west of the den. The pups left the den at 1000 and did not appear cautious.

App. E, Case History 2 (Present study 1976)

At 1822 on 28 June an eagle flew over the Hulahula den which was occupied by all four pups. It flew around the area a short while, lighting briefly on three occasions on a large rock near the den. The last time it lighted, a wolf (apparently barking) raced from the south to chase the eagle. The eagle rose in the air and flew from the area.

App E, Case History 3 (Present study 1976)

At 2207 on 3 July four pups were following an adult wolf near the Hulahula den. The adult walked toward and flushed an immature golden eagle. The eagle flew toward the den and landed 15 m from it. The adult wolf lay down on a rock near the pups some 50 m from the den. At 2250 the adult was no longer visible. The pups were slowly moving toward the den. The eagle was perched on a rock 10 m above the den. At 2315 the eagle was still perched; the pups were

in some brush. At 2320 the adult wolf stood and walked toward the eagle, and, when 5 m from the eagle, charged. The eagle flew off to perch on a knoll approximately 100 m from the den. The adult wolf lay near the den with the pups. The eagle eventually left the area.

App E, Case History 4 (Present study 1976)

At 1727 on 20 July an immature golden eagle flew directly over a rendezvous site near the Hulahula River occupied by four adults and four pups. At 1731 a pup climbed and sat on a large rock apparently to watch the eagle fly around (the pup was looking toward the eagle). One adult wolf looked up briefly but the other three, including the mother, never raised their heads. At 1733 the pup walked out of sight. At 1737 two eagles were calling and flying around the mountain peaks north of the wolves. The eagles eventually left the area.

App. E, Case History 5 (Present study 1976)

At 1137 on 23 July a golden eagle flew near and landed approximately 70 m from two pups that were walking near a creek adjacent to a rendezvous site on the Hulahula River. The eagle was soon joined by another one. At 1150 both eagles flew off and left the area.

App. E, Case History 6 (Murie 1944:98)

"...Eagles have also been observed swooping low over grizzlies and wolves at times when there was no intent of predation. Once an eagle dove at an adult wolf which was standing near its den. About a dozen times the eagle swooped, barely avoiding the wolf which each time jumped into the air and snapped at it. The eagle turned upward at the right moment to avoid the leap, and apparently was enjoying the game."

APPENDIX F. - Interactions between wolves and other mammalian predators at wolf homesites.

Fox

App. F, Case History 1 (Present study 1976)

At 0703 on 16 June at the whelping den on the Hulahula River a red fox was seen approximately 50 m from the den and walking toward The mother wolf and three other adults were near the den. fox saw the mother wolf, and it became a gray streak as it ran from the area. The mother saw the fox and began chasing it. She ran approximately 50 m, stopped, and leapt on her hind legs a few times (observation leaps) apparently to gain a better view. With body rigid, tail erect, and hackles raised, she began barking. The other three wolves responded. The wolf that appeared to be the alpha-male stood and looked up toward the mother. One of the other wolves ran up to the mother. The third wolf ran above the den and lay Both the mother and the wolf that had run to her continued to walk uphill, and they investigated the area. The mother urinated in the squat position. The wolf with the mother walked another 50 m or so and lay down. The mother remained nervous and continued to investigate. At 0710 she, too, lay down.

App F, Case History 2 (Present study 1975)

The remains of an adult red fox were found approximately 20 m from a wolf den on the Canning River, northeastern Alaska. This den was last used by wolves in 1973. The bones were not scattered. Cause of death was unknown. Perhaps wolves had killed this fox.

App. F, Case History 3 (Present study 1975)

A set of red fox mandibles was found at a wolf rendezvous site on the Marsh Fork of the Canning River, northeastern Alaska. The rendezvous site was last used in 1973. Cause of death was unknown.

Bear

App. F, Case History 4 (Present study 1976) See text page 89.

App. F, Case History 5 (Present study 1975)

On 30 June at the den on the Echooka River the young female left the den apparently to hunt. At 2332 when approximately 1.5 km from the den she saw a grizzly bear approximately 30 m away. Both looked at one another. The bear ran. The wolf took chase but did not make much of an effort to catch the bear. The wolf soon slowed and stopped. The bear continued to run. At 2334 the bear stopped running. At 2335 the bear stood on its hind legs and looked toward the wolf some 50 m or so away. The bear slowly walked away but periodically turned to look toward the wolf. The wolf at this time was apparently hunting small animals and was wandering back and forth over the tundra. The bear stopped and watched the wolf for a short while. At 2336 the bear began walking again. At 2337 it stood on its hind legs to look at the wolf. It trotted, then galloped 50 m away from the wolf, frequently turning back to look toward the wolf. At 2340 the wolf lay down, facing the bear some 100 m away. The bear slowly approached the wolf. When the bear was about 30 m from the wolf, the wolf stood and, with tail high, chased the bear. The wolf came very close but the bear veered off and the wolf ran by. The bear then chased the wolf, though neither were running rapidly. The wolf kept looking over its shoulder at the bear and maintained a 5-10 m advantage at all times. At 2343 the wolf apparently tired of the game, stopped, faced the bear in what was obviously a threat posture and stared at the bear for 10-15 seconds. This immediately caused the bear to stop the chase. After a few seconds the bear took a couple of steps back and rolled onto its back and wriggled back and forth as if scratching its back, though I interpret this as possible displacement behavior. The bear stood and chased the wolf again. The bear stopped at 2344 and wandered away. The wolf lay down and, in fact, curled up, apparently unconcerned about the bear a mere 50 m away. After a minute or so the wolf began watching the bear. At 2347 the wolf stood and trotted to the den. She arrived at 0001 on 1 July.

App. F, Case History 6 (Present study 1975)

At 1815 on 11 August approximately 16 km from the den on the Echooka River, we spotted a grizzly bear, and a few seconds later a raven, on the gravel bar. We soon saw a gray wolf lying near the bear. The wolf stood, walked a few steps and lay down. The bear also lay down. The bear was 5 m from a bull caribou carcass. The wolf was 10 m from the bear. The wolf stood, changed beds, and lay down with its head up. The bear stood and walked past the carcass. The wolf stood, trotted to the north, and entered some willows after the bear walked toward him. A different wolf was soon seen in the vicinity of the carcass. There appeared to be no animosity between the wolves and the bear. The wolves often had their backs to the bear even when the bear was walking around.

For some reason, the bear began sniffing the air, stood on its hind legs, then sprinted into the willows. It may have scented us. While the bear was acting up, the visible wolf became concerned and watched the bear closely, particularly when the bear came within 3 m or so when running to the willows. I doubt that the wolves knew we were in the area, though it is possible that they did. They seemed very concerned, however, about the behavior of the bear.

Both wolves trotted down river, looking back often. Both wolves appeared to have full stomachs. They soon entered an extensive stand of tall willows and poplars approximately 0.4 km from the caribou carcass. They were lost to view at 1845. At 1857 a wolf pup was seen where the adult wolves had previously entered the large stand of willows. At 1907 we heard a pup howl. During the next 8 min, 10 more howls were heard. At 1917 another pup was seen on the

gravel bar, and a different pup was heard howling. By 1918 no wolves could be seen or heard. We accounted for the presence of at least two and possibly three different pups at this rendezvous site. The presence of the pups nearby may explain the concern the adult wolves showed when the bear acted as it did.

We continued to watch the area and at 2147 a wolf trotted to the carcass from the west. It began feeding. It was very wary and stopped to look around every 20-30 seconds. At 2200 the wolf gave the carcass a hard tug. The left front leg of the carcass swung over and hit the wolf squarely on the head. Startled, it jumped back quickly and looked around. It resumed feeding. At 2206 it stopped feeding, looked east, trotted 20 m east, stopped, looked intently to the east, trotted 10 m east, stopped to stare again, then trotted back to the carcass. At 2208 it began feeding again. It finished feeding at 2225, picked up a bone with some meat on it, and trotted west. It was out of view at 2230. Observations were terminated shortly thereafter due to darkness. The next day we hiked to the carcass and the rendezvous site. Very little meat remained on the carcass. The wolves were no longer at the rendezvous site.

App. F, Case History 7 (Carbyn 1974b:43, 45)

"May, 1972 - large pieces of wolf hide and extensive matting of hair attested to the death of a wolf at an abandoned den site (den-4). The wolf may have been a lone wolf or it could have been part of a pack denning in the area, presumably in 1971. Circumstances of the death of this animal are not clear but it is possible that a bear killed it. This conclusion is based on the location of the dead animal, i.e. open area, a few meters from the den entrance."

App. F, Case History 8 (Joslin 1966, summary by Mech 1970:282-283)

"What might happen to a wolf if a bear connects with it was discovered by Joslin (1966) in Ontario. He found the fresh carcass of a female wolf near her den of pups in Ontario. Eleven of the

wolf's ribs were broken, as were the tips of two of her neck vertebrae. Black-bear hair in the den entrance showed what kind of animal had probably caused the wolf's violent death."

[The pups were moved from this den by the other adults of the pack probably because of this incident.]

App. F, Case History 9 (Murie 1944:205)

"At the East Fork wolf den, two encounters were observed. The first one, which took place on June 5, I did not see, but it was reported to me...A female with three [2-year olds]...approached the den from down wind....They were not noticed until they were almost at the den, but then the four adult wolves that were at home dashed out at them, attacking from all sides....The four bears remained at the den for about an hour, feeding on meat scraps and uncovering meat the wolves had buried. During all this time, the bears were under attack..."

App F, Case History 10 (Murie 1944:205-206)

"The following morning I was at the wolf den a little before 8 o'clock....At 10 o'clock the black male wolf returned to the den, carrying food in his jaws...a grizzly...appeared to be following a trail, probably the trail of the female grizzly with the [2-year olds]....The five wolves did not see the grizzly until it was a little more than 100 yards away. Then they galloped toward it, the black male far in the lead. When the bear saw the approaching wolves, it turned and ran back over its trail, with the black wolf close at its heels. The bear retreated a few jumps at a time but had to turn to protect its rear from the wolves which tried to dash in and nip it. When all the wolves caught up with the bear they surrounded it. As it dashed at one wolf another would drive in from behind, and then the bear would turn quickly to catch this aggressor....After about 10 minutes the two female wolves withdrew toward the den and shortly thereafter the wolf identified as Grandpa moved off.

"The black male and the black-mantled male worried the bear for a few minutes and then the latter lay down about 75 yards away. A few minutes later the black father also departed. Left alone, the bear resumed his travels in a direction which would take him a little to one side of the den, but not for long. The black-mantled male quickly attacked and the other four wolves approached at a gallop. After another 5 minutes of worrying the bear, the wolves moved back toward the den, the black male again being the last to leave. The bear turned and slowly retraced his steps, disappearing in a swale a half mile or more away..."

Wolverine

App. F, Case History 11 (Present study 1975)

The weathered skull of a wolverine was found near the wolf den on the Echooka River. It is possible that this animal was killed or scavenged by a wolf and the skull carried to the den.

Lynx

App. F, Case History 12 (Stephenson 1975:5)

"Food remains at the den on the Sagavanirktok River...consisted of a lynx skull (Lynx canadensis)....The presence of a lynx skull is notable since this area lies about 50 miles north of the normal range of this species..."

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PERSONAL COMMUNICATIONS

- Steven Buskirk, National Park Service, Mount McKinley National Park, Alaska.
- Dr. Kim Clark, P. O. Box 353, Pembroke, Ontario, Canada.
- James Curatolo, Renewable Resources Consulting Services, Ltd., Fairbanks, Alaska.
- Dr. Frederick Dean, Cooperative Park Studies Unit, University of Alaska, Fairbanks, Alaska.
- John Johnson, National Park Service, Mount McKinley National Park, Alaska.
- Dr. David Klein, Cooperative Wildlife Research Unit, University of Alaska, Fairbanks, Alaska.
- Dr. Peter Lent, Cooperative Wildlife Research Unit, University of Alaska, Fairbanks, Alaska.
- Carol Linkswiler, Wildlife and Fisheries Program, University of Alaska, Fairbanks, Alaska.
- Dr. David Mech, U. S. Fish and Wildlife Service, Northcentral Forest Experiment Station, St. Paul, Minnesota.
- Wilbur Mills, Ambler, Alaska.
- Dr. Rolf Peterson, Dept. of Biology, Michigan Technological University, Houghton, Michigan.
- Robert Ritchie, Renewable Resources Consulting Services, Ltd., Fairbanks, Alaska.
- Daniel Roby, Wildlife and Fisheries Program, University of Alaska, Fairbanks, Alaska.
- Diane Tracy, Wildlife and Fisheries Program, University of Alaska, Fairbanks, Alaska.
- Patrick Valkenburg, Wildlife and Fisheries Program, University of Alaska, Fairbanks, Alaska.
- Kenneth Whitten, Alaska Dept. of Fish and Game, Fairbanks, Alaska.