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DYNAMICS, MOVEMENTS, AND FEEDING ECOLOGY OF A NEWLY PROTECTED WOLF POPULATION IN NORTHWESTERN MINNESOTA

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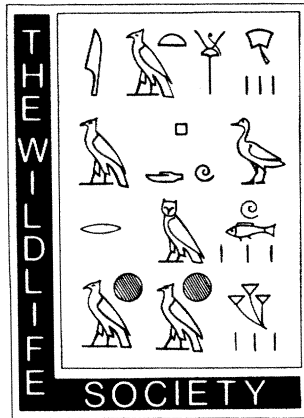
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by

STEVEN H. FRITTS AND L. DAVID MECH

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FRONTISPIECE. The senior author attaches a radio collar to a drugged wolf.

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Steven H. Fritts¹ and L. David Mech²

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INTRODUCTION

The gray wolf *Canis lupus* occupies only about 1 percent of its former range in the lower 48 states (Mech 1974a). Most of the range is in northern Minnesota, where the resident population is classified as "threatened" by the U.S. Department of the Interior. Wolves have been and will continue to be the subject of considerable controversy in Minnesota.

The first scientific study of wolves in Minnesota was conducted by Olson (1938a,b). That and all subsequent research was in the Superior National Forest (SNF) of northeastern Minnesota even though wolves inhabit approximately the northern third of the state. Consequently, until the present study, little was known about wolves in northwestern Minnesota, although it is highly desirable to have such information if wolves throughout Minnesota are to be managed wisely.

This study was inspired by the need for information from a place where, in contrast to the Superior National Forest, wolf densities appeared to be low and prey densities high. Fieldwork was conducted between August 1972 and March 1977, but was most intensive in summer 1973 and from May 1974 through September 1976.

The Beltrami Island State Forest (BISF) was selected as the primary study site because: (1) it is 230 km northwest of the Superior National Forest at the edge of the wolf's primary range; (2) it has a different type of habitat that supports a higher prey density; (3) it is bordered on 3 sides by farmland; (4) the wolf population appeared to be much lower than in the Superior National Forest, and seemed to be related to the vulnerability of wolves in that area to persecution by humans; (5) in addition to white-tailed deer *Odocoileus virginianus*, moose *Alces alces*, and beaver *Castor canadensis*, livestock is a potential prey of wolves in the area, and the resultant potential for wolf-human conflicts is of interest.

The purpose of this study was to collect

information on the biology of wolves in northwestern Minnesota, emphasizing population dynamics and spatial organization, movements, and feeding ecology.

An original hypothesis was that the apparent low density of wolves in the State Forest was a result of human persecution, and, that because of their low density, wolves would exist primarily in small packs (Rausch 1967) that occupied large home ranges. Such biological factors as physical characteristics of wolves and litter size were expected to reflect a low level of intraspecific competition. Testing the hypotheses was facilitated greatly when wolves in Minnesota were given total legal protection in August 1974. That unexpected event permitted an appraisal of the effects of legal protection on the population. Also, deer were more abundant in the study area than in the Superior National Forest, so wolves were expected to feed primarily on deer and to be highly selective for individuals easy to capture. Packs whose ranges bordered farmland were expected to feed on livestock to some extent.

ACKNOWLEDGMENTS

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The cooperation, assistance, and interest of the Minnesota Department of Natural Resources (DNR) is gratefully acknowledged. The department provided

housing and office space at Norris Camp during fieldwork, permitted use of state vehicles, snowmobiles, and other equipment, and provided for the use of a state pilot and plane at minimal cost. P. G. Watt and W. E. Berg were of assistance to the study in numerous ways, including conducting radiotracking during the early stages of the project. Other local departmental personnel who assisted in special ways were Larry Bernhoft, Everett Clem, Gary Gorton, Ervin Hanson, Robert Slick, and Neil Slick. Patrick Karns provided for ageing of deer killed by wolves and for analysis of bone marrow samples.

John Parker, Minnesota Department of Natural Resources, and Les Ellingson, Warroad, Minnesota skillfully piloted the aircraft. The late Bob Himes trapped the first 5 wolves instrumented during the study.

Individuals who assisted in the field include Jackie Boyd, Steve Frendin, Diana Fritts, Todd Fuller, Gary Gorton, John Klein, Randy Stinchfield, Jerry Szal, and George Weed. Tom Meier who conducted the fieldwork alone during August and September 1976 deserves special mention. Nancy Peterson typed the manuscript. Diane Boyd and Tom Meier assisted in preparation of the illustrations. Special thanks are due Diana Fritts for contributing to the project in numerous ways.

STUDY AREA

This research was conducted in and around the Beltrami Island State Forest in northwestern Minnesota and headquartered at Norris Camp (Fig. 1A, 1B). The Forest comprises 2,700 km² in Beltrami, Lake-of-the-Woods, and Roseau counties (95° west longitude, 48°30' north latitude). Much of the southern and central part of the Forest is part of the state managed Red Lake Wildlife Management Area. Land within the Forest is mostly stated owned, but several parcels are administered by the federal government or are part of the Red Lake Indian

Reservation. Private ownership is minimal, although it had been substantial until the 1930s.

Most of northwestern Minnesota was once covered by Glacial Lake Agassiz (Wright 1972a, Schwartz and Thiel 1976). The Forest is basically a flat and poorly drained lowland with extensive bogs. Several ridges of sand and gravel are evident, formed as wind-driven waves deposited ridges along the successive shorelines of Lake Agassiz (Wright 1972b). The highest elevation in that part of Minnesota (399 m) is in the central Forest near Norris Camp. Being higher than surrounding areas, much of the Forest had been an island in Lake Agassiz at various times in the past.

Several slow-moving streams originate in the Forest and drain into Hudson Bay. Lake-of-the-Woods, Red Lake, Thief Lake, Mud Lake, and the few shallow lakes within and around the Forest are remnants of Lake Agassiz (Wright 1972a). Less than 0.1 percent of the Forest currently is covered by open water, compared to 15 percent of the Superior National Forest (Minnesota Department of Conservation, Division of Waters, Soils, and Minerals 1968).

The climate of the study area is characterized by short, warm summers, and long, cold winters. Average mean monthly temperature in nearby Warroad ranges from -16.6 C in January to 19.7 C in July (U.S. Weather Bureau 1976). Temperatures below -30 C are common in January and February. Average annual precipitation in the area is about 53 cm, and normal annual snowfall is about 127 cm (Baker et al. 1967). Snowcover usually is continuous from late November into April.

More than half the study area is covered with peat. Exposed mineral soils are mostly sands or sandy loam with a wide range of textures (Arneman 1963). Excluding the 4 southernmost townships, about 70 percent of the Forest is wooded. About 35 percent of the Forest is covered by conifers. Generally pines *Pinus banksiana* Lamb, *P. resinosa* Ait., *P. strobus*

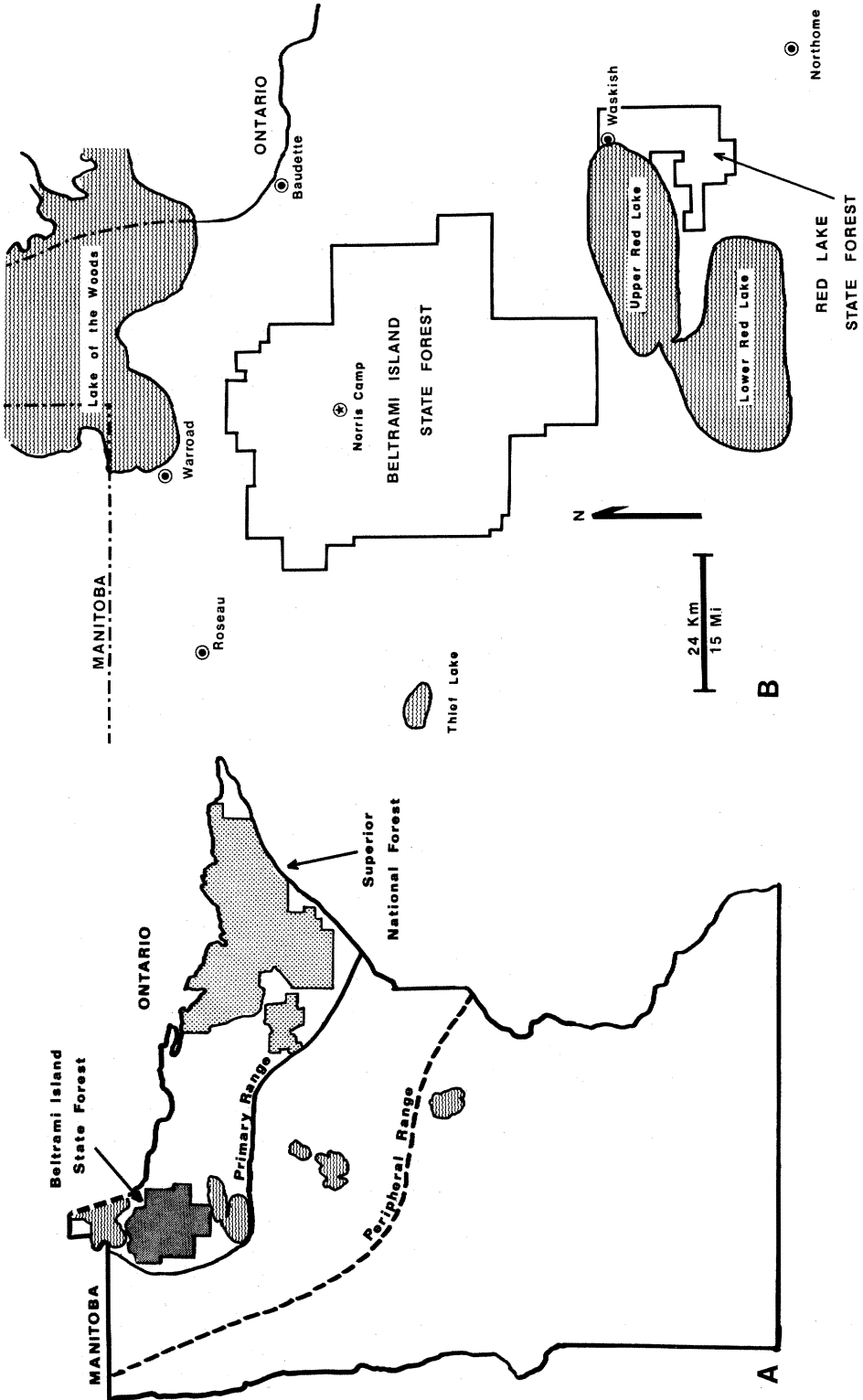


FIG. 1. A. Location of the Beltrami Island State Forest, the Superior National Forest (site of most previous research on wolves in Minnesota), and the primary and peripheral ranges of wolves in Minnesota. B. Detail of study area showing locations of towns referred to in the text.

L., are found on the sand ridges, with spruce *Picea glauca* (Mornch) Voss and *P. mariana* (Mill.) BSP, balsam fir *Abies balsamea* (L.) Mill., white cedar *Thuja occidentalis* L., and tamarack *Larix laricina* (Du Roi) K. Koch at more poorly drained sites. Trembling aspen *Populus tremuloides* Michx. and paper birch *Betula papyrifera* Marsh cover 30 percent of the area. About 17 percent is treeless marsh, and 14 percent is scrub conifers or willows *Salix* sp. and alders *Alnus* sp.

Extensive logging and fires have occurred in the Forest as well as in most of northern Minnesota (Jesness and Nowell 1935). Just to the south and east lies probably the largest expanse of peatland in the world (Heinselman 1963; Hofstetter 1969, unpublished doctoral dissertation, University of Minnesota, Minneapolis, Minnesota). North and west, the major land use is agricultural, although blocks of aspen, willow, and alder remain in some areas, especially on poorly drained land and some state owned property. The major type of agriculture involves production of small grains and livestock (Minnesota Crop and Livestock Reporting Service 1976).

Over 1,600 farmers settled in what was to become the Beltrami Island State Forest during an ill-fated land boom in the early 1900s. A massive drainage project resulted in about 2,900 km of ditches for draining peatlands for agricultural improvement (Manweiler 1938). However, the peat beds did not drain well, the land soon proved unsuitable for agriculture, and the economic condition of the settlers reached a critical level. Starting in 1934, the Beltrami Island Resettlement Project began purchasing farms and relocating families on more fertile soil. That project essentially was completed by 1936 (Dana et al. 1960). Shortly thereafter, the state began managing the area for wildlife production (Manweiler 1939). Several old fields, homestead openings, and cabins still are evident, as are the drainage ditches and old roads.

Hunting, trapping, and logging currently are the major human activities

within the Forest. A fairly extensive road system in all but the south-central part of the Forest permits easy access to less swampy areas. Nonetheless, human activity and its impact on wildlife currently are less than when homesteaders occupied the area.

The population of deer in the study area apparently has declined over the past 3 to 4 decades, but is still substantially higher than in northeastern Minnesota. Counts of tracks and deer pellet groups by the Minnesota Department of Natural Resources indicated a deer density of 4 to 6/km² during the study. Density of moose was at about 0.3/km²; the western part of the Forest supported the higher numbers (W. E. Berg, pers. comm.). Beaver live along ditches and natural waterways where there was about 0.33 active colony/km during the study (V. E. Gunvalson, pers. comm.).

Wolves probably were abundant in the study area before settlement. Interviews with some longtime residents of the area, including some former residents of the Forest itself, indicated that wolves were rare to nonexistent during the period of human occupancy. Wolves reoccupied the area after removal of the homesteaders in the mid 1930s and have survived there since. Seeking a substantial bounty, several local persons took wolves in the 1940s, 1950s, and early 1960s by trapping and aerial hunting. Minnesota Department of Conservation (now Minnesota Department of Natural Resources) personnel were active in wolf control during that period.

The number of wolves bountied during the 1940s and 1950s is unknown, as wolves and coyotes *Canis latrans* were not distinguished in records. However, approximately 15 wolves were estimated to have been taken annually from the Forest in the 1950s (E. Clem, pers. comm.). The population may have increased after about 1960, because of less exploitation (E. Clem, pers. comm.). Prior to that time, coyotes were thought to outnumber wolves in the Forest. Even during the early 1960s, the ratio of coy-

otes to wolves bountied at Norris Camp was 20:1. A bounty on wolves was in effect in Minnesota until 1965 (Van Ballenberghe 1974). Total legal protection was granted in August 1974 by the Endangered Species Act of 1973. The U.S. Department of the Interior reclassified the wolf in Minnesota from "endangered" to "threatened" in spring 1978.

METHODS

Data collection in this study required capturing and radiocollaring (Kolenosky and Johnson 1967) as many wolves as possible throughout the study area. Therefore, a major portion of field time was devoted to trapping. Numbers 4 and 14 Newhouse traps were set mainly along forest roads where tracks or other wolf "sign" had been located, or near centers of wolf activity (Mech 1974b). Traps were checked each morning. Most trapping was conducted from May to October when access to all regions of the study area was easiest and wolf packs were least mobile. Beginning in July, attempts were made to capture pups near rendezvous sites.

Captured wolves were anesthetized with phencyclidine hydrochloride (Sernylan, Parke-Davis Co.) and promazine hydrochloride (Sparine, Wyeth Laboratories) administered via a jabstick, with dosages as recommended by Seal et al. (1970). Pups that weighed up to 16 kg were handled without drugs. All wolves were examined, eartagged, and weighed, and measurements of body length and canine teeth length were taken. Testes were measured, or extent of nipple development was noted. Pups less than 7 months old were distinguished from adults by tooth replacement or length of permanent canines (Van Ballenberghe and Mech 1975). Blood samples of up to 60 cc from adults and 30 cc from pups were drawn for examination. Any wolf whose foot might have been injured by the trap was injected with 1,200,000 units bicillin (Wyeth). Some wolves were given vitamin injections to ensure viability

until movement and behavior became normal.

Forty-one collars of denture acrylic (Mech 1974b) fitted with transmitters from AVM Instrument Co.¹ were placed on 35 wolves (including recaptures). Transmitters functioned for up to 27 months, and although they generally performed well, at least 11 transmitted intermittently for part of their lives. Signals from 2 became weak, and another expired prematurely because of increased battery drain due to an accelerated pulse rate. Despite the satisfactory performance of most radios, many potential data were lost as a result of the few malfunctions.

Failure to obtain the signal from a transmitter could indicate (1) the transmitter had failed, (2) the wolf had moved out of tracking range, or (3) the wolf had been killed and its transmitter damaged.

Most location data and virtually all observational data were obtained by homing, using aerial radiotracking (Mech 1974b). A Cessna 180, a Cessna 172, and a Piper Supercub were employed to determine 2,295 locations of instrumented wolves during about 840 hours of flying. Instrumented wolves were located an average of about once every 3 days during summer 1973 and from May 1974 through September 1976. Flights before and after those dates were less frequent. We attempted to locate wolves in early morning as much as possible, because they are more active and more likely to be seen then (Mech 1970).

After instrumented wolves were found, their location was plotted on a map or aerial photo, and the number of wolves present, time, behavior, and habitat were noted. Wolves were observed 850 times, and the rate of observation of instrumented wolves ranged from 13 percent in June to 74 percent in December and January. The size of territories was estimated by measuring with a planimeter

¹ 3101 W. Clark Rd., Champaign, Illinois 61820. Mention of brand name does not constitute endorsement.

the minimum area covered (Mohr 1947). Aerial and ground searches for tracks produced information on location and size of noninstrumented social units. Estimates of wolf density followed procedures described by Mech (1973, 1977b) and Van Ballenberghe et al. (1975).

Aerial checks of known dens and rendezvous sites were made, whether or not instrumented pack members were present, so that pups could be counted. Presence or absence of wolves at such sites also was checked by ground telemetry and by attempts to induce howling (Joslin 1967) whenever accessibility permitted. Some attempts to locate instrumented wolves from a vehicle and from 2 fire lookout towers were successful. Observation from the ground was not possible because of the flat terrain and dense vegetation. Ground checks of wolf locations were made when the signal was inexplicably stationary.

Wolf scats were collected from forest roads and trails and den and rendezvous sites. Wolf scats often were distinguishable from those of other species by size and the presence of wolf tracks at the site of defecation (Weaver and Fritts 1979). The 2 species whose scats might most readily be confused with wolf scats are dogs *Canis familiaris* and coyotes. Because both species were rare in the forest during the study, we believe the number of nonwolf scats in the collection was negligible.

Date of scat deposition was recorded as accurately as possible. Precise dating occurred only when certain roads were cleared at intervals of up to 2–3 months in summer. Scats were collected from unplowed roads as soon as they became passable by vehicle in spring, thus permitting only a “winter” classification. Scats collected at dens and rendezvous sites of instrumented packs were dated according to period of known occupancy.

Identification of prey remains in scats was based on comparison with remains in wolf scats of known content derived from feeding trials (Floyd et al. 1978) or comparison with parts of museum speci-

mens. Identification usually was possible from gross examination of hairs (Stains 1958); however, microscopic examination of hair medulla (Mayer 1952) and scale pattern (Adorjan and Kolenosky 1969) frequently was helpful. In an identification test of an assemblage of wolf scats of known content, Fritts identified 38 of 39 correctly. He was unable to distinguish between hair from deer and moose in all cases. The scale pattern of hairs from those 2 species may differ slightly, but differences were not distinct enough to allow classification of all scats containing cervid hairs (Peterson 1974).

Food items were grouped into 9 categories, and the percentage relative estimated bulk (% REB) of each category was calculated (Lockie 1959). For that calculation it was necessary to estimate the proportions of different foods in scats that contained more than 1 food species (15.7% of the sample). For example, a scat with about equal proportions of deer hair and moose hair would have 0.5 occurrence of each food. The total number of food occurrences was always 1.0 for each scat. We chose that method of dietary comparison over the more common percentage “frequency of occurrence” because of the inherent tendency of the latter method to overestimate uncommon prey and underestimate common prey (Scott 1941, Lockie 1959). Annual and seasonal differences in number of occurrences of foods were tested for significance by chi-square analyses (Snedecor and Cochran 1967:215).

The approximate relative biomass and relative numbers of different prey species in the diet were calculated (Floyd et al. 1978). The known relationship between prey size and weight of prey per collectable scat (Floyd et al. 1978), together with number of occurrences of each prey in scats and weights of prey species taken from the literature, were used in those calculations. Calculations were made for both summer and winter and were refined by considering age ratios of deer and moose eaten and weights of subadults at different seasons.

Figures of biomass and numbers for deer and moose in summer represent averages of the figures calculated independently for April–May, June–July, and August–September. It usually was possible to classify hair from deer and moose in scats collected from May to July as either fawn/calf or adult, which made possible a direct estimate of fawn and calf representation in the diet through July. However, all scats with cervid remains collected during that period could not be distinguished as fawn/calf or adult. We assumed that the ratio of juvenile remains to adult remains was the same in the unidentified samples as in the identified samples. Therefore the unidentified scats collected during that portion of the summer were allocated accordingly.

However, during April–May, August–September, and winter (October–March) it was impossible to distinguish age cohorts of cervids by their hair, so it was necessary to use the known or estimated age structure of deer and moose killed by wolves to estimate biomass and total numbers of prey represented. The fawn:adult ratio of deer in winter was known from examination of deer killed by wolves located during aerial telemetry. Because no such data were available for moose, we used ratios of moose that died from natural causes in northwestern Minnesota in 1969–1974 (Berg 1975). These ratios probably were similar to age ratios among the moose that were eaten by wolves because most of the moose eaten were believed to have been scavenged.

The identity of prey seen near wolves during telemetry flights was recorded. Carcasses were examined on the ground whenever possible, and an effort was made to determine their sex, age, and physical condition. Deer killed by wolves were aged by tooth replacement (Severinghaus 1949) and dental annulation (Gilbert 1966).

Reports of wolf depredations on livestock were solicited and investigated. Farmers near the Forest or near territories of radiocollared wolves were ques-

tioned regarding possible loss of livestock to wolves, and were encouraged to report losses. The U.S. Fish and Wildlife Service's Animal Damage Control Office contributed information on complaints received and investigated near the study area from 1974 through 1977.

CAPTURE DATA

Thirty-nine wolves were captured and 35 were radiocollared between August 1972 and June 1976 (Table 1). One wolf was radiocollared 3 times and 5 were collared twice. Many wolves escaped from traps. At first capture, 22 wolves were adults or yearlings and 17 were pups. The sexes of the combined age groups were 16 males and 23 females. The color of most captured wolves was gray or gray with rufous guard hairs. Three were a light shade of gray, and 1 was white. Three additional white wolves were seen during aerial observation of the study packs. No black wolves were captured or observed.

Trap nights for the study totaled 7,882. Most of the trapping was conducted during summer and, when possible, near activity centers. Other Canidae captured incidentally were 81 red foxes *Vulpes vulpes* and 3 coyotes.

DESCRIPTION AND HISTORY OF INSTRUMENTED SOCIAL UNITS

All but 2 instrumented wolves associated with 1 or more other wolves while under study. Altogether, 16 packs and pairs were radiotracked for periods that ranged from a few days to 4 years (Fig. 2). The number of groups followed in the main study area was higher after 1974 because of more intensive trapping effort and an increase in number of social units. In 3 cases, instrumented wolves dispersed from and settled outside the Forest and contributed to the formation of new groups.

Clear River Pack (CRP)

The Clear River Pack was the first and most intensively studied group (Fig. 3).

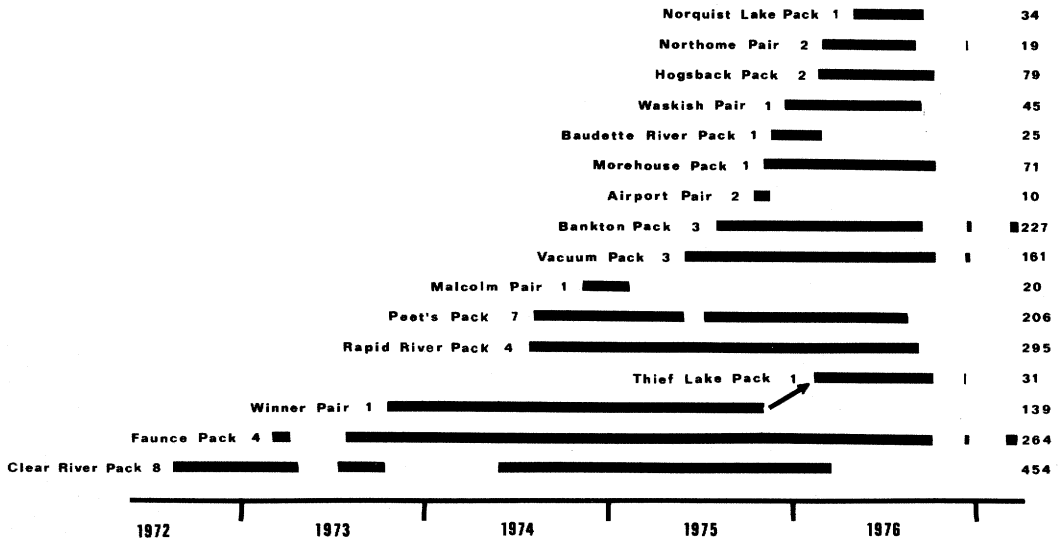


FIG. 2. Periods of radio contact with wolf social units. Numbers left of bars indicate the numbers of wolves instrumented; numbers at right indicate numbers of aerially determined radio fixes for each group.

Its territory was near the northern edge of the Forest and was relatively accessible to humans. Thus, that pack was highly persecuted early in the study. According to local residents and Minnesota Department of Natural Resources personnel, a pack had occupied that particular area for several years. In addition to the animals represented in Fig. 3, 2 wolves without radiocollars were shot within the pack's range in November 1973.

The pack may have accepted a new alpha male in winter 1972–1973. Its breeding male, 2451, was shot on 24 January 1973, by which time he probably had not bred the white adult female that whelped that spring. A female pup from the litter of 1972 bred in 1974 and held the alpha position until her death in early 1976.

Two pups captured from the Clear River Pack were too small for radiocollaring; they were male 5101 in 1973 and female 5117 in 1974. Female pup 5143 separated from the pack in February 1975 but remained within or near the edge of the territory for a month before loss of her signal.

In view of the number of adults present

in spring 1975 and the production of what seemed (from induced howls) to be several pups, the Clear River Pack was surprisingly small in autumn 1975. In November, the group abandoned the eastern two-thirds of its territory and began to explore the area to the southwest. Movements in January 1976 were as far as 18 km southwest of any previous radio fixes and were clearly within the Winner Pair's range.

Around 20 January 1976, alpha female 2455 was killed by a pack, possibly a group that had usurped the eastern part of the Clear River Pack's territory. Her probable daughter, 5151, and 2 other wolves survived in the western part of the original territory until at least mid-March 1976. That trio may have reproduced in 1976, because reports of considerable wolf activity in that area were received, and tracks of 4 or more wolves were seen there in winter 1976–1977.

Faunce Pack (FP)

Male 5051 was observed twice in the eastern Forest during a 10-day period of tracking in late March and early April

TABLE 1.—SEX, AGE GROUP, WEIGHT, PACK AFFILIATION WHEN FIRST CAPTURED, NUMBERS OF RADIO FIXES, TIMES OBSERVED, AND FATE OF 39 WOLVES CAPTURED IN THE BELTRAMI ISLAND STATE FOREST, MINNESOTA, 1972–1976. P = PUP, Y = YEARLING, A = ADULT

Number	Date captured	Sex	Age	Weight (kg)	Pack affiliation	No. aerial fixes	No. ground fixes	No. times observed	Fate
2451	18 Aug 1972	M	A	47.6	Clear River	20	0	5	Shot 24 Jan 1973
2453	18 Aug 1972	F	P	12.2	Clear River	20	1	4	Trapped 3 Feb 1973
SHF 67 ¹	20 Aug 1972	F	Y or A	—	Clear River	—	—	—	Died at capture
2455	24 Aug 1972	F	P	13.6	Clear River	192	32	69	Killed by wolves Jan 1976
2457	21 May 1974	F	2 yrs	34.0	Clear River	7	1	2	Shot 19 Nov 1972
5051	24 Aug 1972	M	P	12.2	Clear River	—	—	—	—
	3 Mar 1973	M	A	38.6	Faunce?	—	—	—	—
	17 Aug 1973	—	A	34.0	?	—	—	—	—
5101 ¹	1 Jun 1975	—	A	35.8	Vacuum	101	15	65	Survived at least until 17 Dec 1976
5105	15 Jul 1973	M	P	13.6	Clear River	—	—	—	?
	15 Jul 1973	F	Y or A	27.4	Clear River	215	8	82	Trapped at farm and euthanized 7 Jul 1980
	4 Jun 1975	—	3+ yrs	30.4	Winner	—	—	—	—
5109	23 Jul 1973	M	Y or A	33.1	loner	16	4	1	Shot 18 Nov 1973
5111	28 Jul 1973	F	A	27.7	Faunce	26	18	8	Killed by wolves Mar 1974
5113	17 Aug 1973	M	Y or A	33.1	loner?	5	1	0	? Signal lost Sep 1973
SHF 125 ¹	11 Sep 1973	F	P	11.3	Faunce	—	—	—	Killed in trap by humans
5115	18 Sep 1973	M	P	15.4	Faunce	115	31	30	Survived at least until 5 Aug 1977
5117 ¹	10 Jul 1974	F	P	8.6	Clear River	—	—	—	?
	14 Jul 1974	F	P	8.6	Clear River	—	—	—	?
5119	23 Jul 1974	F	A	32.0	Clear River	—	—	—	?
	20 Aug 1974	—	A	36.3	Rapid River	—	—	—	?
	3 Sep 1975	—	3+ yrs	38.1	Rapid River	173	11	88	Survived at least until 9 Sep 1976
5103	28 Jul 1974	M	Y or A	40.8	loner	41	0	18	Shot 15 Feb 1975
5123	3 Aug 1974	M	P	11.8	Peet's	6	0	0	Died Aug–Sep 1974
5107	3 Aug 1974	F	A	33.6	Peet's	71	4	40	Survived at least until 11 Feb 1976
840	17 Aug 1974	M	P	12.2	Rapid River	5	3	0	Died of capture injury Sep 1974
5141	22 Aug 1974	M	P	15.0	Clear River	173	35	53	Survived at least until 15 Sep 1976
	20 Sep 1974	F	Y or A	31.3	loner	—	—	—	—
	24 Jul 1975	—	A	31.3	Faunce	142	25	54	Survived at least until 16 Mar 1977
5143	23 Sep 1974	F	P	20.9	Clear River	41	2	15	? Signal lost Mar 1975
5145	24 Sep 1974	F	P	16.3	Rapid River	125	3	64	Survived at least until 12 Dec 1976
5151	9 May 1975	F	Y or A	33.1	Clear River	51	16	10	Survived at least until 16 Mar 1976
5153	1 Jun 1975	M	Y or A	34.9	Vacuum	41	9	12	Survived at least until 17 Jan 1976
5155	2 Jun 1975	F	Y or A	27.7	Vacuum	106	13	45	Survived at least until 10 Oct 1976
5157	19 Jul 1975	M	A	33.6	Peet's	8	0	4	Died Aug 1975

TABLE 1.—CONTINUED

Number	Date captured	Sex	Age	Weight (kg)	Pack affiliation	No. aerial fixes	No. ground fixes	No. times observed	Fate
5159	21 Jul 1975	F	P	10.0	Peet's	9	1	3	Died Sep 1975
5161	21 Jul 1975	F	P	10.0	Peet's	10	1	3	Shot 8 Sep 1975
5165	30 Jul 1975	F	A	29.0	Bankton	95	2	49	Killed by wolves 4 Mar 1978
5167	31 Jul 1975	M	P	13.6	Bankton	99	4	31	Killed by humans 21 Jan 1979
5169	10 Aug 1975	F	Y or A	26.3	loner	49	1	24	Survived at least until 28 Feb 1976
5171	31 Aug 1975	F	Y or A	30.8	Rapid River	38	11	14	Killed by humans Feb 1976
5173	9 Sep 1975	F	P	12.7	Peet's	95	3	41	Survived at least until 28 Oct 1976
5175	13 Sep 1975	M	P	20.0	Peet's	17	2	3	Shot Nov 1975
376	22 Feb 1976	M	A	37.6	Hogsback	54	35	13	Died (killed by humans?) Sep-Oct 1976
844	22 Feb 1976	F	A	27.7	Hogsback	25	22	10	Died Jun 1976
848	1 May 1976	F	Y or A	29.5	Norquist Lake	34	3	5	? Signal lost Sep 1976
5510	10 May 1976	F	Y	27.2	Bankton	33	3	8	Killed by wolves Mar 1977

¹ Not instrumented.

1973. He was seen with a white wolf on both occasions and with another gray wolf at least once. That trio was considered to be the Faunce Pack (Fig. 4). Male 5051's radio failed in April. In August, he was recaptured about 25 km west of the pack's range, and subsequent radiotracking indicated he resided there.

A white female, 5111, that had pups was instrumented in July near where a white wolf had been seen with male 5051. Thus, female 5111 was assumed to be male 5051's previous associate. The relationship of 5051 and 5111 was not understood. However, the male's dissociation from the Faunce Pack apparently was not a case of normal dispersal, because he was already a "middle aged" wolf at that time as indicated by tooth wear. Either 5051 or the other adult sized wolf seen in March could have sired 5111's litter in 1973.

The presence of a second adult wolf in the Faunce Pack was not confirmed in summer and autumn of 1973. Possibly, the adult female was without assistance in feeding her pups. Local trappers took 2 male wolves from the pack's range in winter 1972–1973. Conceivably, one of them could have been 5111's mate.

Female 5111 and her instrumented male pup, 5115, were separated on all 19 days they were located between 7 October 1973 and 7 March 1974. The adult ranged over at least 487 km² before being killed by wolves within the Oaks deer yard, a few km south of the pack's probable range.

Male pup 5115 and 2 companions ranged over at least 880 km², trespassing into territories of the Rapid River Pack and Peet's Pack, before restricting themselves to about 555 km² in the east-central Forest. The latter range corresponded well with locations of adult male 5051 in March 1973, and of adult female 5111 and 5115 as a pup in summer and autumn 1973. The 2 companions of 5115 might also have been pups from the 1973 litter. The group did not reproduce in 1974, and 5115, as a yearling, appeared to be the

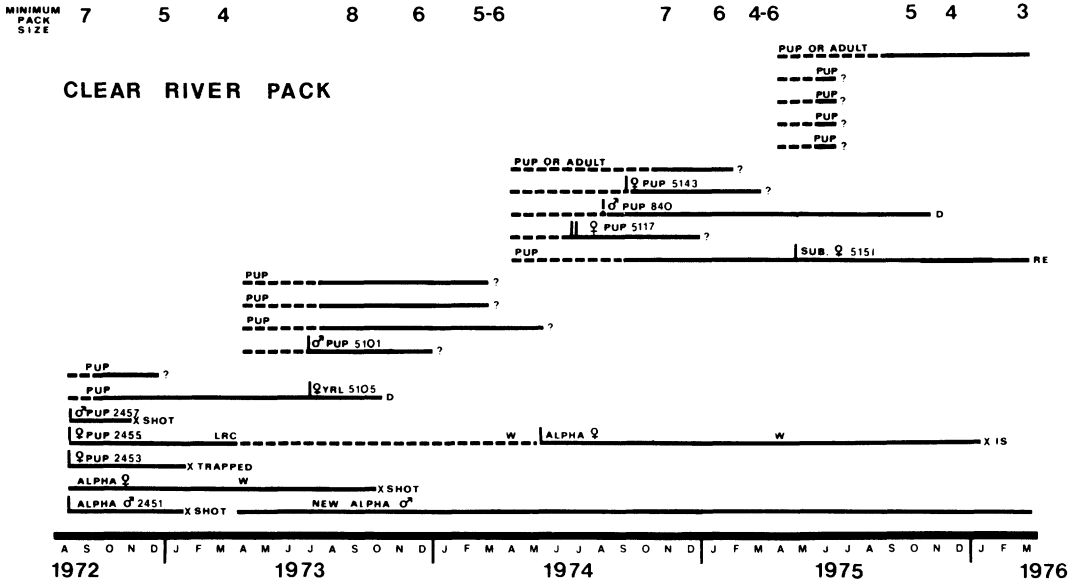


FIG. 3. Flow chart of data on Clear River Pack. Solid line = presence known; dashed line = presence inferred; | = captured and radiocollared; D = dispersal; IS = intraspecific strife; LRC = lost radiocollar; RE = radio expired; W = whelped; X = death; ? = fate unknown.

dominant member of the trio, at least by autumn 1974.

The new pair of male 5115 and female 5141 (previously a lone wolf) settled in the northwestern part of the Faunce Pack's range in spring 1975 and produced pups. The fate of 5115's 2 companions is unknown. Possibly they were among the progenitors of 3 new packs that formed within the original territory of the Faunce Pack.

In summer 1977, 5115, another adult or yearling male, and a female pup were captured by a U.S. Fish and Wildlife Service control trapper at a nearby farm where wolf predation on swine had been reported.

*Winner Pair (WP)/Thief
 Lake Pack (TLP)*

After leaving the Clear River Pack in October 1973, nonbreeding female 5105

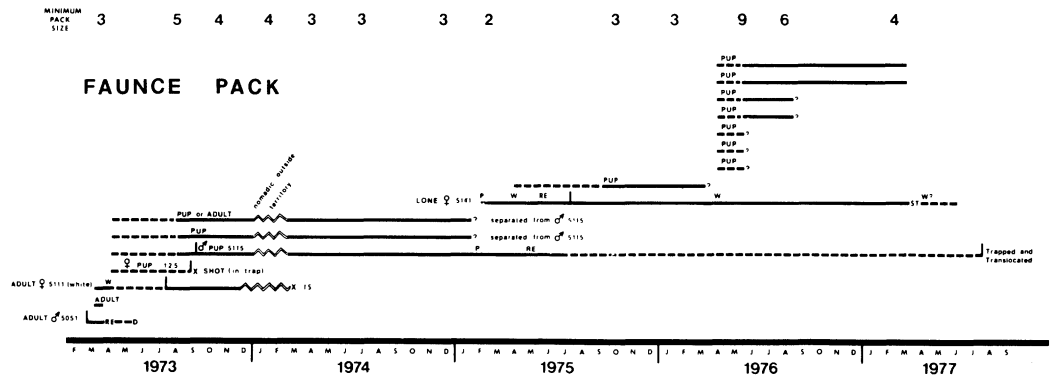


FIG. 4. Flow chart of data on Faunce Pack. Solid line = presence known; dashed line = presence inferred; | = captured and radiocollared; IS = intraspecific strife; P = paired; RE = radio expired; ST = stopped tracking; W = whelped; X = death; ? = fate unknown.

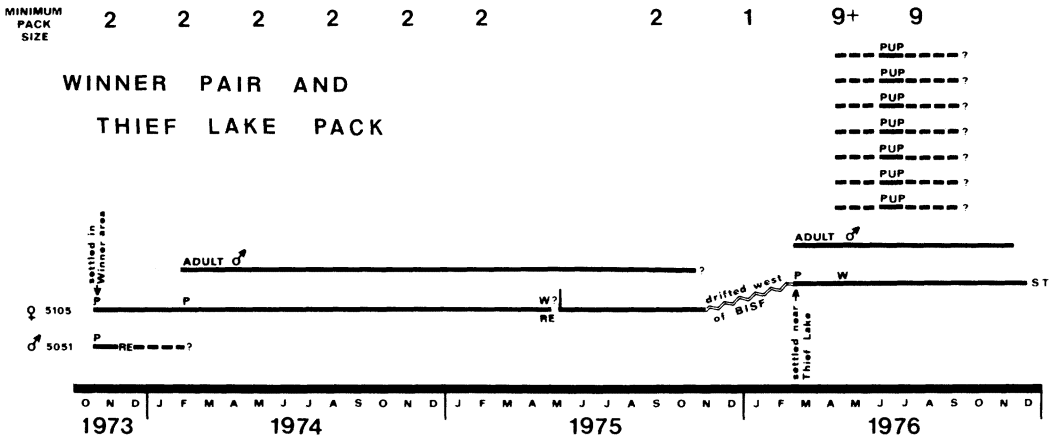


FIG. 5. Flow chart of data on Winner Pair and Thief Lake Pack. Solid line = presence known; dashed line = presence inferred; | = captured and radiocollared; P = paired; RE = radio expired; ST = stopped tracking; W = whelped; ? = fate unknown.

immediately settled in an area adjoining the parent territory to the southwest (Fig. 5). The scarcity of wolf sign in that area indicated no pack was present. Adult male 5051 (previously with the Faunce Pack) used part of that area from August to November and was located with 5105 on 3 occasions over a 20-day period. This was a short-lived relationship, however. The female paired with a different male in midwinter 1973–1974 but produced no pups in 1974.

It was not clear whether the Winner Pair produced pups in 1975. Female 5105 dened and later frequented 3 locations that could have been rendezvous sites. Her teat development in early June indicated she probably had suckled 2 pups. Howls were induced from what seemed to be a pup at one of those locations, but no pups were observed. An event that might have influenced early pup survival was the capture and escape of an adult wolf from a trap within 100 m of the den on 29 May 1975 and the subsequent abandonment of the site.

After disappearance of her mate in November 1975, 5105 gradually abandoned her territory and began drifting within an adjacent undeveloped area west of the Forest. At that time, the neighboring Clear River and Vacuum packs began in-

truding into her range, which might have been responsible for her final abandonment of it. No. 5105 and a mate that was not habituated to the tracking aircraft and thus probably was from a nonradiocollared pack, colonized a marshy, undeveloped area north of Thief Lake and became the progenitors of the Thief Lake Pack. In July 1977, a U.S. Fish and Wildlife Service control trapper captured 2 pups near the group's 1976 den. No. 5105 remained in the area until July 1980, when she was captured at a nearby farm where wolves were killing sheep (Fritts, unpubl.). Examination of teat development indicated she probably had suckled pups in 1980.

Rapid River Pack (RRP)

The Rapid River Pack was known to exist in summer 1973 but was not instrumented until 1974 (Fig. 6). Radio locations of pack members were closely associated with the Rapid River and nearby vegetation; peatbogs are found north and south of the river in that part of the Forest.

We had little success in counting pups from the Rapid River Pack in 1974 and 1975. A den was visited on 20 May 1975, and 2 pups were outside, while at least

MINIMUM
PACK
SIZE

6 5 5

9 7 6

8+

RAPID RIVER PACK

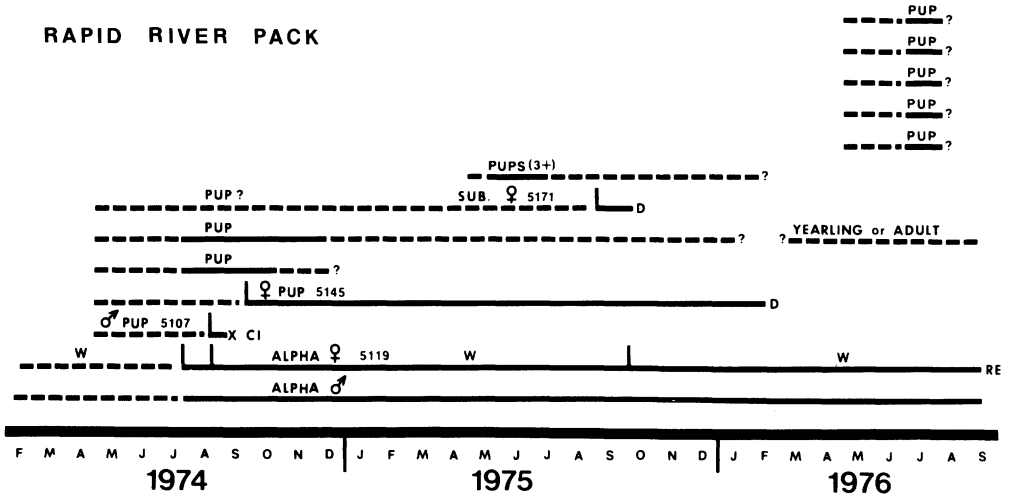


FIG. 6. Flow chart of data on Rapid River Pack. Solid line = presence known; dashed line = presence inferred; | = captured and radiocollared; CI = capture injury; D = dispersal; RE = radio expired; W = whelped; X = death; ? = fate unknown.

l more whined within the den. Induced howls suggested good pup production both years.

A yearling female, 5145, spent little time with the pack during its sedentary phase in 1975. Most of her locations were at the edge of the territory or southwest of it.

Size of the Rapid River Pack's territory was about 330 km², much of which was peatland. The territory shifted a few kilometers to the west during the study to include part of what earlier had been the eastern edge of Peet's Pack's territory.

Peet's Pack (PP)

As with the Rapid River Pack, Peet's Pack was discovered in summer 1973, but efforts to capture a pack member were not successful until 1974 (Fig. 7). The territory used by Peet's Pack diminished during the study, as the Rapid River Pack to the east and the nonradiocollared Moose River Pack to the west began infringing on parts of the range utilized by this group in 1974.

Adult male 5157 was in poor condition

at capture and died of undetermined causes in August. Several blood characteristics were deviant (U. S. Seal, pers. comm.). Examination of the skeleton revealed an advanced case of osteoarthritis (Fritts and Caywood 1980).

Malcolm Pair

Adult male 5121 drifted throughout the southern two-thirds of the Forest as a lone wolf in late summer and autumn 1974. Beginning in mid-November he was seen with a smaller companion. The 2 wolves appeared to be colonizing an area in the southwestern part of the Forest where there was no resident pack. They remained together consistently until mid-November, after which the smaller wolf was seen with 5121 on less than half of 5121's observations. The companion was frightened of the tracking aircraft throughout all observations.

Beginning in mid to late January, some of 5121's locations (apparently alone) were outside the jointly used area, but he was with the smaller companion again on 5 and 8 February. He was shot on 15 Feb-

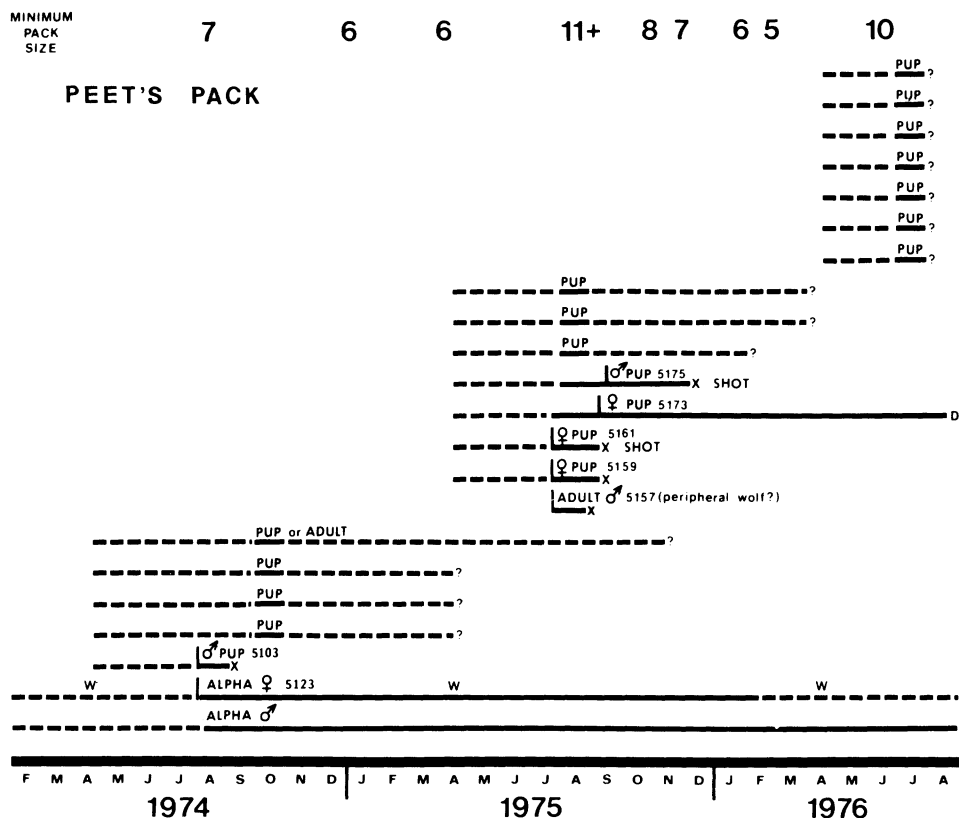


FIG. 7. Flow chart of data on Peet's Pack. Solid line = presence known; dashed line = presence inferred; | = captured and radiocollared; D = dispersal; W = whelped; X = death; ? = fate unknown.

ruary. It was not clear at that point whether those wolves had pair bonded and would have formed a pack.

The progenitors of the nonradiocollared Moose River Pack may have been establishing a territory in the same general area, or possibly just north of the Malcolm Pair, during winter 1974–1975. Presence of that group might have influenced the behavior of 5121 and his companion and thus explain his erratic movements and the ambiguity of his relationship with his companion.

Vacuum Pack (VP)

This pack probably was present at the beginning of the study (Fig. 8). Though it was not instrumented until summer 1975, considerable information on size

and movements of the group was obtained by snowtracking in winter 1974–1975. Adult male 5051 was a member of the Vacuum Pack in June 1975, and, based on observations of social interactions with other members of the pack, he appeared to be the alpha male. Previous known associations of that wolf were with female 5111 of the Faunce Pack in March 1973 and female 5105 in the western Forest in November 1973.

The Vacuum Pack's territory overlapped considerably with an area to the west used by the Winner Pair. In winter 1975–1976, the territory changed considerably. Much of the Winner Pair's range was annexed, whereas some area at the southwestern side of the territory was relinquished to female 5155 and her mate (Morehouse Pair). During that winter,

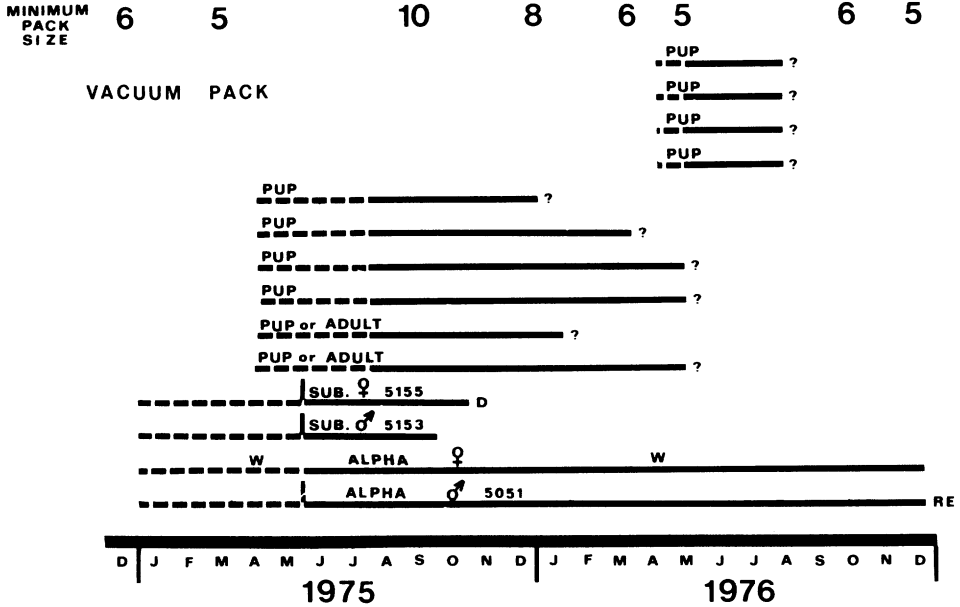


FIG. 8. Flow chart of data on Vacuum Pack. Solid line = presence known; dashed line = presence inferred; | = captured and radiocollared; D = dispersal; RE = radio expired; W = whelped; ? = fate unknown.

movements of the Vacuum Pack were the most extensive of any pack in the Forest, and covered about 500 km².

Bankton Pack (BP)

The Bankton Pack originated in winter 1974-1975. At that time, tracks of a pair

were found in the southeastern part of the 555-km² range used by the Faunce Pack (Fig. 9). Telemetry data indicated little, if any, use of this area by the Faunce Pack (male 5115 and 2 associates) after midwinter. The Bankton Pack relinquished some of the northeastern part of its newly acquired territory to the new

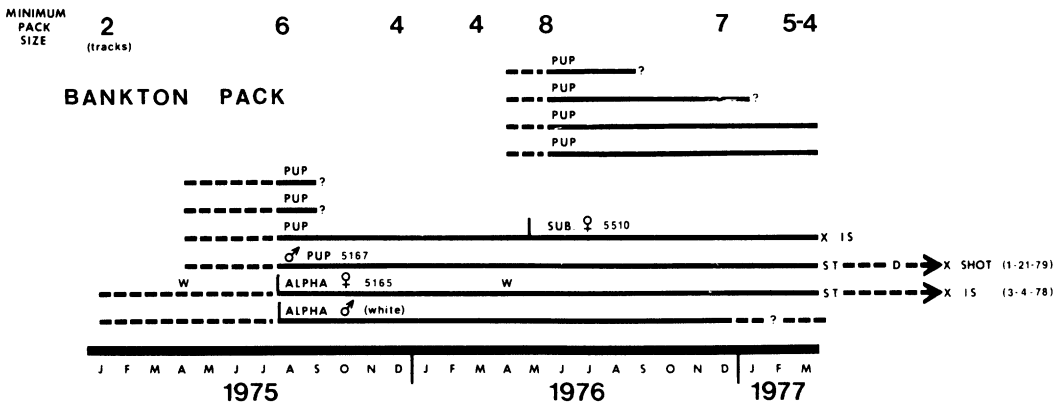


FIG. 9. Flow chart of data on Bankton Pack. Solid line = presence known; dashed line = presence inferred; | = captured and radiocollared; D = dispersal; IS = intraspecific strife; ST = stopped tracking; W = whelped; X = death; ? = fate unknown.

Baudette River Pack by winter 1975–1976. Pack members 5510 and 5165 were killed by wolves in March 1977 and 1978, respectively. We were unable to determine which packs were responsible. Female 5165 was killed at the edge of their territory, whereas 5510 died well within their territory and near a deer carcass from which the Bankton Pack fed. Female 5165 was carrying 7 embryos when killed.

Airport Pair

Between 2 and 7 October 1975, male 5153 dispersed from the Vacuum Pack and female 5171 left the Rapid River Pack. By 21 October, the 2 wolves were traveling together. The pair remained together until about 21 November and spent much of that period near the Norris Camp airstrip.

After breakup with 5171, male 5153 was located only twice because of a malfunctioning radio. On the second occasion (January 1976), he was with another wolf in the northern part of the Forest. Snowtracks revealed the pair had heavily scent marked roads near the location. Therefore, they may have been attempting to establish a territory in that area (Rothman and Mech 1979). That duo is referred to later as the Bednar Pair.

Female 5171 eventually left the Forest and dispersed into Canada. She was killed by humans near the Canadian border in February 1976.

Morehouse Pack (MP)

The Morehouse Pack originated in autumn 1975 after 5155, a subordinate female, left the Vacuum Pack about 25–28 October and paired between 31 October and 4 November. By December, the duo settled at the southwestern edge of the Vacuum Pack's territory. Locations during the remainder of the winter were in a narrow 68-km² strip that was generally among the territories of the Vacuum, Peet's, and Moose River packs. Female 5155 denned in spring, and at least 4 of

her pups survived until mid-September 1976.

The new territory expanded toward the northwest in summer 1976, as the Morehouse Pack began to utilize the southern part of the Winner Pair's abandoned range. Female 5155's radio evidently failed that autumn, for she could not be located in December.

Baudette River Pack (BRP)

As was also true for the Bankton Pack, the Baudette River Pack became established in part of the large range used by the Faunce Pack from 1972 through 1974.

In August 1975, a nonbreeding female, 5169, was radiocollared at the eastern edge of the Forest. She drifted alone until November, after which she was with 2 other wolves in a more restricted area in the northeastern corner of the study area. The group was radiotracked within a 67-km² area until March 1976 when female 5169's radio expired prematurely. Attempts to reinstrument the Baudette River Pack in summer 1976 were unsuccessful. The group produced pups in 1976; howling was induced from at least 3 in July.

Waskish Pair

Yearling male 840 of the Clear River Pack dispersed southeastwardly from that pack's territory in November 1975. By mid-December he was accompanied by a smaller wolf that consistently fled from the tracking aircraft. The pair drifted around the large bog north and northeast of Upper Red Lake before settling in the Red Lake State Forest southwest of Waskish in April 1976. The pair was seen at a den in April, but there was no confirmation that pups were produced. Male 840's radio expired in late September 1976. A pack was reported in that area in winter 1976–1977.

Hogsback Pack

In November 1975, tracks of 2 wolves and intensive scent marking were noted

along the Hogsback Ridge in the central Forest. This, too, was an area where searches for wolf sign previously had indicated very little usage, although the Faunce Pack occasionally visited the area until 1975. The area also had been visited by female 5141 as a lone wolf, and the Airport Pair had been located there or just to the northwest in October and November 1975. A mated pair, male 376 and female 844, was instrumented in this area in February 1976. The female denned, but no pups were seen at the site. She died of undetermined causes in early June. Radiotracking of the male during summer suggested he was frequenting rendezvous sites. The presence of pups finally was confirmed when at least 1, and probably 2, were seen at a deer carcass bait in late August (G. Nordquist, pers. comm.).

Beginning in early July, male 376 was accompanied by a smaller and lighter colored adult wolf which presumably became his new mate. The pair was seen scent marking together on 12 July.

Each of 5 locations of male 376 in September and 1 in October were 4–7 km outside the group's known range and definitely within the Faunce Pack's territory. He died there in late September or early October. Cause of death was uncertain, but human involvement appeared likely. Fate of the other pack members was unknown. Tracks of 4 wolves were seen within the range in December 1976, but it was not known whether they represented survivors of the Hogsback Pack or some other group.

Northome Pair

Yearling female 5145 of the Rapid River Pack dispersed southeastwardly in late February 1976. By 29 February she had paired with a nomadic adult male that had been radiocollared in the Chippewa National Forest, some 90 km from the Rapid River Pack, by W. E. Berg, Minnesota Department of Natural Resources. The duo appeared to be settling into the Armstrong Creek area north of Northome,

about 30 km east of Lower Red Lake. There was no confirmation of pup production in spring, although the female's movements in spring and summer were rather restricted. Contact with the male was lost in June. Female 5145's radio functioned only intermittently throughout 1976, which greatly hampered tracking efforts. She was located last in December 1976 when she was seen with another wolf in the same general area.

Norquist Lake Pack (NLP)

As mentioned earlier, the eastern two-thirds of the Clear River Pack's territory was usurped in winter 1975–1976 by a nonradiocollared pack. Snowtracks of the unmarked group indicated about 6 wolves were present. Attempts to instrument the pack in winter 1975–1976 failed. A nonbreeding female, 848, was instrumented in May 1976. Presence of that animal, probably a yearling, was evidence that a pair had colonized the area and produced pups in 1975 without being detected. Their range must have overlapped considerably with that of the Clear River Pack, which continued to visit the eastern part of its range until about October 1975. Pups were produced by the Norquist Lake Pack in 1976; 4 or 5 were seen in late July. Tracks of at least 4 adult-sized wolves were seen within the pack's territory in May 1976.

Female 848's radio was last heard in mid-September 1976. Presence of at least 6–7 pack members was suggested by snowtracks followed in December 1976.

Moose River Pack (not instrumented)

In autumn 1975, a new pack was discovered near the southwestern corner of the Forest. Previously, there had been very little evidence of wolf activity there, except that the Malcolm Pair had used the same general area in winter 1974–1975. Possibly another pair had successfully colonized the area that winter. Attempts to instrument the group in autumn and early winter of 1975 were

unsuccessful. A sighting of the pack and several observations of tracks indicated 4 wolves were present in December 1975, and a pack was still in that area in summer 1976.

Shilling Pair (not instrumented)

Tracks of 2 wolves were observed repeatedly at the southern edge of the study area during aerial searches for wolf sign in winter and spring 1976. We continued to observe tracks of a pair in the same area into early summer 1976, but failed to capture the wolves. Activity in July was concentrated within a small area, as if pups were present there. However, existence of pups was never confirmed, and fate of the group was not determined before termination of fieldwork.

POPULATION DYNAMICS

Density and Numerical Trend

Several lines of evidence suggest that wolf density was low in 1972 when the study began. The Minnesota Department of Natural Resources conducted aerial surveys for wolf sign in the Beltrami Island State Forest in December 1969 and February 1971. Twenty-two of 31 (70%) track sightings were of 2-3 sets of tracks, and 5 sets were the most seen together (V. E. Gunvalson, pers. comm.). Searches for wolf sign in the Forest by Mech and assistants in 1970-1972 suggested a low density of wolves. Searches for wolf tracks along forest roads in late 1972 and in 1973 also indicated a low population, as did a few aerial searches for wolf sign in winter. Tracks found appeared to represent groups of 4 or fewer, as might be expected in a low density population if pack size is an index of density (Rausch 1967, Zimen 1976). Discussions with trappers and other local persons familiar with the study area also indicated wolves were not abundant when the study began.

During the study, knowledge of the number of wolves in social units (groups

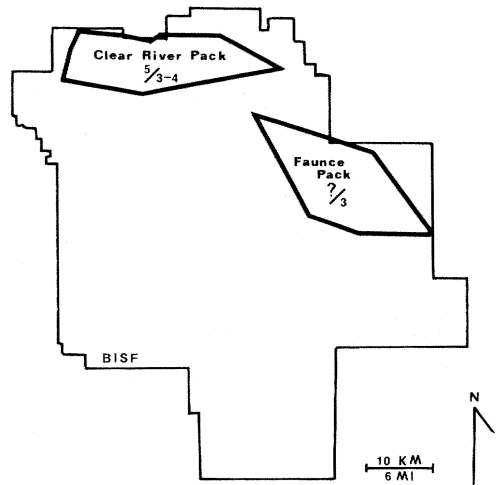


FIG. 10. Size and minimum area occupied by Clear River Pack and Faunce Pack in 1972-1973. Numbers above lines indicate pack size in winter; numbers below lines indicate pack size in spring.

of 2 or more) and of the size of territories permitted objective estimates of population density. The highest counts of each social unit during December-February and March-April were considered the

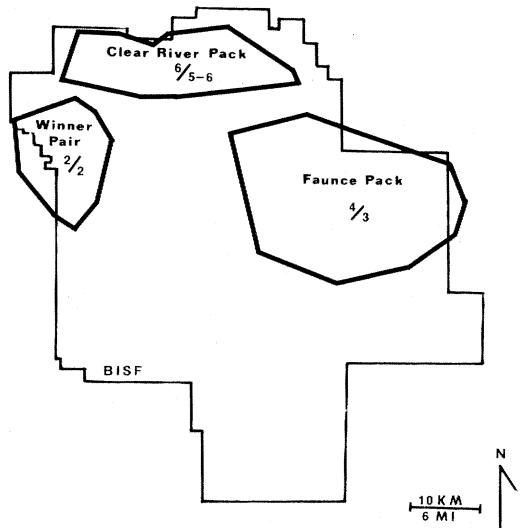


FIG. 11. Size and minimum area occupied by Clear River Pack, Faunce Pack, and Winner Pair in 1973-1974. Numbers above lines indicate pack size in winter; numbers below lines indicate pack size in spring.

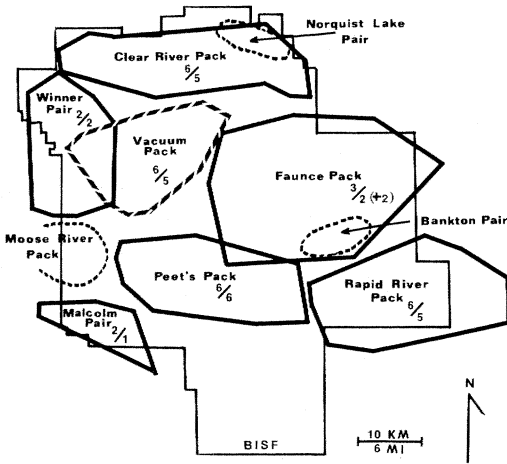


FIG. 12. Size and areas occupied by 10 different social units of wolves in 1974-1975. Numbers above lines indicate pack size in winter; numbers below lines indicate pack size in spring. Dashed lines indicate approximate locations of noninstrumented groups.

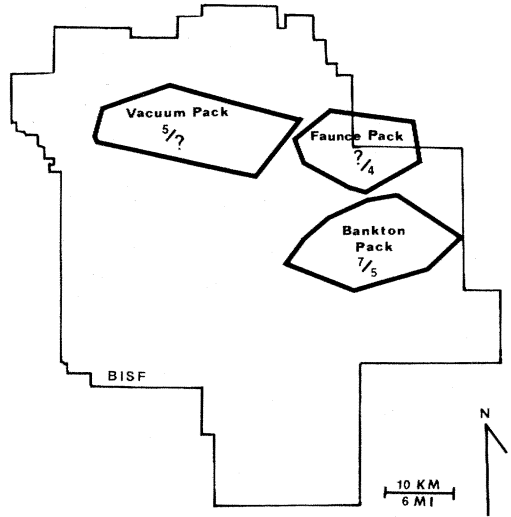


FIG. 14. Size and minimum area occupied by Faunce Pack, Vacuum Pack, and Bankton Pack in 1976-1977. Numbers above lines indicate pack size in winter; numbers below lines indicate pack size in spring.

winter and spring sizes (Mech 1973, 1977b). An estimate of intrapack density was possible for 15 percent of the Forest in winter 1972-1973 (Fig. 10) and 34 percent in winter 1973-1974 (Fig. 11). During the winters of 1974-1975 and 1975-

1976, a greater number and distribution of instrumented social units and more extensive aerial and ground work permitted estimates of total area density over about 2,600 km², corresponding closely to the entire Forest (Figs. 12, 13). In estimating the number of wolves present in winter 1974-1975, we assumed that 3 groups first discovered in summer 1975 existed as pairs the previous winter. Radios remained operative in 3 packs in 1976-1977, permitting an estimate of intrapack density for 20-32 percent of the Forest (Fig. 14). The census area during each year was exclusive of approximately 3 townships of open marsh habitat at the southern edge of the Forest.

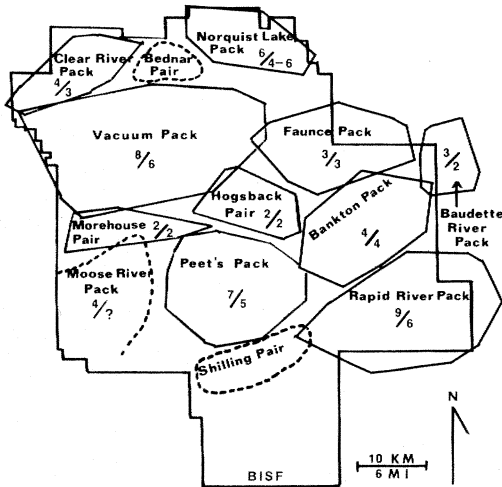


FIG. 13. Size and areas occupied by 13 social units of wolves in 1975-1976. Numbers above lines indicate pack size in winter; numbers below lines indicate pack size in spring. Dashed lines indicate approximate locations of noninstrumented groups.

Although data are too sparse to determine with certainty whether the population was changing early in the study, the available evidence suggests that it was (Table 2). A substantial increase (35%) clearly occurred between winters of 1974-1975 and 1975-1976. The population was expected to be higher during the winter of 1976-1977 because at least 3, and probably 5, new groups produced pups for the first time in 1976.

TABLE 2.—ESTIMATES OF WOLF DENSITY WITHIN THE BELTRAMI ISLAND STATE FOREST, MINNESOTA, 1972–1977

Year	No. wolves observed		Area utilized (km ²)	Population density (wolves/100 km ²)	
	Winter	Spring		Winter	Spring
1972–1973	8+	6–7	395 ¹ –872 ²	0.9–2.0	0.7–1.6
1973–1974	12	10–11	915	1.3	1.1
1974–1975	38 ³	34	2,584	1.5	1.3
1975–1976	58	47	2,563	2.3	1.8–1.9
1976–1977	16	9	538 ¹ –873 ²	1.8–3.0	—
			(winter)		
			313	—	2.9
			(spring)		

¹ Area utilized as indicated by current-year relocations, which probably were too few to describe territories.

² Area utilized as suggested by subsequent relocations.

³ Includes a lone wolf not represented in Fig. 12.

The estimates of total areal density probably gave the most accurate indication of density within the Forest. The total area approach allowed inclusion into the census area of areas between territories, such as open marsh, where wolves rarely visited. Therefore, estimates of density for 1974–1975 and 1975–1976 probably are more accurate than those for other years.

Estimates of population density for each year must be considered minimal. The number of observations of radiocollared groups was sufficient to determine group size in almost all cases, but a few nonradiocollared pairs and lone wolves might have gone undetected. For example, the progenitors of 2 new packs escaped detection in winter 1974–1975, and it is possible that unknown pairs also were present the following winter. Lone wolves appeared to be a temporary and minor component of the study population as it increased. Dispersing wolves and wolves that were loners at capture in summer usually paired before winter. Therefore, no attempt was made to estimate their numbers and adjust the population estimates accordingly (Mech 1973). Lone wolves probably are more common in saturated populations (Mech 1977b) or in very low density populations (Hendrickson et al. 1975).

Less objective evidence also suggested a population increase. For example, wolf sign was much more abundant in the For-

est in 1976 than in 1972 and 1973. Persons living near the study area, and Minnesota state personnel working there, believed that an increase in wolf numbers was occurring. Also, coyote tracks frequently were seen within the Forest from 1972 to 1974, but rarely thereafter. Wolves are intolerant of coyotes (Young and Goldman 1944, Young and Jackson 1951, Stenlund 1955, Mech 1970, Berg and Chesness 1978), so the decrease in coyotes could have indicated increased wolf numbers.

Estimates of wolf density for each winter were lower than estimates from northeastern Minnesota. Densities there ranged from 7.1 wolves per 100 km² along the north shore of Lake Superior to 3.7 per 100 km² in the interior of the Superior National Forest (Mech 1973, Van Ballenberghe et al. 1975). However, by 1976 the wolf populations in northeastern and northwestern Minnesota undoubtedly were at a more comparable density than previously because of the long-term decline in the northeast (Mech 1977a,b) and the increase in the northwest. The increase in the population in the Beltrami Island State Forest is believed to have resulted from the total legal protection provided wolves in August 1974.

Number and Size of Social Units

The number of social units in the Forest increased sharply while the study was

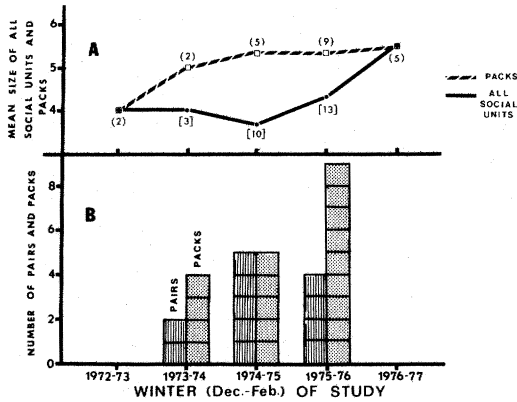


FIG. 15. A. Trends in mean sizes of packs and all social units (packs and pairs), 1972-1973 to 1976-1977. Numbers in parentheses and brackets indicate sample size. B. Minimum numbers of pairs and packs (3 or more wolves) in the Beltrami Island State Forest, 1973-1974 to 1975-1976. Minimum numbers were believed to be very close to actual numbers.

in progress. At least 8 of the 13 social units known to be present in mid-1976 formed during the study. The increase in the wolf population was primarily the result of formation of new groups rather than increased size of groups already present.

Considering the entire study period, 1972-1977, size of social units observed in winter ranged from 2 to 9 (Figs. 10-14) and averaged 4.3 (5.3 with pairs excluded). This indicates a smaller average social unit in the study area than in Superior National Forest. Eleven packs in the eastern National Forest averaged 7.2 members in autumn and early winter of 1971 (Van Ballenberghe et al. 1975). Mean annual pack size in the central National Forest ranged from 4.1 to 7.3 in winters of 1970-1971 to 1975-1976 (Mech 1977b).

The mean size of wolf social units in the State Forest did not increase until late in the study, and mean size of reproducing units alone increased only slightly (Fig. 15A). Some established groups (Peet's Pack, Rapid River Pack, Vacuum Pack) showed small increases, whereas others (Clear River Pack) decreased, or

remained essentially stable through 1976-1977 (Faunce Pack). The greatest increase in size was by colonizing pairs that reproduced and began their own packs. The high number of pairs in the population (Fig. 15B) depressed mean group size, which increased only after some of these colonizers produced pups. The increase in average size of social units in winter 1975-1976 occurred after 3 colonizing pairs present in 1974-1975 (Bankton Pack, Moose River Pack, Norquist Lake Pack) had produced their first litters, and 2 pairs (Malcolm Pair, Winner Pair) had dissolved. All groups known to us in winter 1976-1977 were packs (groups of 3 or more). The number of colonizing pairs in the population at the end of the study was unknown because few wolves were instrumented in 1976. However, the number probably was lower than previously, because all available areas appeared to be filled by 1976-1977.

The failure of reproductive packs to increase significantly in size as the density increased appeared to be in part the result of a high rate of dispersal by yearlings before their second winter of life.

Productivity

A minimum of 4 litters was produced within the Forest in 1974, 7 to 9 in 1975, and 9 to 13 in 1976. The mean minimum size of litters as determined primarily by aerial observation during July and August of those years was 4.0, 4.5, and 4.8 pups (Table 3). Mean size of 3 litters from 1972 and 1973 was 4.0. The uterus of female 5165 contained 7 fetuses in March 1978. Counts of pups in 1976 may have been more complete than in previous summers because of the use of a more maneuverable aircraft and more early morning flights.

Productivity varied considerably among groups. Reasons for failure of the Winner Pair to produce or sustain pups in 1974 and 1975 and for the low pup production or survival in the Faunce Pack and Clear River Pack in 1975 are unknown. Considering all litters of known size during the

TABLE 3.—MINIMUM LITTER SIZE IN SUMMER AND MAXIMUM NUMBER OF PUPS THAT SURVIVED UNTIL WINTER IN 13 SOCIAL UNITS OF WOLVES, BELTRAMI ISLAND STATE FOREST, MINNESOTA, 1972–1976. NUMBERS IN PARENTHESES ARE MEANS IF SOCIAL UNITS THAT PRODUCED NO PUPS ARE EXCLUDED. UNDERLINED NUMBERS REPRESENT KNOWNS

Year	Social unit	Maximum pups observed		Maximum number pups surviving until December ¹
		Number	Month	
1972	Clear River Pack	5	Oct	3
1973	Clear River Pack	4	Jul	<u>4</u>
1973	Faunce Pack	3	Aug	3
Mean		3.5		3.5
1974	Clear River Pack	4	Sep	5
1974	Faunce Pack	Did not den		—
1974	Winner Pair	Did not den		—
1974	Rapid River Pack	4 ²	Aug	4
1974	Peet's Pack	4	Sep	3–4
1974	Vacuum Pack	?		4
Mean		2.4 (4.0)		2.8 (4.1)
1975	Clear River Pack	3 ³		1
1975	Faunce Pack	3 ³		<u>1</u>
1975	Winner Pair	?		<u>0</u>
1975	Rapid River Pack	3+ ²	May	6
1975	Peet's Pack	7	Aug	5
1975	Vacuum Pack	4+	Aug	6
1975	Bankton Pack	4	Aug	<u>2</u>
1975	Moose River Pack	?		<u>2</u>
Mean		4.5		2.9 (3.3)
1976	Faunce Pack	7	May	2
1976	Thief Lake Pack	7	Jul	?
1976	Rapid River Pack	5	Jul	?
1976	Peet's Pack	7	Jul	?
1976	Vacuum Pack	4	Aug	3
1976	Bankton Pack	4	Jul	<u>3</u>
1976	Morehouse Pack	4	Aug	<u>?</u>
1976	Baudette River Pack	3–4 ⁴	Jul	?
1976	Hogsback Pack	2 ⁵	Aug	?
1976	Norquist Lake Pack	4–5	Jul	4–5
Mean		4.8		3.1

¹ Procedure of calculation as described by Mech (1977b).
² Presence of more animals suggested by howling induced from litter.
³ Howls induced from a litter in July.
⁴ Minimum number heard howling. Pups not observed.
⁵ Single observation; may be low.

study period, the mean size of 5 litters by new pairs was 4.1, compared with 4.6 for 15 litters of established packs. However, these means were not significantly different ($t = 0.745, P > 0.05$).

Total pup production within the Forest increased dramatically during the study because of the addition of new reproductive units to the population. In both 1975 and 1976, at least 3 new groups were added. Probably no more than 16 pups were present in summer 1974 and no

more than 35 in 1975. In 1976, at least 40 pups were counted exclusive of any pups born to the Clear River Pack, Moose River Pack, and Shilling Pair, all of which probably reproduced, and of a litter of 7 born to the Thief Lake Pack just west of the Forest. Assuming the Clear River Pack, Moose River Pack, and Shilling Pair produced a total of 10–12 pups, productivity within the Forest would have at least tripled from 1974 to 1976.

Mean litter sizes in the interior of the

TABLE 4.—RATES AND CAUSES OF MORTALITY OF WOLVES INSTRUMENTED IN THE BELTRAMI ISLAND STATE FOREST, MINNESOTA, 1972–1977

Year ¹	No. wolves with active transmitters	No. instrumented wolves that died	% Dying	Cause of mortality				
				Humans	Unknown, suspect humans	Unknown, probably natural	Intra-specific strife ²	Capture injury
1972–1973 ³	5	3	60	3	0	—	—	—
1973–1974	6	2 (?3)	33	1	—	—	1	—
1974–1975	12	3 (?4)	25	1	1 ⁴	—	—	1
1975–1976	24	7	29	3	—	3 ⁴	1	—
1976–1977 ³	13	2	15	—	1 ⁴	—	1	—

¹ 1 Jul–30 Jun.

² Another wolf succumbed to intraspecific strife after fieldwork was completed.

³ Entire year not represented; therefore, mortality rate probably underrepresented.

⁴ Decomposed.

Superior National Forest during June–August of 1972–1975 were 3.0, 3.3, 3.0, and 3.4 (Mech 1977b). Some packs there did not produce pups in 1974 and 1975; if those are included, the mean litter sizes for those years were 1.5 and 1.9. Combining data from different years, the mean number of pups observed in the study area was 4.4 (4.1 including groups not denning) versus 3.2 (2.5 including groups not denning) in the National Forest. Therefore, litter size and early survival of pups were greater in the State Forest during this period when the population was increasing there and declining in the National Forest. The difference probably can be attributed to nutritional levels of the 2 populations (Seal et al. 1975, Van Ballenberghe and Mech 1975, Mech and Karns 1977). Litter size in the State Forest, based on pup counts, was within the range reported for populations believed to have adequate food (Mech 1970).

Mortality

The amount of mortality between birth and 4 months of age was not determined because pups were not instrumented before midsummer. The earliest date on which a litter was observed was 22 May when 7 pups were seen with the Faunce Pack. Only 5 pups seemed to have been present on 5 July. Pups that were instrumented in late summer generally survived longer than those radiocollared in

midsummer. Of the 14 pups radiocollared in July, August, and September, 8 (57%) survived until December, and 6 (43%) until spring. After 1972–1973, the effective reproduction (percentage of pups born that survived for 1 year) was 5–6 of 10 (50–60%). Survival of adults and yearlings radiocollared in summer was 16–18 of 20 (80–90%) until December and 10–13 of 20 (50–65%) until spring. Van Ballenberghe et al. (1975) calculated a 57 percent survival rate of pups until early winter and 39 percent until 1 year of age in the Superior National Forest.

Seventeen (49%) of the 35 instrumented wolves died while their transmitters were functioning, and signals were inexplicably lost from 3 others. One instrumented wolf was reported dead in 1978 after fieldwork was completed and another in 1979. Length of survival after capture ranged from 21 to 1,246+ days for monitored wolves. Male 5115 survived at least 1,417 days after his original capture as a pup, and female 5105 survived for 2,548 days after her capture as a probable yearling (Table 1). One pup was killed by humans while still in the trap and before it could be radiocollared.

In calculating mortality rates, we assumed that the percentage of wolves with active transmitters within a given year that died that year approximated the annual mortality rate of the population (Mech 1977b). Mortality rates calculated in this manner were moderate except in 1972–1973 when 3 of the 5 instrumented

wolves were killed by humans within 6 months of capture (Table 4). Annual mortality rates in the Superior National Forest ranged from 5 to 51 percent from 1968 to 1976 (Mech 1977b, corrected by Mech, unpubl.). Van Ballenberghe et al. (1975) calculated a rate of 40 percent for their study area in the eastern Superior National Forest. Thus, the rate of mortality in the study area (at least after 1972–1973) was lower than indicated for stable or declining populations elsewhere in Minnesota.

Humans appeared to be the major cause of mortality for this population before it was legally protected and continued to be an important factor afterward. Humans were responsible for deaths of at least 4 of 5 instrumented wolves that died while the species was unprotected, compared to at least 4, and possibly 6 of 12 that died after legal protection was granted in August 1974 (Table 4). Among the 8 instrumented wolves that definitely were killed by humans, 1 was trapped, and 6 were known to have been shot, 4 by deer and moose hunters. Human related mortality of wolves in northeastern Minnesota apparently decreased after 1973, although some poaching did continue (Mech 1977b).

The actual decrease in persecution of wolves may have been greater than indicated by these mortality data. Trapping and shooting of wolves were known to be commonplace in the study area before the species was protected. Eleven unmarked wolves were known to have been killed within the northern State Forest during winters of 1972–1973 and 1973–1974. About half that number were trapped. Trapping and snaring for wolves involves a much greater risk of detection than does incidental shooting. After 1974, no instrumented wolves were known to have been trapped or snared within the study area. After legal protection was granted, killing of wolves probably was limited to incidental shooting, primarily during the autumn hunting seasons. That type of mortality probably decreased too, because we encountered several persons

(e.g., deer hunters, loggers, State Forestry personnel) who claimed to have passed up opportunities to shoot wolves because of their protected status. The poaching that continued probably was sufficient to moderate the increase in density. Legal protection has not totally halted persecution of wolves in other areas (Weise et al. 1975, Robinson and Smith 1977, Mech 1977b).

Intraspecific strife was recorded in 4 instances, 3 of which occurred after the population had increased (Table 4). However, the killing of female 5111 in early 1974 demonstrated that this type of mortality is not always related to high population density. Yearling female 5510 was completely eaten by other wolves in March 1977, after the population had increased. Intraspecific strife related to food stress was the cause of all natural mortality recorded in the Superior National Forest in 1974 and 1975 and half of all natural mortality recorded there from 1970 through 1976 (Mech 1977b). Death from malnutrition was not recorded in this study, although Mech (1977b) considered it an important cause of pup mortality in the National Forest during the same period.

Mortality of instrumented wolves occurred mainly in late summer, autumn, and winter. Overwinter losses in the monitored social units were about 11 percent in 1974–1975 and 17–21 percent in 1975–1976. The percentage of pups in the monitored part of the population for winters 1972–1973 through 1976–1977 were 67 (1 pack only), 28–45, 31–46, 28–47, and 31–50, respectively. All indications were that recruitment of young wolves into the population exceeded mortality after legal protection became effective.

Sex and Age Ratios

It has been suggested that unbalanced sex ratios may influence the growth rate of wolf populations (Cowan 1947). Among 22 adults and/or yearlings captured, 8 were males and 14 were females; among

17 pups there were 8 males and 9 females. If 3 pups trapped from study packs by a federal livestock depredation control trapper in 1977 are included, a total of 9 male and 11 female pups were captured during the study. The sexes of nonbreeding wolves (most of which probably were yearlings) were 4 males and 9 females. Based on the instrumented samples, this discrepancy apparently was not the result of better survival of female pups. Yearling females might be easier to capture than males. Although alpha males and females should be equally abundant in wolf populations, alpha females were captured more often in this study and in the Superior National Forest (Mech, unpubl.). One possible bias is that alpha females probably are more easily recognized because of evidence of lactation. Van Ballenberghe et al. (1975) reported 19 males and 18 females among adults they captured, 17 males and 18 females among wolves thought to be yearlings, and 29 males and 20 females among pups. Stenlund (1955) found a ratio of 64 males to 36 females among wolves of unreported age in northeastern Minnesota.

Mech (1975) compared the sex ratios of pups captured from 3 areas of Minnesota, including the present study area, and found indications that the proportion of males in the 3 areas was directly proportional to population density and inversely related to estimated nutritional level. The ratio reported from the Red Lake area (Beltrami Island State Forest) at that time was 6 males and 6 females. There was no apparent increase in proportion of males in the population as it increased.

Ratios of age groups of wolves trapped in summer probably do not reflect their relative proportions in the population. Difficulty of trapping a wolf increases markedly with its age and experience. Nevertheless, the adult : nonbreeder (yearling?) ratio of 9:13 might be a crude representation of those 2 cohorts in the population during summer. That ratio possibly can be interpreted as supporting telemetry data by indicating good survival of juveniles into their second summer

of life. The population appeared to include a high percentage of young wolves during all seasons, which is consistent with the independent finding of increasing density.

Most adult wolves captured in this study appeared to be fairly young. Tooth wear of 2 individuals (female 5111, and male 5157) indicated they were exceptionally old. The exact or minimum age of some adults can be determined from information in Table 1.

The Role of Dispersal

As previously stated, the size of reproductive packs either remained stable or increased only slightly as the population increased. The size of most older packs (i.e., Clear River Pack after 1973, Peet's Pack, Vacuum Pack, Rapid River Pack) in winter was surprisingly small in view of the number of members present the previous spring, the number of pups produced in summer, and the available information on mortality rates. Such circumstances suggested a high rate of dispersal prior to winter. Data on instrumented nonbreeding wolves (either known or thought to be yearlings) supported this conclusion.

Eight radiocollared wolves (3 males and 5 females) clearly left the territory of their original pack while the study was in progress. All except possibly male 5051 had been nonbreeders, as far as could be determined. In addition, female pup 5143 separated from her pack at 10.5 months of age but remained within or near the territory for 6 weeks until her signal was lost. Male 5167 left his pack sometime between 16 March 1976 and 21 January 1979, after completion of fieldwork. Known ages of 3 dispersers were 16, 19, and 22 months. An additional 4 were young wolves that were thought to be yearlings, and 1 was an adult, based on tooth wear. The adult, male 5051, is considered a disperser here although the evidence was less clear than for the other wolves. Except for 1 possible instance in 1977, there were no known cases of in-

strumented juvenile wolves staying with their pack past breeding age (assumed to be 22 months, Mech 1970) unless they became breeders after the death of alpha animals.

Four wolves dispersed in October, and one each in August, November, and February. Another nonbreeding female may have left the study area in late September or early October 1976 during a period when no telemetry flights were made.

Dispersal appeared to contribute to the minor overwinter reductions in pack size. However, the greatest loss to packs from dispersal probably occurred in autumn. In one such case, both instrumented nonbreeders in the Vacuum Pack in 1975 left in October, thereby reducing the group from 10 to 8 members. Mortality to pack members also may have peaked at that time of year because of the hunting seasons.

At least some dispersing wolves remained within the Forest to play a major role in the population increase. Whereas 3 left the Forest, at least 3 or 4 settled there. One wolf that left later returned, but its ultimate fate is unknown. Dispersing radiocollared wolves were involved in the formation of new groups inside the Forest as well as in adjacent areas. Female 5105, male 5153, and female 5155 colonized areas at the edge or just outside the parental territory. This probably would not have been possible in a high density population. Wolves that emigrated from the Forest (female 5105, female 5171, female 5173, female 5145, and male 840) did so after the density within the Forest had increased substantially.

For 6 of the 7 dispersing nonbreeders that were located regularly, the maximum number of days before initial pairing was 8, 10, 14, 18, 19, and 30. The yearling that left and later returned to the Forest in 1976 apparently had not paired or settled after 60 days.

At least 4 wolves were loners when captured during summer. Lone wolves have previously dispersed from a pack (or are the sole survivors of a decimated

pack) and are searching for a mate and a territory (Mech 1972, 1973; Rothman and Mech 1979). Whereas 1 loner was shot by a deer hunter 118 days after capture, the other 3 paired and/or settled within 95, 104, and 148 days after capture. Two paired in November and 1 in February.

If dispersal occurred mostly in autumn, it follows that the greatest opportunity for finding a mate also occurred at that time. The relatively short interval between dispersal and pairing of instrumented wolves is evidence that the population contained an abundance of dispersers in autumn. Moreover, it is interesting that lone wolves instrumented in summer did not pair until autumn or winter.

The extent to which immigration might have contributed to the formation of new social units is unknown. However, we believe that most of the progenitors of new groups originated within the local population.

In summary, the wolf population in the Forest apparently had been held at a low density by persecution from humans prior to about 1974, but increased rapidly when mortality was reduced by legal protection. Mortality rates were moderate and pup production and survival were high after the population was protected. Nevertheless, humans were still the primary cause of mortality.

The population increased mainly by way of increased numbers of social units. Progenitors of the new groups were, at least in many cases, dispersers radio-tracked from existing social units who paired, reproduced, and started their own packs. Others were lone wolves, which no doubt had already dispersed from existing packs. Rather than attempting to breed within their natal packs, most young wolves appeared to be following a breeding strategy of early dispersal and formation of new social units. Although not all dispersing wolves reproduced, the individuals who chose this strategy (Packard and Mech 1980) experienced a high probability of reproductive success after legal protection was granted and as the population increased. The opportu-



FIG. 16. Minimum area covered plotted against number of relocations for alpha female 5119 of the Rapid River Pack, Beltrami Island State Forest, Minnesota. Period represented is July 1974 to September 1976.

nity for finding a mate and colonizing an unused area (Peters and Mech 1975, Rothman and Mech 1979) was unusually good during that period, and the selective advantage of dispersing and doing so at minimum breeding age undoubtedly was great.

MOVEMENTS AND TERRITORIALITY

Size and Stability of Territories

For each instrumented social unit of wolves, the minimum area covered (Mohr 1947) was plotted as a function of the cumulative number of relocations (Odum and Kuenzler 1955). Territories were considered defined when the curve of the area covered reached an asymptote (Fig. 16). By that criterion, the number of relocations was sufficient to define 8 territories (Table 5). Nine additional territories were not fully defined. However, knowledge of the locations of neighboring social units indicated that the areas covered were close to the actual size of territories in most of the latter groups. From 35 to 120 ($\bar{x} = 79$) radio fixes were required to reach an asymptote for all groups except the new Baudette River Pack. Only 18 relocations were necessary to define its area, probably because of its small size. Additions to minimum area covered that occurred after 40 to 50 fixes (multiple asymptotes) were known in

some cases to represent shifts or expansions in territories.

The 8 territories considered to have been defined ranged from 195 to 555 km² and averaged 344 km² (Table 5). Territories in the Superior National Forest are reported to be relatively stable with exclusive areas of 52 to 310 km² (Mech and Frenzel 1971; Mech 1972, 1973, 1974b, 1977a; Van Ballenberghe et al. 1975).

Basically, packs used the same areas in summer and winter. No distinct summer and winter ranges were observed. Specific areas within territories were used more intensively during different seasons. In summer, a large percentage of relocations was at dens and rendezvous sites, whereas many of the relocations in winter were associated with deer wintering areas.

Intensity of use patterns within territories were influenced greatly by physiography. Within all territories there were areas in which the wolves were seldom or never found. Generally they corresponded to the treeless marshes or to homogeneous conifer cover. For example, within the territory of the Vacuum Pack there was a 50-km² marsh in which the pack never was found. Being near the center of the territory, that marsh undoubtedly had a major influence on movements of the pack. Marshes and conifer swamps also functioned as natural buffer zones between some territories (e.g., Bankton Pack and Rapid River Pack; Faunce Pack and Clear River Pack; Peet's Pack and Vacuum Pack).

Related to the increase in the population, territory size generally decreased during the study. Territories of 3 packs present early in the study compressed as density increased. The territory of the Clear River Pack was stable from 1972 until late 1975 when it decreased by approximately 68 percent. The area covered by the Faunce Pack decreased by 65 percent, and the territory of Peet's Pack decreased by 17 percent from 1974–1975 to 1975–1976.

Territories of the Winner Pair, Rapid River Pack, and Vacuum Pack were not

TABLE 5.—SIZE OF TERRITORIES OF INSTRUMENTED SOCIAL UNITS OF WOLVES, BELTRAMI ISLAND STATE FOREST, MINNESOTA, 1972–1977. THE EFFECTIVE PERIOD IS GIVEN FOR TERRITORIES CONSIDERED FULLY DEFINED (UNDERLINED)

Social unit	Size of social unit in winter (range)	Territory size			Approximate effective period
		Greatest length (km)	Greatest width (km)	Minimum area utilized (km ²)	
Clear River	5–6	39	12	<u>330</u>	Aug 1972–Nov 1975
Faunce (original)	3–4	34	22	<u>555</u>	Aug 1973–Feb 1975
Faunce (new)	3+	23	13	<u>195</u>	Aug 1975–Mar 1977
Winner	2	23	17	<u>283</u>	Oct 1973–Nov 1975
Thief Lake ¹	?	12	8	64	—
Rapid River	6–9	34	17	<u>410</u>	Jul 1974–Sep 1976
Peet's	6–7	25	15	<u>250</u>	Oct 1975–Aug 1976
Malcolm	2	22	7	98	—
Vacuum	5–8	37	22	<u>520</u>	Jun 1975–Dec 1976
Bankton	4–7	26	12	<u>210</u>	Jul 1975–Mar 1977
Morehouse	2+	20	9	116	—
Baudette River	3	11	10	67	—
Waskish ¹	2	18	9	117	—
Hogsback	2	19	9	130	—
Northome ¹	2	13	5	54	—
Norquist Lake	6	21	8	115	—

¹ Outside Beltrami Island State Forest.

known to compress during the study (Figs. 10–14). However, the Winner Pair's territory was abandoned in December 1975 following encroachments by neighboring packs. The Vacuum Pack's territory may have increased slightly in winter 1975–1976; acquisition of most of the Winner Pair's abandoned territory compensated for area lost to the colonizing Morehouse Pair that winter.

New social units that colonized areas both inside and outside the Beltrami Island State Forest occupied considerably smaller territories than packs that had been present since the beginning of the study (Table 5, Figs. 10–14). Minimum territory size for 8 groups during their first year in the Forest ranged from 67 to 167 km² and averaged 136 km². The mean territory size for packs that were monitored in both 1974–1975 and 1975–1976 decreased from 377 km² to 217 km² between those years. When the new social units from 1975–1976 are included in a comparison of the same years, the mean

territory size in 1975–1976 was about 189 km². The trend toward smaller territories was most evident in the eastern Forest where the 555-km² area covered by the Faunce Pack until about February 1975 eventually became occupied by 4 packs (Figs. 10–14).

The range in territory sizes was greater after the increase in population density because 2 older pack territories (Vacuum Pack and Rapid River Pack) did not compress. Based on pack size and estimated availability of prey, the Vacuum Pack's territory remained considerably larger than necessary at the end of the study. Nonetheless, by 1976 the space available to new groups was relatively limited throughout most of the study area. Beginning then, population growth probably was being moderated by territoriality. The establishment of new breeding units probably was considerably more difficult than before because of the territorial behavior of resident packs.

Apart from decreases in overall size,

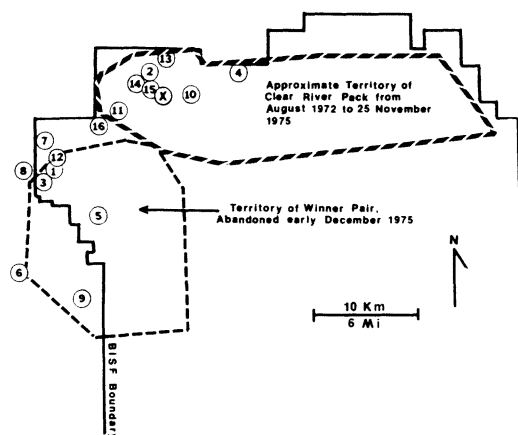


FIG. 17. Progressive relocations of alpha female 2455 and Clear River Pack between abandonment of eastern part of the territory around 25 November 1975 and 18 January 1976 when 2455 was killed by other wolves ("X" indicates death site). Mean interval between relocations was 3.5 days.

some shifting of certain boundaries or entire territories was evident, beginning in winter 1974–1975. These changes resulted primarily from the establishment of several new territories and the abandonment of one. The most dramatic shift was by the Clear River Pack in late 1975, after a new pack became established in the eastern part of its territory (Figs. 12, 13). After November, movements within the original territory were restricted to the western end. Concurrently, the group explored the recently abandoned territory of the Winner Pair to the southwest and may have added some of that area to its territory (Fig. 17). The Clear River Pack's alpha female, 2455, was killed by a pack about 18 January 1976, probably by the same nonradiocollared pack that claimed most of the Clear River Pack's territory.

Establishment of the Moose River Pack probably caused Peet's Pack to relinquish the western part of its territory after autumn 1974 (Figs. 12, 13). The boundary between the Rapid River Pack and Peet's Pack shifted westward between 1974–1975 and 1975–1976 (Figs. 12, 13). In association with those losses of area at the east and west sides of its territory, the geometric center of activity (Hayne 1949,

Mech et al. 1966) within the territory of Peet's Pack shifted 2.4 km toward the northeast from winter 1974–1975 to winter 1975–1976.

A southwestward shift in the territory of the Bankton Pack apparently resulted from formation of the Baudette River Pack in November 1975 (Fig. 18). Similarly, formation of the Morehouse Pack in winter 1975–1976 resulted in a northward shift in the southern boundary of the Vacuum Pack's territory (Fig. 19). During summer 1976, the Morehouse Pack was found several kilometers farther north, apparently claiming even more of the Vacuum Pack's territory.

The demise of the Winner Pair in late 1975 resulted in a major disruption in the spatial organization within the western Forest (Figs. 12, 13). The male member of the pair was not seen with the instrumented female (5105) after 13 November. His disappearance could have occurred between 4 and 13 November, because the pair was not observed during that period. Fate of the male is unknown, but human involvement is a strong possibility. The wolf disappeared during the deer hunting season at a time when there was a high density of hunters within the pair's territory. The neighboring Vacuum Pack was found within the Winner Pair's territory by 21 November, and the Clear River Pack was there on 25 November (Fig. 17). On 21 November, the Vacuum Pack was within 1.1 km of 5105, and on 1 December the Clear River Pack was within 1.7 km of her. By 11 December, 5105 began to explore the area west of her territory. She then abandoned her territory and resettled farther west. Possibly the Vacuum Pack and Clear River Pack forced her out of her territory, as each claimed part of it. It is significant that the alpha female of the Clear River Pack at the time, 2455, probably was a littermate of 5105, who had dispersed from that pack 2 years earlier.

Additional compression and shifting of territories could have escaped detection. The perceived boundaries based on telemetry data probably lagged behind ac-

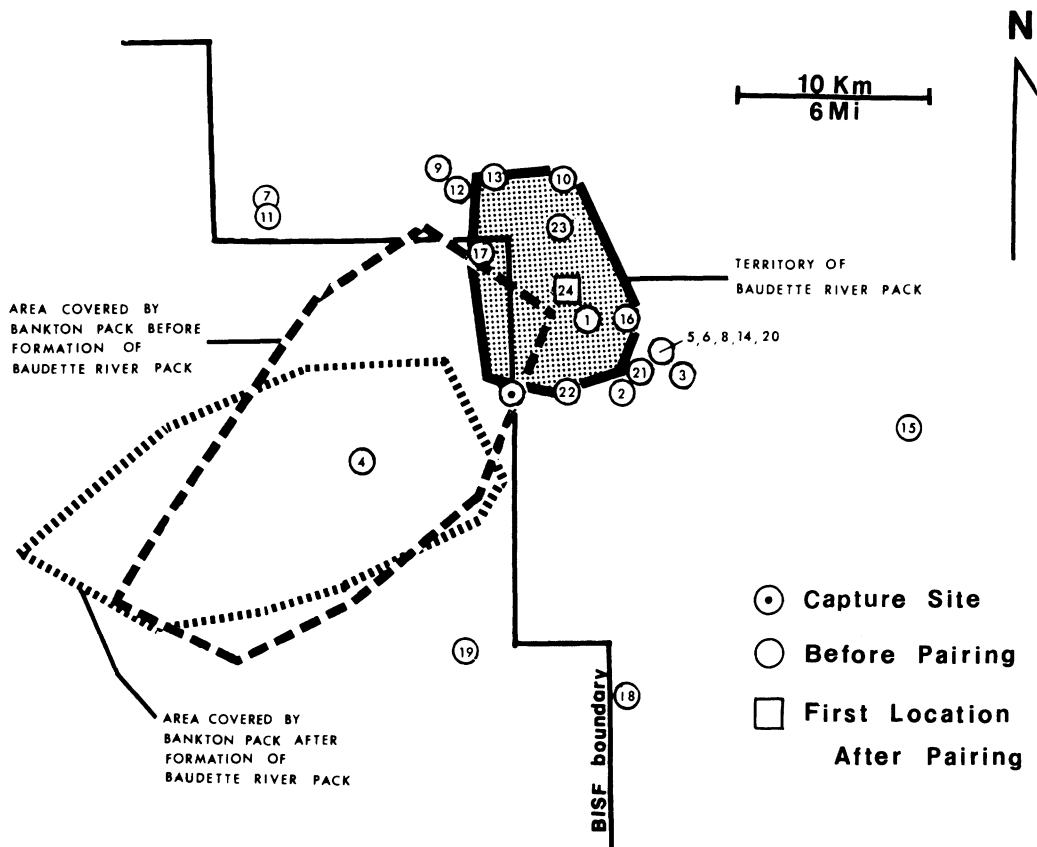


FIG. 18. Movements of lone female 5169 from capture through pairing as indicated by progressive relocations between 10 August and 21 November 1975. Mean interval between relocations was 4.5 days. Shaded area represents approximate territory of 5169 and 1 or 2 companions (Baudette River Pack) between 21 November 1975 and 23 March 1976. Shift in territory of Bankton Pack believed related to establishment of Baudette River Pack also is indicated.

tual boundaries somewhat because of the low rate at which telemetered wolves were relocated.

It probably is significant that the 2 territories with the highest perimeter to area ratio prior to the population increase (Clear River Pack, Peet's Pack) underwent major reductions in length and in total area. The perimeter to total area ratio of oblong territories probably renders them more difficult to defend than those that are more circular.

Perceived overlap in territories was slight in most cases. Among well-established territories the amount of overlap probably was similar to the 2-km boundary strip of shared area thought to exist in

the Superior National Forest (Peters and Mech 1975). A contact zone did not appear to exist between some adjacent territories due to the presence of wide unused marshes. In some cases areas utilized by new groups were known to overlap existing territories temporarily. For example, the Norquist Lake Pack probably was present near the north edge of the study area as early as winter 1974-1975, but the Clear River Pack continued to visit that area until autumn 1975.

The greatest amount of range overlap by 2 established groups involved the Winner Pair and the Vacuum Pack. From June through October 1975, while both packs were being radiotracked, the ex-

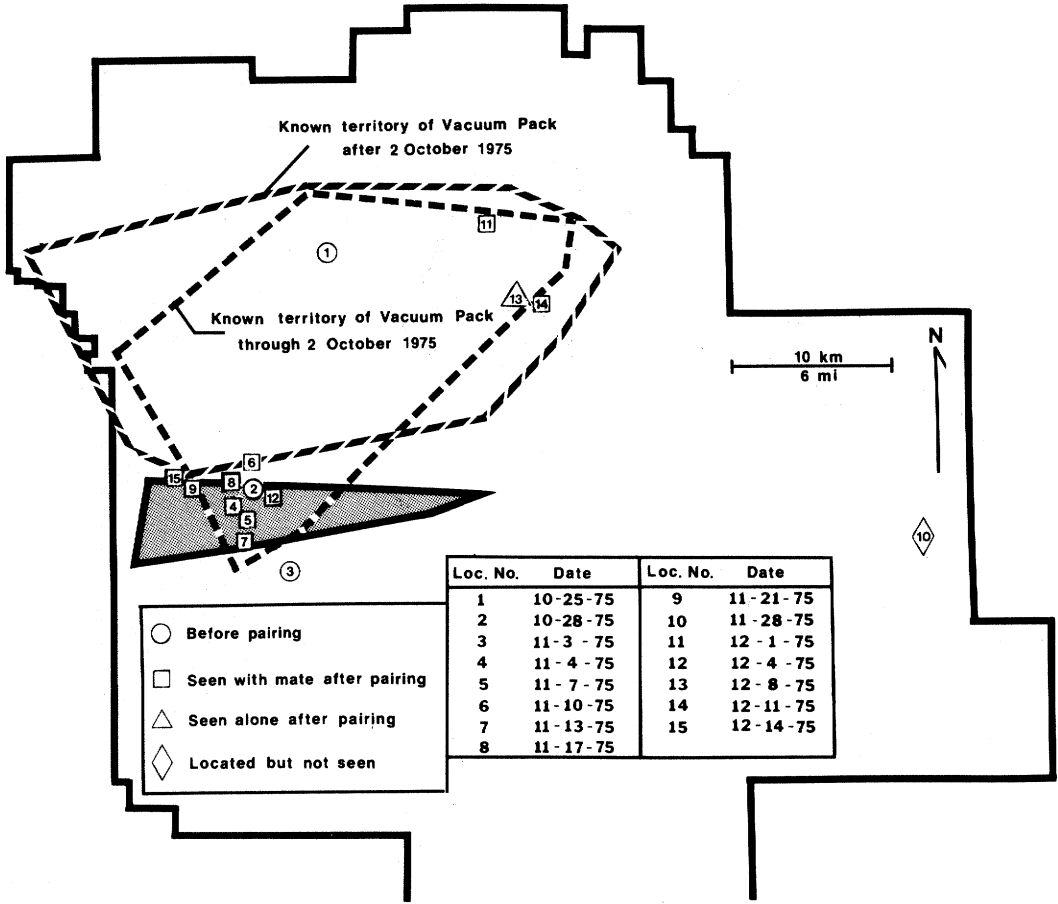


FIG. 19. Relocations of female 5155 after dispersal from the Vacuum Pack through pairing, drifting, and colonization of the edge of the parental territory. Shaded area represents the approximate territory of 5155 and her mate (the new Morehouse Pair) as indicated by relocations in winter 1975-1976 after 14 December. Shift in territory of Vacuum Pack also is indicated.

tent of overlap was an area about 7 km wide (Fig. 20). A similar amount of overlap existed in winter 1974-1975, based on radiotracking of the Winner Pair and snowtracking of the Vacuum Pack (Fig. 12). It may be significant that male 5051, as a lone wolf, had associated with female 5105 (future member of the Winner Pair) in the area that was to become her territory before he became alpha male of the Vacuum Pack.

Territories of genetically related groups (i.e., Clear River Pack and Winner Pair, Vacuum Pack and Morehouse Pack) showed no greater tendency to overlap

than did those of other groups. Dynamics of range boundaries of related versus unrelated packs have not been reported in the literature.

Dispersal, Movements of Lone Wolves, and Pack Formation

Five wolves were loners when captured. Only 2 of the 5, males 5109 and 5113, apparently did not associate with others while being monitored (Fig. 21). Contact with male 5113 was lost after 5 relocations. He last was found close to a human residence. Probably he either was killed near the last location or he moved

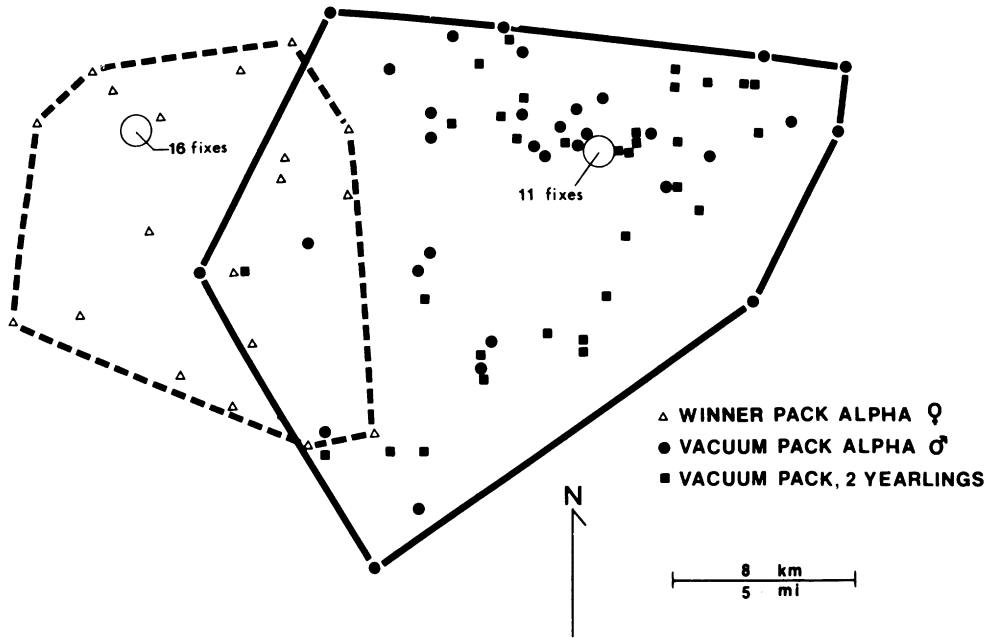


FIG. 20. Spatial relationship of Winner Pair and Vacuum Pack from June through October of 1975 as indicated by relocations of telemetered pack members.

completely out of the study area. The movements of male 5109 covered at least 1,400 km²; he appeared to be a nonterritorial resident of the Forest.

Three wolves that were loners when captured paired while being followed (male 5121, female 5141, female 5169); 2 were involved in the formation of new packs.

Lone male 5121 initially was nomadic over at least 650 km² in the southern and southwestern Forest where no packs were thought to exist (Fig. 22). His travels probably covered a larger area than indicated because he was not found on 3 attempts in late summer of 1974. Observations of 5121 and a companion (Malcolm Pair) were within a 98-km² area at the southwestern corner of the Forest. After apparently pairing with this nonradiocollared wolf, he ranged in and out of the area apparently used by her. He was shot on 15 February before it was determined whether his movement pattern would culminate in pair bonding and successful colonization of that area.

Lone female 5141 was captured at the edge of the Faunce Pack's territory, and most of her relocations (covering at least 886 km²) during the next 5 months were near the periphery of that territory (Fig. 23). After she and yearling male 5115 of the Faunce Pack paired in February 1975, movements of both wolves became restricted to an area of 86 km² at the northwestern edge of the Faunce Pack's territory for the remainder of the winter. After pairing with the female, male 5115 was not subsequently located with his 2 former companions from the Faunce Pack.

Although pair 5141–5115 did not form until shortly before the breeding season, there was evidence that female 5141 produced pups that spring. Settlement of that pair into a territory at the northern portion of the Faunce Pack's original range occurred at the same time as a nonradiocollared pair (progenitors of the Bankton Pack) colonized its southern region. Raised leg urinations (RLUs) were abundant in the area used by 5115 and

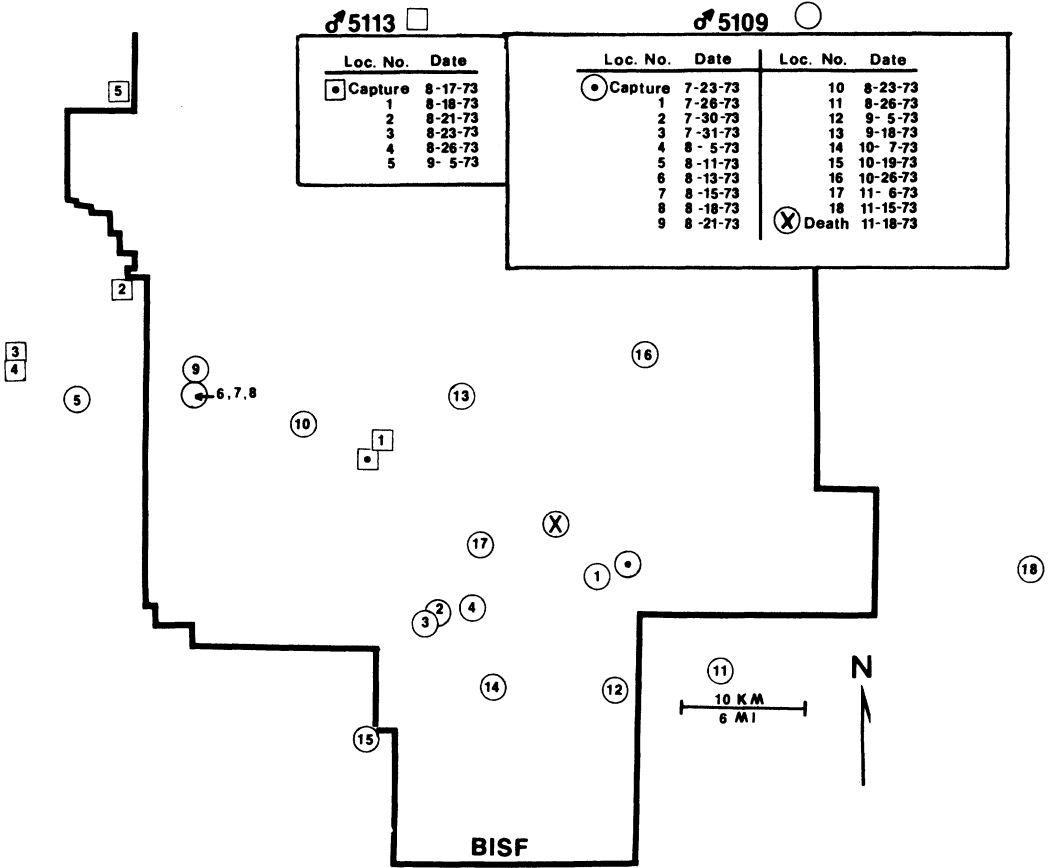


FIG. 21. Relocations of lone male 5109 and lone male 5113.

5141 for at least 5 weeks after they paired. Newly formed pairs scent mark at a high rate, behavior thought to be critically related to courtship and pair bonding (Rothman and Mech 1979).

Lone female 5169 ranged over at least 476 km² before she paired (Fig. 18). Her movements indicated an affinity for a specific area at the edge of the Forest between farmland and 1 or 2 packs. That area was the focal point of her movements prior to pairing, even though she drifted in and out. One site there received especially heavy use. After being seen with 2 other wolves in her area on 21 November, she was not found outside it again. The movement pattern of female 5169 before pairing suggests she had selected an area that was suitable for a fu-

ture territory. Perhaps the periodic movements away from the area were attempts to find a mate.

Eight wolves dissociated from their packs and left the parental territory while being monitored. In addition, 1 pup separated from its pack at 10 months of age but remained near the territory.

Wolves that dispersed demonstrated a variety of movement patterns prior to and after leaving the parental territory. In some cases dispersal appeared to be gradual, preceded by a series of relocations at the edge of the territory and little association with other pack members, for periods ranging from 10 to 30 days, e.g., females 5155, 5171, and 5173. Other wolves left their packs and territories without any prior detected changes in

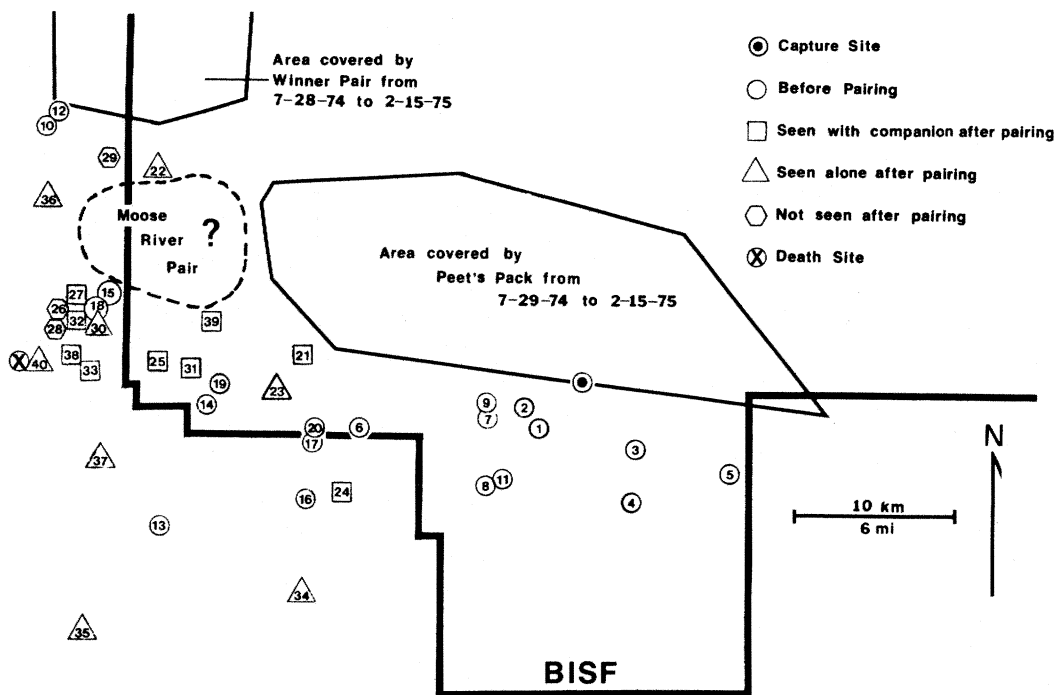


FIG. 22. Relocations of adult male 5121 from capture on 28 July 1974 through drifting and pairing phases and until death on 15 February 1975. Mean interval between relocations was 4.9 days.

their movements or associations, e.g., males 840 and 5153 and female 5145.

Yearling female 5173 was the only disperser not known to associate with other wolves while being monitored. She traveled at least 138 km (straight line distance) from her pack and then returned to the vicinity of its territory (Fig. 24). She was alone when observed once during that trip, which involved traversing farmland. Little suitable habitat for wolves exists in the areas visited by her, so her failure to settle was not surprising. On 7 and 10 October 1976, she was within an area of extensive forest and grass fires, and on 10 October she virtually was surrounded by fire (Fig. 24). Possibly the trauma from that event contributed to her return to a familiar area in October. The single relocation after her return to the Forest was just outside the territory of her pack. She might have left the Forest again, because her signal was not heard

during an extensive search in December 1976.

Seven wolves were monitored through dispersal and pairing, and are discussed in the following order: female 5105, male 5051, female 5155, female 5171, male 5153, male 840, and female 5145.

Female 5105 dispersed from the Clear River Pack's territory in October 1973. She immediately settled in an adjoining area not used by a pack and spent the next 2 years there (Fig. 25). The same area already had been explored by male 5051, whose movements were concentrated there for at least 2 months prior to the arrival of female 5105. Five consecutive relocations of male 5051 in August and September were at the edge of the Clear River Pack's territory. A possible explanation is that he was attempting to attract a mate from that pack. Female 5105 was not found at that edge of her territory while with the Clear River Pack,

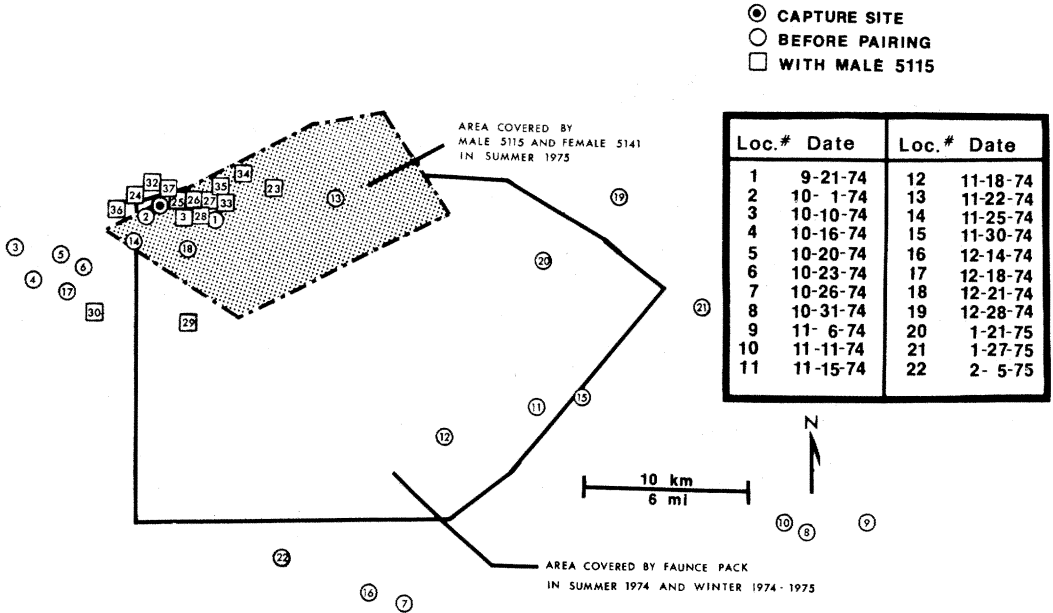


FIG. 23. Relocations of female 5141 as a lone wolf from 20 September 1974 through 5 February 1975, and with male 5115 in winter 1974–1975 after pairing on 11 February. Mean interval between relocations of the pair was 3.3 days. Shaded area indicates area covered by the pair in summer 1975.

although a radio fix on 15 August was within about 3 km of the edge. After 5105 dispersed in October, she and 5051 began traveling together there after a maximum of 15 days and possibly much sooner. They were together at each of 3 relocations over the next 3 weeks and then were found apart twice before the male's radio failed in early December. The period over which male 5051 remained with female 5105 is unknown. The female was accompanied by another wolf in the same area from February 1974 until November 1975. Male 5051 was a member of the neighboring Vacuum Pack when recaptured in June 1975. Therefore, he and female 5105 separated and the female was joined by another male sometime between November 1973 and June 1975.

Female 5105 gradually abandoned her territory of 2 years after the apparent loss of her mate in November 1975 (Fig. 26). From 12 December 1975 through 11 February 1976, she drifted nomadically over an area of about 95 km² immediately west

of the previous territory where no pack was known to exist. She was with another wolf on 6 of 7 observations from 18 December through 20 January. She apparently separated from that wolf, because she was alone during the 8 observations from 24 January through 24 February. By 29 February, she and a nonradiocollared wolf paired and settled in a wooded area about 20 km from her previous territory. The presence of established packs probably did not influence the selection of the territory, because it was virtually surrounded by farmland.

Subordinate female 5155 dissociated from the Vacuum Pack between 25 and 28 October 1975. She frequented the southern edge of the pack territory and was seen with a mate there within 10 days (Morehouse Pair) (Fig. 19). After being found within that area for about a month, the pair (or at least female 5155) drifted at least 45 km from it over a period of from 3 to 13 days. She and a mate were back in the original area by 4 December. They remained in the future territory for

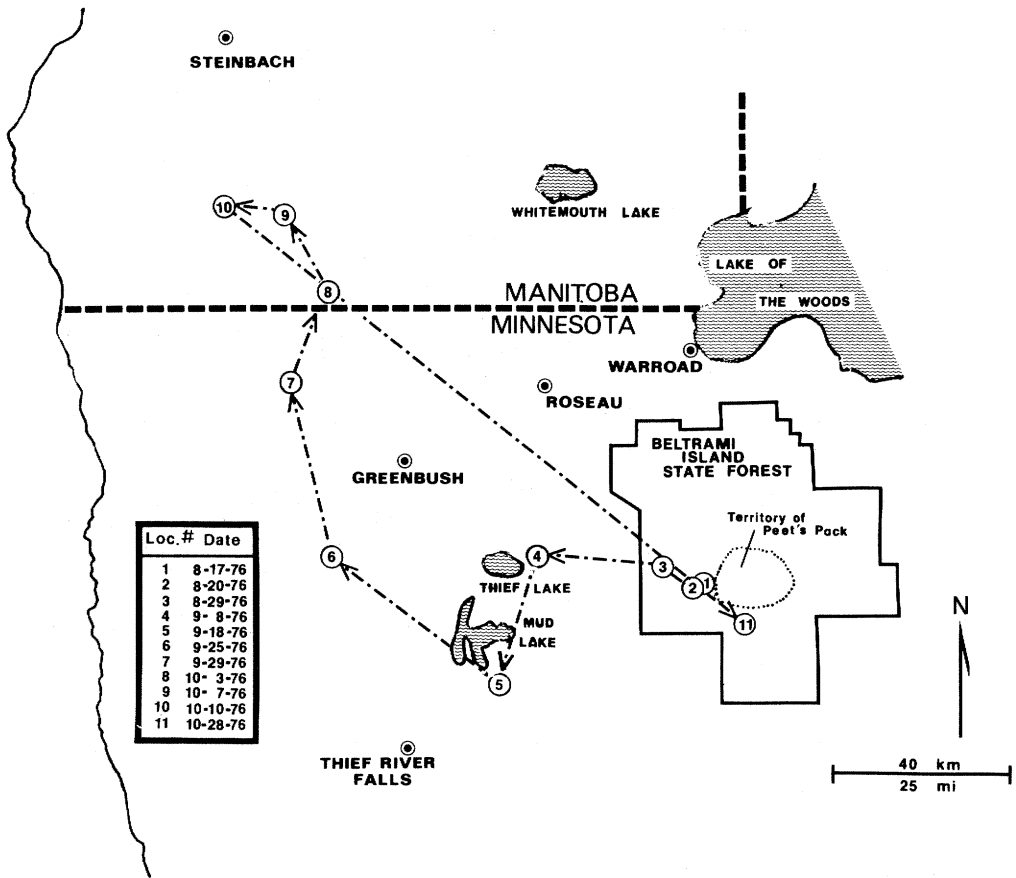


FIG. 24. Dispersal from and return to the Beltrami Island State Forest by yearling female 5173. Lines indicate sequence of relocations, not travel routes. Note relocation no. 11 near original territory.

1 to 7 days, left again, and settled along the eastern edge of the Vacuum Pack's territory for 3 to 10 days before again returning to their original area by 14 December. The male was seen urinating with raised leg (Peters and Mech 1975, Rothman and Mech 1979) outside the area into which they settled, perhaps indicating an unsuccessful attempt at establishing a territory elsewhere (8 December 1975, Fig. 19). Female 5155's intermittent radio made it impossible to relocate her on each attempt, and thus other moves prior to settling could have been missed. Roads through the new territory were heavily scent marked in winter, and the male was observed urinating with raised leg there on 2 occasions. This

pair had a high kill rate during winter 1975–1976. Presence of a major deer wintering area at the east end of their range probably contributed to their successful colonization of the area.

Another newly formed pair that may have attempted to colonize the edge of a parental territory was female 5171 and male 5153. After dissociating from the Rapid River Pack, female 5171 remained near the edge of her parental territory until found by male 5153, who recently had dispersed about 25 km from his pack (Fig. 27). Relocations of the duo (Airport Pair) were at the edge or between pack territories. The pair traveled toward the territory of the Vacuum Pack, from which 5153 dispersed, and became somewhat

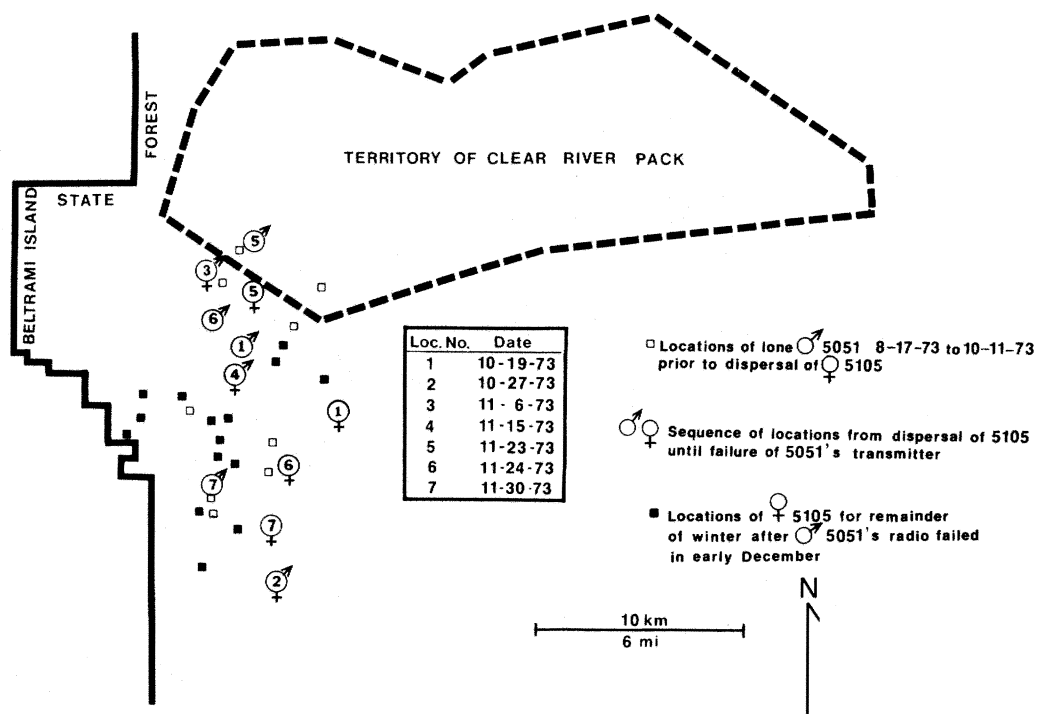


FIG. 25. Settlement of female 5105 into an area adjacent to her parental territory shown with relocations of lone male 5051. Subsequent movements of the 2 as a pair also are shown.

sedentary at the edge of the territory. They separated after 21 November. The Vacuum Pack was known to have traveled within at least 2 km of the pair at about the time of breakup, and might have been involved. Rothman and Mech (1979) reported an incident in which a newly formed pair broke up after it ventured into a pack's territory. They also pointed out that a successful pair bond is not assured when 2 loners meet. Individual preferences in canids (Le Boeuf 1967, Beach 1970, Beach and Merari 1970) may be a major factor in determining whether or not pairs remain together.

Male 5153's radio nearly failed at the time of breakup with female 5171. In mid-January, he and a mate were found at the north edge of the Vacuum Pack's territory (Bednar Pair in Fig. 13). They had heavily scent marked roads near their location. A new pack was suspected to reside there in summer 1976; so, male 5153 may have colonized the edge of his

parental territory after all, but along a different edge and with a different mate than during his first attempt.

After her breakup with male 5153, female 5171 remained in the same vicinity for another week before becoming nomadic (Fig. 28). Even during the period of drifting she revisited the area. In January, she suddenly left the Forest, crossed considerable farmland, and found a forested area in Manitoba where she appeared to settle. She was killed by humans near the Canadian border, approximately 87 km from the territory of her original pack.

Another disperser, yearling male 840, moved across and outside the Forest within 2 to 4 weeks of leaving the Clear River Pack, and was with a mate within a maximum of 19 days after dispersal (Fig. 29). His movements prior to leaving the Forest were not determined, so any attempt to find a territory there would have been missed. The only relocation

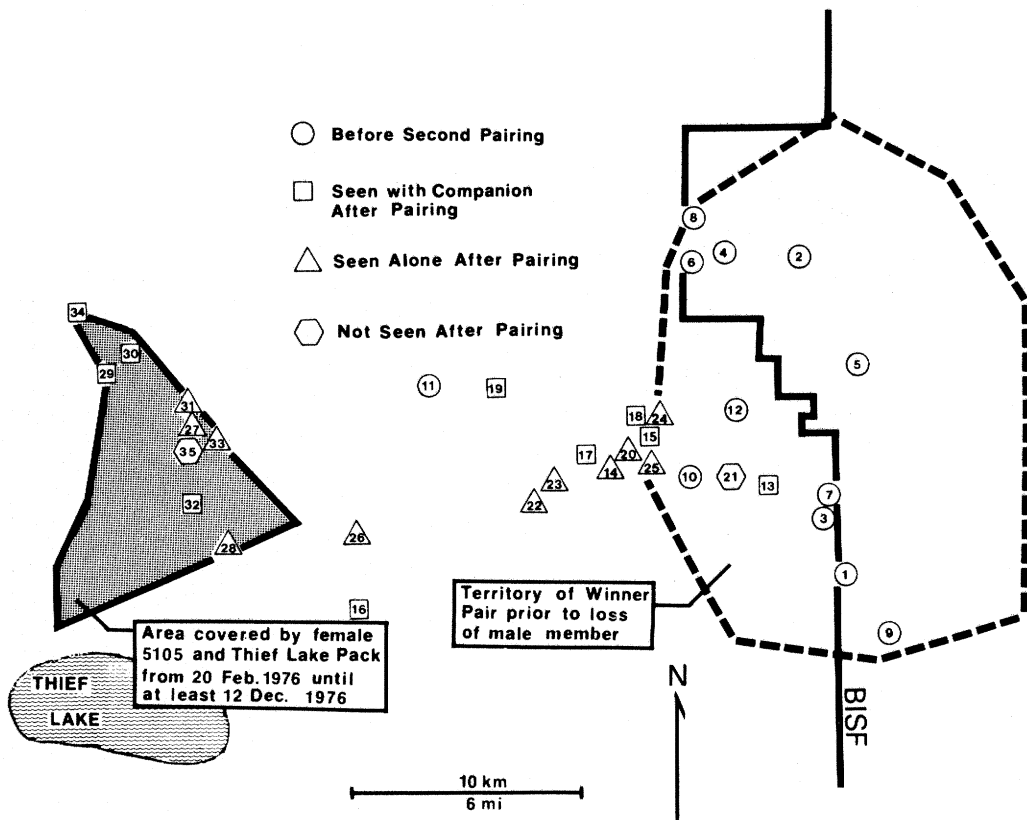


FIG. 26. Abandonment of territory, drifting, pairing, and resettling of adult female 5105, as indicated by progressive relocations between 4 November 1975 (last date male member of Winner Pair was seen) until 1 April 1976. Mean interval between relocations was 4.2 days. Shaded area indicates territory of 5105 and Thief Lake Pack from 20 February to 12 December 1976.

within the Forest after dispersal was at a kill in a tamarack swamp between territories of 2 resident packs. As with the Airport Pair and the Morehouse Pair, 840 and his companion (Waskish Pair) drifted together before they settled into a territory. While they drifted, the female was extremely frightened of the tracking aircraft and was difficult to observe. Therefore, she probably was with 840 more often than indicated in Fig. 29. The Waskish Pair did not settle into their future territory on first finding it by early March, but continued to drift until early April. They were seen at a den in late April, and a pack was thought to inhabit that area the following winter. If pups were produced, they were conceived before

the pair possessed the territory where it finally settled.

Yearling female 5145 paired within 9 days after dispersing from the Rapid River Pack's territory (Northome Pair, Fig. 30). Her mate was a wide-ranging lone male who had been instrumented 90 km southeast of the Rapid River Pack in the Chippewa National Forest by the Minnesota Department of Natural Resources. It was not known whether those 2 wolves first associated in the vicinity of the Rapid River Pack's territory or if they met south of Waskish. Whichever the case, the initial pairing occurred outside the area into which they appeared to settle.

In June 1976, either the male's radio failed, or he separated from 5145 and left

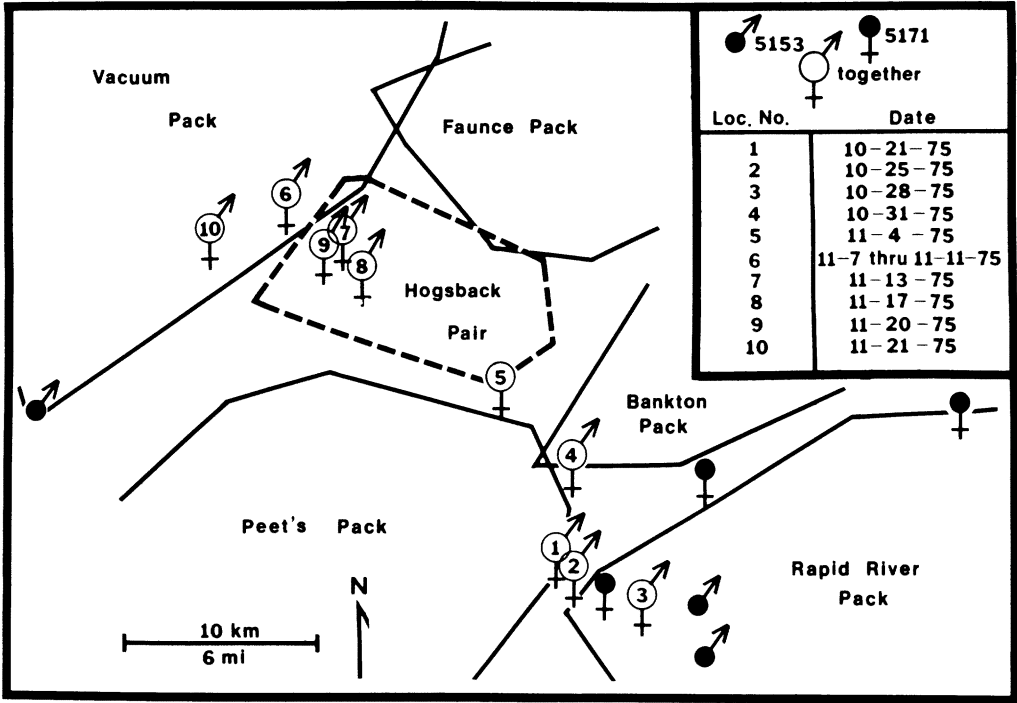


FIG. 27. Temporary association of male 5153 from the Vacuum Pack and female 5171 of the Rapid River Pack as indicated by relocations of both wolves from dispersal until pair breakup.

the area. Female 5145 was observed only twice during summer 1976 because of a faulty radio. It is not known whether a mate and pups were present during that period. Pairing of those wolves occurred during the latter part of the breeding season. Female 5145 remained in the same area until at least 12 December, at which time she was accompanied by a nonradiocollared wolf. A possible interpretation of these data is that the female chose to remain within the territory after the loss or departure of the instrumented male until she was found there by another male.

The only known case of a pup dissociating from its pack involved female 5143 when she was 10 months old. She remained within or near the parental territory, but appeared to be avoiding her pack during a 6-week period prior to loss of her signal after 19 March (Fig. 31). Some relocations were within the territory of the neighboring Winner Pair.

However, the pair was not known to visit that edge of their territory while 5143 was there. The pup was alone when observed on 2 occasions following separation from the Clear River Pack. She fed from the carcass of a snared deer during part of the period.

The longest move by a wolf marked during this study was by male 5167, who was shot about 56 km west of Thunder Bay, Ontario, on 21 January 1979. This location was about 390 km east of his capture site. Dispersal occurred sometime after 16 March 1976 when telemetry work ceased. The only published report of a longer move by a wolf is a 670-km move in western Canada (Van Camp and Gluckie 1979).

Movements of all nonterritorial wolves (including loners, dispersers, and newly formed pairs) were greatly influenced by packs. Relocations of those wolves were almost exclusively in areas not utilized by packs or along the periphery of pack

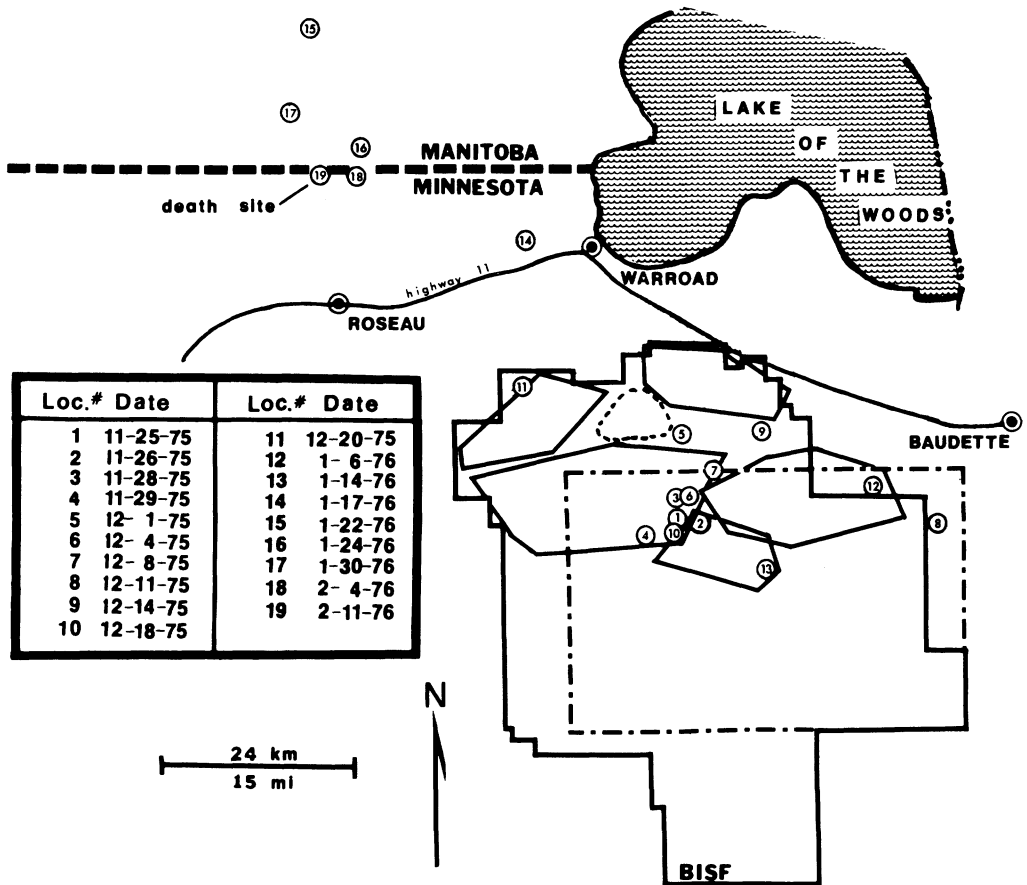


FIG. 28. Relocations indicating nomadic movements of female 5171 after breakup with male 5153. Rectangle within map of the Beltrami Island State Forest indicates area included in Fig. 27. She was killed near location no. 19.

territories, and this appeared to be true both before and after the increase in population density. Lone or single wolves have been reported to avoid territories of packs in high density populations (Jordan et al. 1967, Mech and Frenzel 1971, Van Ballenberghe et al. 1975, Peterson 1977, Rothman and Mech 1979). Lone or single wolves may be chased and killed if encountered by packs (Murie 1944, Mech 1966, Mech and Frenzel 1971, Mahrenke 1971, Van Ballenberghe and Erickson 1973, Mech 1977b).

Lone wolves in the Superior National Forest respond little to imitations of howling (Harrington and Mech 1979). Neither do they scent mark, although

they show considerable interest in scent marks encountered (Rothman and Mech 1979). "Reading" of scent marks probably permits loners to avoid contact with packs, and to detect potential sites for colonization based on the absence or infrequency of marking (Peters and Mech 1975, Rothman and Mech 1979). Loners in the Beltrami Island State Forest probably had less difficulty avoiding resident packs, at least early in the study, because of the low density of wolves. Related to their avoidance of packs, loners were more often found in marginal habitat such as open marsh and tamarack swamps between some territories or close to the interface of farmland and forest. On the

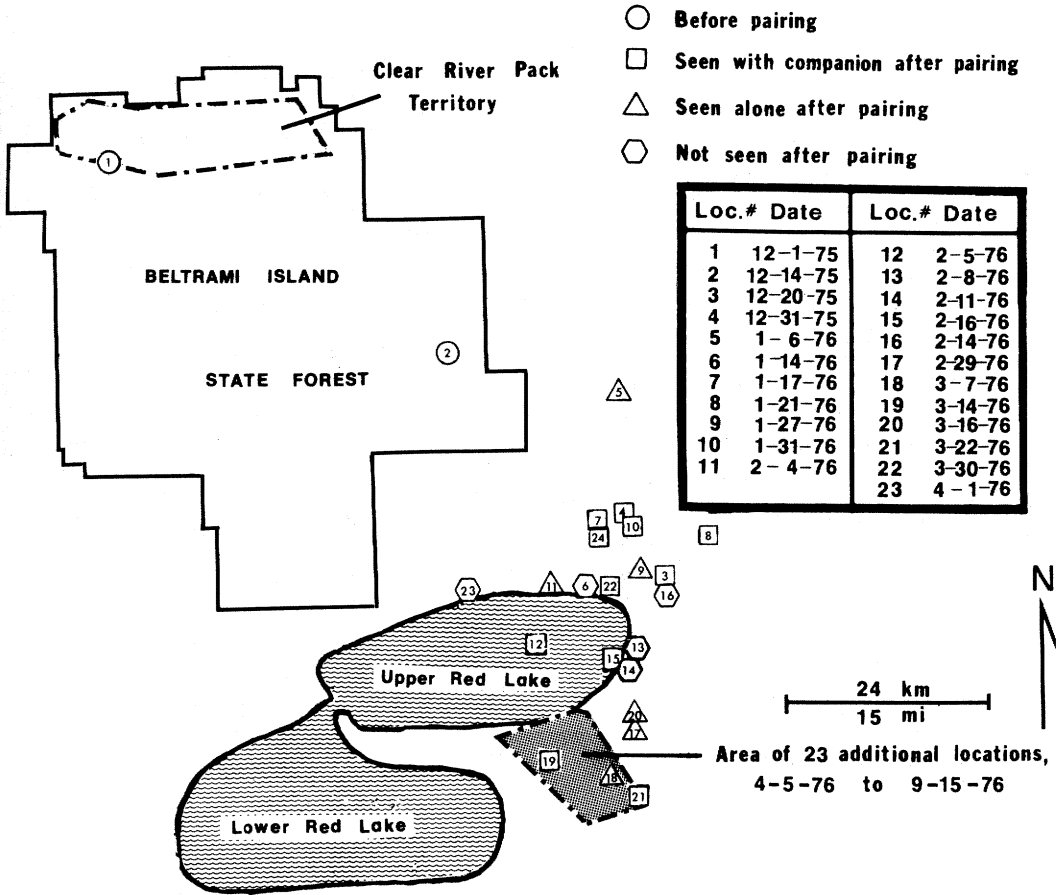


FIG. 29. Relocations indicating dispersal of yearling male 840 from the Clear River Pack, pairing, and drifting prior to settling into a territory. Shaded area indicates territory of the pair from 5 April to 15 September 1976, as indicated by 23 relocations of 840.

other hand, 2 loners were able to utilize a major deer yard between territories of 2 groups and apparently not used by either.

Lone wolves appeared to have little difficulty finding an unused area (at least early in the study) and a mate. Colonizing wolves attempted to establish territories either between those of established packs or at the edge of the forest, i.e., between a pack and farmland. Wolves that settled outside the Forest apparently had found vacant areas near human settlements. Persecution of wolves in these peripheral areas undoubtedly is high, but probably eased when legal protection

was granted. Colonization of the edge of a parental territory by progeny of that pack might be a common process of pack formation in increasing populations. When ample space and prey are available, breeding pack members might increase their genetic fitness by being tolerant of progeny that attempt to colonize part of their territory.

Rothman and Mech (1979) concluded that pair formation in the Superior National Forest occurs after a lone wolf finds a vacant area and is discovered there by another wolf of the opposite sex. That pattern also was observed in the Beltrami Island State Forest. However,

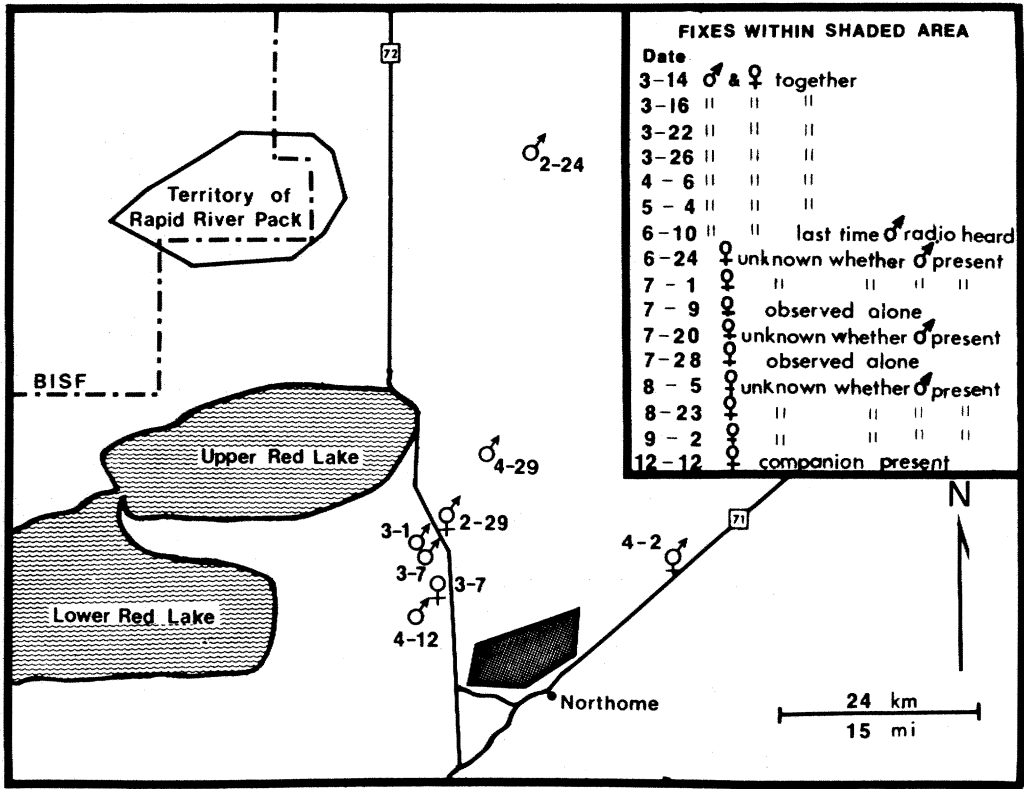


FIG. 30. Relocations indicating dispersal of yearling female 5145 from the Rapid River Pack in February 1976, pairing with lone male 903, and movements prior to settling. Shaded area indicates the eventual territory of the pair in 1976, as indicated by 16 relocations of one or both wolves. Pair may have been together on 1 March and on 12 and 29 April (female's radio was not functioning on those dates).

in 4 cases it was seen that possession of an unused area by one wolf was not a prerequisite to pair formation. The Washish, Morehouse, Northome, and Airport pairs were formed before a territory was found and drifted together until a potential site was located. Thus, considerable variation was evident in the early stages of pack formation.

Acceptance of Lone Wolves by Packs

There is only one record of a lone wolf being accepted into an established pack (Rothman and Mech 1979); yet, non-instrumented wolves are thought to have joined packs in at least 1, and possibly 3, cases during this study. Death of a breeding pack member preceded acceptance of the loner in at least 1 of those.

The evidence for a loner joining a pack was best in the case of the Hogsback Pack in 1976. In May 1976, that group consisted of mated pair 376-844 and an unknown number of pups. After female 844 died in early June, the male remained in his territory and evidently provided for the pups. He was accompanied by another female by 12 July, and the 2 remained together until at least 29 August. At least 1 or 2 pups survived for a minimum of 6 weeks after the pairing; however, the role of the new female in caring for the pups is unknown. Male 376 died outside the territory in late September or early October. The fate of his new mate and the pups is unknown.

In another case, male 5051 apparently joined the Vacuum Pack between No-

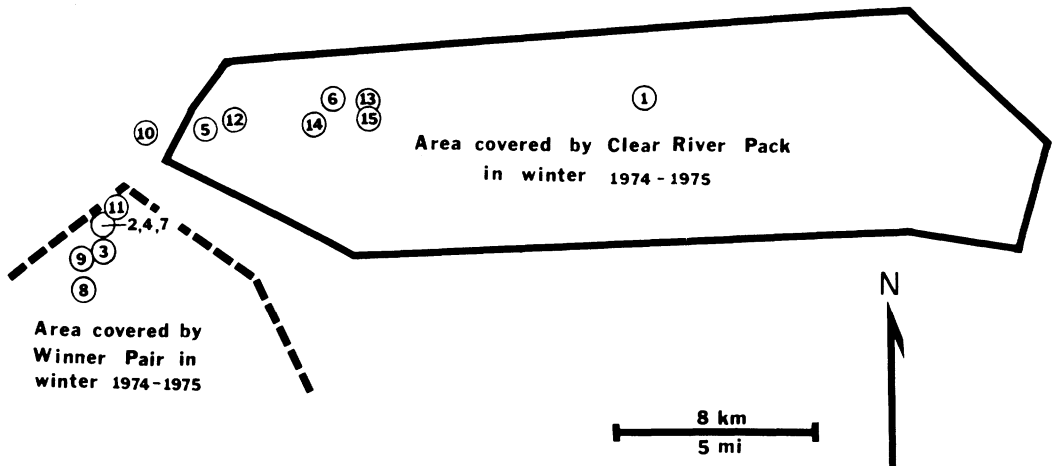


FIG. 31. Movements of female pup 5143 between dissociation from Clear River Pack on 5 February 1975 until last found on 19 March 1975, as indicated by 15 relocations. Mean interval between relocations was 3.1 days.

vember 1973 and June 1975. There was strong evidence that the Vacuum Pack was present at least by mid-1973, although it was not instrumented until 1975. During 1973, 5051 associated first with the Faunce Pack in March and April and then with lone female 5105 in November before contact was lost in early December. He was alpha male of the Vacuum Pack when recaptured in June 1975.

Another possible case of an established pack accepting an outside wolf, at least temporarily, involved the Clear River Pack in early 1973. The only known adult male member of the pack was killed on 24 January. No wolves of a possible 1971 litter remained with the pack. The alpha female whelped that spring, but because 24 January is earlier than breeding is known to occur at this latitude (Van Balenbergh and Mech 1975, Peterson 1977, Mech and Knick 1978), it is unlikely she had been bred at the time of her mate's death. A loner might have joined the group and bred the alpha female. Another possibility is that an unknown peripheral pack member might have sired the pups, although there was no evidence for the existence of such an animal.

In all those cases, it is possible that the

individual that apparently was accepted into a pack had previously dispersed from it or had associated with some members. Whatever the case, acceptance of lone wolves by packs apparently helps to maintain pack structure in high mortality populations, resulting in greater productivity and a more stable social and spatial organization than otherwise would be possible.

Movements of Pack Members in Summer

In late winter or spring the nomadic movement pattern of winter gives way to a stationary phase when pregnant females become sedentary at dens (Ognev 1962, Mech 1970). Dens and rendezvous sites (homesites) become the focal point of pack activities in spring and summer, and pack members usually travel in subgroups or alone to and from these locations (Murie 1944, Joslin 1967, Voigt 1973, unpublished master's thesis, University of Guelph, Guelph, Ontario).

Adults

Dates by which the instrumented breeding females settled at dens ranged over a 45-day period from about 13 March

TABLE 6.—SPATIAL RELATIONSHIPS OF ALPHA FEMALE WOLVES AND THEIR PUPS DURING SUMMER, BELTRAMI ISLAND STATE FOREST, MINNESOTA, 1972–1977

	Apr ¹	May	Jun	Jul	Aug	Sep
Number of days data obtained	56	52	18	7	53	13
Number occasions with pups	46	38	4	2	27	10
Number occasions not with pups	10	14	14	5	26	3
Number times located ² away from pups	9	7	6	5	16	3
Mean distance from pups when away (km)	6.0	3.2	6.7	1.7	9.1	14.9
Maximum distance from pups (km)	23.7	4.8	11.9	2.7	28.2	26.5

¹ After settling at dens. Parts of April not included.

² Aerially determined (daytime) relocations only. Inclusion of ground fixes would bias the data.

until 26 April. The median date ($n = 9$) was 8 April. Dates on which those females first were located away from their dens ranged from 16 April to 29 May, the median date ($n = 9$) being 29 April. The actual dates of settlement at dens and first movements away from them undoubtedly were slightly earlier than indicated here because most females were not located daily.

In spring 1975, female 2455's den was checked daily by ground based telemetry, so a more precise record of her sedentary period with pups could be obtained. She became sedentary at her den on 20 March and was known to leave it first on 16 April when she was 12 km away. Female 2455 probably was the first to produce pups that year. Female 5119 of the Rapid River Pack was the last breeding female to become sedentary both in 1975 and 1976. In both years, she settled around 21 or 22 April. The relatively small size of her pups in midsummer of both years was further evidence that she whelped later than the other females. Late breeding and whelping of 5119 might have been related to food supply, as there probably were fewer deer within her territory than in any other in the Forest.

Other data also may help to define the reproductive period. Female 5155 was seen digging a den on 8 April. Bloody urine was noted while snowtracking different packs on 2, 6, and 11 February. Young and Goldman (1944) indicated vaginal bleeding could precede estrus by as much as 45 days. Rothman and Mech (1979) found blood in urine of wolves in

northeastern Minnesota by 4 January and at least through 24 February.

Copulation was observed once: 3 March 1975. The participants were not tied. Copulation has been observed in the Superior National Forest from 28 January to 4 March (Mech and Knick 1978) and on Isle Royale from 4 February to 2 March (Peterson 1977). The size of embryos recovered from female 5165, killed by wolves on 4 March 1978, indicated a conception date of around 2 February and a projected birth date of about 5 April (Evans 1974). In 1975, that wolf settled at her den by 30 March.

Taken together, these data indicate considerable variation in date of whelping. Based on data from Isle Royale and the Superior National Forest, Van Ballenberghe and Mech (1975) concluded that most pups in Minnesota are born during a 2- to 3-week period in late April. Whelping dates appeared to be similar in northwestern Minnesota but the average date may be a little earlier there.

After females began leaving their dens, they were located with their pups intermittently throughout summer (Table 6). For example, female 2455, after first being found away from her pups on 16 April 1975, was found at her den on 16 of 24 occasions between then and 12 May, after which we were uncertain of the location of her pups. Ground checks for instrumented females at their dens and homesites suggested a greater tendency, at least among some, to be with the pups at night than during the day. Female 2455 was thought to be with her pups at only 2 of 21 aerially determined locations

TABLE 7.—SPATIAL RELATIONSHIPS OF ALPHA MALE WOLVES AND THEIR PUPS DURING SUMMER, BELTRAMI ISLAND STATE FOREST, MINNESOTA, 1972–1977

	Apr	May	Jun	Jul	Aug	Sep
Number of days data obtained	13	14	15	5	10	2
Number occasions with pups	6	6	2	2	5	0
Number occasions not with pups	7	8	13	3	5	2
Number times located ² away from pups	4	5	7	3	1	2
Mean distance from pups when away (km)	10.3	7.0	7.2	6.1	1.9	7.7
Maximum distance from pups (km)	18.2	9.7	12.9	8.7	1.9	15.0

¹ After alpha females settled at dens. Parts of April not included.

² Aerially determined (daytime) relocations only. Inclusion of ground fixes would bias the data.

during daylight hours from 22 May through July 1974. Presumably she was with her pups more often at night.

Three alpha males monitored during this study were at known pup locations less frequently than were the alpha females ($\chi^2 = 14.844$, $P < 0.005$, Tables 6, 7). Adult males and females usually were alone when observed away from dens and homesites.

Caring for pups did not prevent alpha females from covering most of their territories during summer. However, the parts of the territories around homesites did receive more intensive use. Activity radii (Dice and Clark 1953, Tester and Siniff 1965) of alpha females from known locations of their pups showed no obvious increase as summer progressed, but data from late summer were too sparse to indicate any definite trends (Table 6). Some of the first relocations away from dens involved considerable distances. For example, female 2455 was found 23 km from her pups as early as 22 April 1975. Yearling male 840, and possibly other wolves, remained at the den while she was away. Adult males usually were found farther from their pups in summer than were the alpha females. Twenty (48%) of 42 aerially determined relocations of alpha females were within 3 km of their litters, whereas only 2 (11%) of 18 relocations of alpha males were within that distance.

Two nonreproducing groups (Faunce Pack in 1973; Winner Pair in 1974) showed no apparent difference in summer and winter movements. During sum-

mer, they traveled extensively throughout their territories, and showed no affinity for any specific site.

Nonbreeding Adults and Yearlings (Subordinates)

Subordinate wolves differed in attendance at homesites and in their association with the breeding members of their packs in summer. Instrumented subordinates were with alpha members of their packs on 75 of 231 (32.5%) possible occasions when located in summer.

When adult females became sedentary at dens, some subordinates (e.g., yearling male 840) initially spent much time at or near the den. Others (e.g., yearling females 5173 and 5145) immediately began a basically solitary movement pattern that frequently took them to the edge of the territory and seldom to the pack's den. Altogether, the subordinates were not with the pups as often as were the breeding females during the April-through-July period ($\chi^2 = 17.039$, $P < 0.005$, Tables 6, 8).

The areas covered by subordinates in summer were much the same as areas covered by alpha members of their packs during that season (Fig. 32). However, some relocations of subordinates were near the edge or outside of the area covered by alphas and outside the territories as they were known from both summer and winter relocation data. Yearling female 5145 of the Rapid River Pack is an example of wolves whose movements demonstrated this pattern. She explored

TABLE 8.—SPATIAL RELATIONSHIPS OF NONBREEDING ADULT WOLVES OR YEARLINGS (SUBORDINATES) AND PUPS FROM APRIL THROUGH JULY, BELTRAMI ISLAND STATE FOREST, MINNESOTA, 1972–1977

	Apr ¹	May	Jun	Jul
Number days data obtained	28	23	33	21
Number occasions with pups	13	10	14	6
Number occasions not with pups	15	13	19	15
Number times located ² away from pups	10	12	10	12
Mean distance from pups when away (km)	4.8	5.1	5.8	4.3
Maximum distance from pups (km)	13.7	15.3	11.4	15.1

¹ After alpha females settled at dens. Parts of April not included.

² Aerially determined (daytime) relocations only. Inclusion of ground fixes would bias the data.

an area southwest of the pack territory in summer (Fig. 32C), at which time we thought she had dissociated from the pack. She was not known to visit the pups or associate with alpha female 5119 between mid-May and mid-September when she returned to the pack. Yearling female 5173 of Peet's Pack also appeared to be exploring the edge of her pack's territory in summer 1976, prior to dispersing in late August. Between the beginning of the stationary phase of her pack on about 22 April and dispersal on 20 August, 10 of 36 relocations of 5173 were 1 to 3 km outside the area covered by the pack during the previous winter. Potential dispersers probably collect information on the possibilities for colonizing adjacent areas by "reading" scent marks and listening for howling at the edge of the parental territory.

Pups

Abandonment of natal dens occurred primarily in June. The earliest known date of den abandonment was 2 June and 12–16 July the latest. Length of the move to the first rendezvous site was determined in 4 cases: 2.4 km by the Rapid River Pack in 1975, 4.8 km by the Clear River Pack in 1975, 5.5 km by the Faunce Pack in 1976, and 10.0 km by the Vacuum Pack in 1975.

As summer progressed, locations of noninstrumented litters became more difficult to determine because instrumented wolves frequently were away

from the pups when located, and many litters were difficult to observe from the air. Attempts to induce howling from pups at sites frequented by instrumented pack members sometimes were successful.

Fourteen pups were radiotracked in middle and late summer. Relative weights of those pups generally were higher than reported for pups captured in the Superior National Forest (Van Ballenberghe and Mech 1975), and no individual showed any abnormally slow development that should have restricted its movements (Fritts, unpubl.). Nonetheless, the extent of movements of those pups at a given time varied considerably. Homesites were used at least into August: male pup 5103 was at a homesite from capture on 3 August until 13 August 1974; male pup 5107 of the Rapid River Pack was at a homesite between 17 and 30 August 1974; female pups 5159 and 5161 of Peet's pack used a homesite for 6 to 8 days in late July 1975, and possibly others thereafter. Male pup 5167 of the Bankton Pack remained at a homesite in late July; he moved 7.3 km to another by 4 August and remained nearby until 15 August. Movements of male pup 5175 of Peet's Pack were confined to an area of about 2 km² between 13 September and 2 October 1975. Observations of noninstrumented litters in August also suggested occupancy of homesites. Instrumented pups that used homesites in July and August were not confined there but ranged a few km away, as also reported

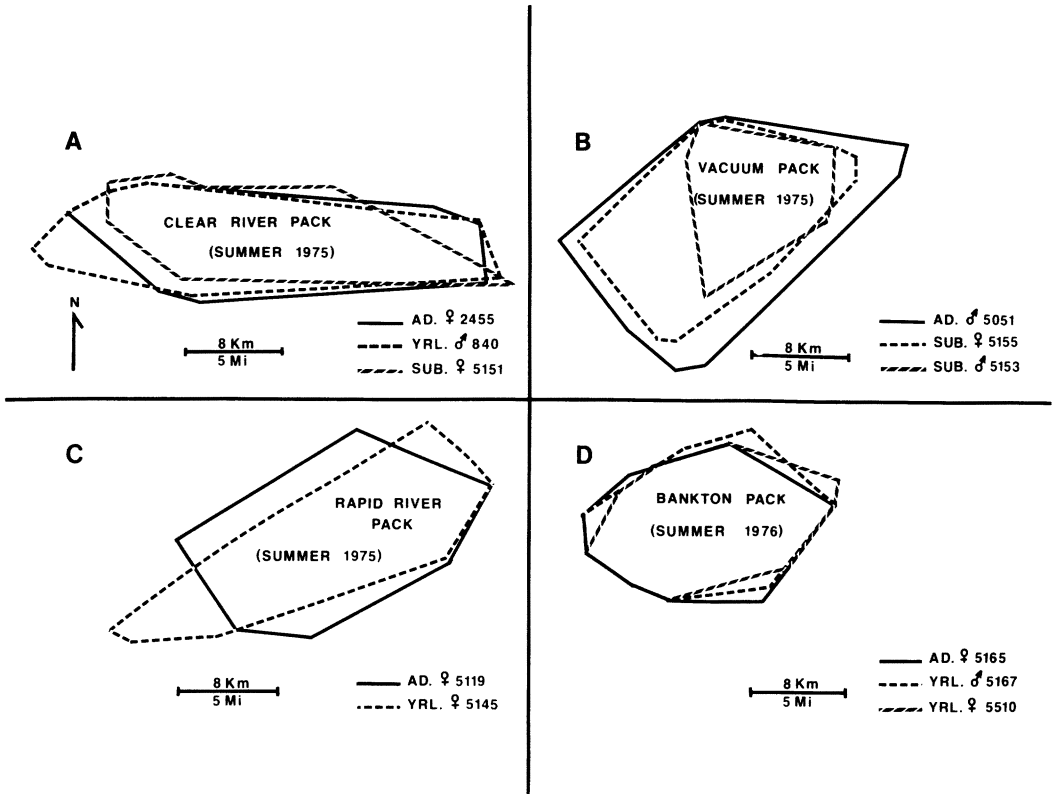


FIG. 32. Comparison of areas covered by adults and subordinates in summer, for Clear River Pack, Vacuum Pack, Rapid River Pack, and Bankton Pack.

by Van Ballenberghe et al. (1975) in northeastern Minnesota.

Pups started becoming nomadic from late August to early October, but primarily during September. They ranged fairly widely, and often were separated from littermates or instrumented adults. For example, on 21 September 1972 alpha male 2451 and littermates 2453, 2455, and 2457 were each at different locations separated by as much as 12.5 km. Mean distance between consecutive relocations (approximately 5 days apart) of instrumented pups increased from 4.5 km for August to 6.0 km for September to 9.8 km for October. If homesites were being used during that period, they were not occupied for long. Occasionally, a pup would be found at a homesite that had been used by the pack earlier in summer.

Movements of Packs in Winter

Generally, pack members began traveling together in late September or early October. The earliest date by which pups began traveling with their packs was 6 September (Clear River Pack in 1974). In that case, 2 radioed pups were with the group consistently after that date. They were indistinguishable from adults by aerial observation in September.

In contrast, 2 instrumented pups from Peet's Pack did not begin traveling regularly with their pack until the first week in November. Both pups ranged widely, apparently alone, before consistently accompanying other pack members. Moreover, male pup 5167 was separated from the remainder of the Bankton Pack at most relocations until the end of Novem-

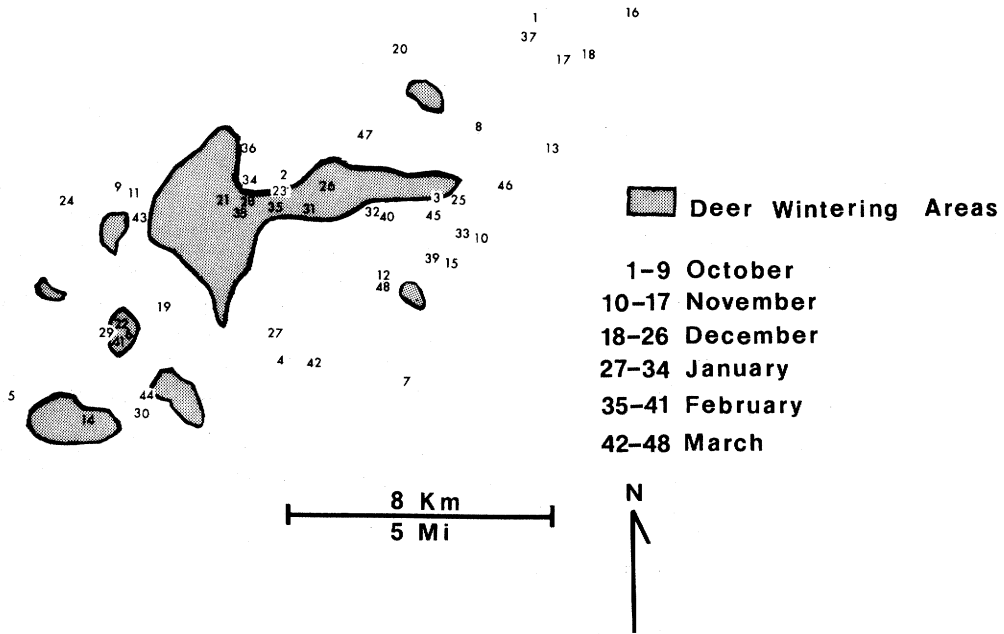


FIG. 33. Progressive relocations of Bankton Pack (alpha female 5165) during winter 1975-1976 in relation to edge of the territory and deer wintering areas.

ber. Van Ballenberghe et al. (1975) reported that abandonment of rendezvous sites by 5 packs in the eastern Superior National Forest occurred as early as 8 September, and that pups from all groups started ranging widely by 10 October. Variation in dates of final abandonment of rendezvous sites was thought to be related to development of pups. Our findings support that conclusion.

Two subordinates, male 5153 and female 5155, were with their pack consistently beginning on 17 and 22 September 1975, after intermittent association with pack members during summer. Yearling female 5145 rejoined her pack about 12 September 1975, after a 4-month period during which she was not known to associate with other wolves.

The instrumented packs traveled extensively during late September, October, November, and occasionally into December (depending on the pack). Perhaps some pups had difficulty keeping up with their packs during that period, which might explain why 3 pups often

were found separated from their packs until November.

During such extensive movements, packs often were found at the edges of their territories (Fig. 33). Similar movements occur in autumn in the Superior National Forest (Van Ballenberghe et al. 1975, Mech, unpubl.).

A function of scent marking is territorial maintenance, and rates of scent marking are higher along edges of territories in winter (Peters and Mech 1975). Perhaps packs are eager to scent mark their territories as soon as possible in autumn in order to avoid encroachments by newly formed pairs that are attempting to colonize edges of territories or by neighboring packs that are becoming mobile at about the same time. Territorial boundaries may be reestablished to some degree at that time of year. The first packs to become mobile might be at an advantage in any attempt to claim additional area. It is noteworthy that the Winner Pair, after failing to produce pups in 1974, began as early as mid-July to spend

an inordinate amount of time near the eastern and southern edges of its territory. Between then and mid-November, 9 of 22 relocations were at the southern and eastern edge, but none were at the northern or western edge. Other packs were located east and possibly south of the pair, whereas farmland set the northern and western limits of the territory. Possibly the pair was taking advantage of its mobility in attempting to claim additional area.

Most packs did not cover as much area in January, February, and March as in early winter. This could have been the result of less favorable snow conditions in late winter and greater concentration of deer. All packs were found frequently in the vicinity of deer wintering areas in late winter (Fig. 33 is an example). However, the areas thought to contain the highest density of wintering deer in the Forest apparently were used little by study packs, and relatively few kills were found there. No incident of a pack trespassing into neighboring territories in search of prey (Mech 1977a) was observed.

Comparison of total area covered in summer versus winter was possible during certain years for 7 packs. Whenever possible, only relocations of alpha animals and their associates were considered in this comparison. The mean area covered by packs in winter was 267 km², compared with 230 km² in summer, a difference of 14 percent. Three exceptions to this pattern of smaller summer ranges included the Faunce Pack and Winner Pair during years when no pups were produced. Another exception was the Bankton Pack, whose movements covered 182 km² in both summer 1975 and summer 1976, but only 143 km² in winter 1975–1976. The presence of a major deer wintering area in the center of the pack's territory may explain its more restricted movements in winter. A similar situation in northeastern Minnesota was reported by Van Ballenberghe et al. (1975) for packs whose ranges bordered the north shore of Lake Superior. Movements in

winter there were restricted to the part of the territories along the shoreline because of the high concentration of deer that winter there. A pack studied in the interior of the Superior National Forest covered 20 percent more area in winter than in summer (Mech 1977a).

Among the larger packs, numerous observations during winter indicated all pack members were not present. Throughout winter (including October and November) instrumented adults and pups were together on 151 (73%) of 207 potential occasions, and yearlings were with adults on 51 (69%) of 74 occasions. In many cases, the wolves that were separated from the main pack appeared to be trailing it.

During winter, instrumented wolves were traveling on 32.6 percent of the occasions they were observed; they were sleeping, resting, and feeding at 20.4, 42.5, and 3.8 percent of observations.

Roads were used intensively as travel routes in the Forest during both summer and winter, even though the probability of contact with humans is increased considerably by such behavior. Extensive use of frozen rivers and lakes, as in the Superior National Forest (Stenlund 1955, Mech and Frenzel 1971) was not possible. Frozen drainage ditches often were traveled in winter, whereas ditch grades were used in summer.

FEEDING ECOLOGY

Scat Analyses

White-tailed deer was the most important food of wolves in the Beltrami Island State Forest in winter and summer, both in terms of biomass and number of individuals eaten (Tables 9, 10). The occurrence of deer in winter scats was significantly higher than in summer ($\chi^2 = 11.62$, $P < 0.005$), and the estimated deer biomass eaten/100 scats was approximately 1.6 times greater in winter, even though the summer diet included more individuals (cf. Tables 9, 10). The literature contains relatively little information

TABLE 9.—PREY REPRESENTED IN 174 WINTER WOLF SCATS RECOVERED IN BELTRAMI ISLAND STATE FOREST, MINNESOTA, 1972–1976, TOGETHER WITH ESTIMATED BIOMASS AND NUMBERS OF PREY CONSUMED (CALCULATED ACCORDING TO FLOYD ET AL. 1978)

Food	% Relative estimated bulk	Biomass eaten/100 scats (kg)	% Biomass eaten	Number individuals eaten/100 scats	Ratio of number individuals eaten
Deer ¹	86.9	121.20	75.3	2.41	1.000
Moose ²	6.2	33.30	20.7	0.14	0.060
Hare ³	1.8	0.75	0.5	0.63	0.260
Livestock ⁴	0.6	4.46	2.8	0.01	0.004
Small rodents ⁵	0.1	0.05	<0.1	0.16	0.060
Other ⁶	0.9	1.13	0.7	0.12	0.030
Deer or moose ⁷	3.5	—	—	—	—

¹ Calculations based on known age ratio in kill of 1 adult : 1 fawn with respective weights of 64 and 35 kg (Erickson et al. 1961).
² Calculations based on assumed age ratio eaten of 4 adults : 2 yearlings : 5 calves (Berg 1975) and respective weights of 360, 260, and 150 kg (Peterson 1974).
³ Assuming weight of 1.2 kg.
⁴ Based on 0.1 occurrence of hog and 0.9 occurrence of cow, with assumed weights of 91 and 400 kg (Spector 1956).
⁵ Probably meadow voles, assumed weight of 30 g.
⁶ Based on 1.0 occurrence of wolf, 0.2 occurrence of grouse, 0.4 occurrence of bear (cub?), with respective assumed weights of 31.75, 1.0, and 90.7 kg.
⁷ Not distinguishable. Assume figures above not significantly altered by omission of this datum from calculations.

on contents of wolf scats collected in winter in the Great Lakes region. However, the available data suggest greater utilization of deer in winter than in summer (Thompson 1952, Pimlott et al. 1969, Van Ballenberghe et al. 1975, Theberge et al. 1978).

The percentage of deer in summer scats increased from 51.9 in April–May to 88.9 in June–July, then dropped to 78.3 in August–September. Percentage relative estimated bulk of deer was especially low in May (36.3%). Estimated deer biomass eaten increased from April–May to August–September at a ratio of 1.00:1.06:1.32 for the 3 summer periods, whereas estimated numbers of deer increased then decreased for the same periods at a ratio of 1.00:2.14:1.24. A distinct ebb in consumption of deer in April–May corresponded to increased consumption of moose. The deer:moose ratio of biomass eaten during April–May was 1:1.7, although an estimated 4.5 deer were eaten per moose consumed.

Remains of deer fetuses appeared in a few scats deposited in winter and spring. During April–May, fetuses or fawns composed only about 3 percent of the total deer biomass eaten; however, the calculated proportions of these age groups in the diet was 1 fawn : 1.6 adults. Fawn re-

mains became common in scats in early to middle June and composed 220.2 of the 275.2 (80%) occurrences of deer in June–July. At that time, the estimated biomass of fawns ingested was about 1.4 times greater than biomass of adults, and the ratio of fawns to adults eaten was approximately 9.0:1. We were unable to distinguish fawn and adult hair in scats deposited after July.

The importance of fawns in the summer diet of wolves is well documented by scat analyses in other areas (Thompson 1952, Pimlott et al. 1969, Van Ballenberghe et al. 1975, Frenzel 1974, Voigt et al. 1976). No previous estimates of the proportion of fawns and adults in the summer diet are available for comparison with our findings, except that Floyd et al. (1978) calculated that fawns composed 45 percent of individual deer (and 15% of deer biomass) represented in the summer scat collection of Van Ballenberghe et al. (1975) from northeastern Minnesota. Relatively high consumption of fawns in the Forest also is suggested by comparison of the percentage of fawn occurrences among deer in this study with results of the studies cited above.

The occurrence of deer in scats differed significantly between years ($\chi^2 = 10.48$, $df = 4$, $P < 0.05$); however, this

TABLE 10.—PREY REPRESENTED IN 670 SUMMER WOLF SCATS COLLECTED IN BELTRAMI ISLAND STATE FOREST, MINNESOTA, 1972–1976, TOGETHER WITH ESTIMATED BIOMASS AND NUMBERS OF PREY CONSUMED (CALCULATED ACCORDING TO FLOYD ET AL. 1978). NUMBER OF SCATS FROM APRIL–MAY, JUNE–JULY, AND AUGUST–SEPTEMBER PERIODS WERE 135, 310, 59, RESPECTIVELY

Food	% Relative estimated bulk	Biomass eaten/100 scats (kg)	% Biomass eaten	Number individuals eaten/100 scats	Ratio of number individuals eaten
Deer ¹	74.8	75.22	56.8	3.12	1.00
Moose ²	10.1	44.75	33.8	0.21	0.07
Hare ³	3.4	1.36	1.0	1.13	0.36
Beaver ⁴	3.1	1.82	1.4	0.18	0.06
Livestock ⁵	2.4	8.17	6.2	0.07	0.02
Fruit	2.7	—	—	—	—
Small rodents ⁶	0.5	0.20	0.2	0.18	0.06
Other ⁷	1.3	0.84	0.6	0.37	0.12
Deer or moose ⁸	1.7	—	—	—	—

¹ April–May calculations based on known age ratio in kill of 1 adult : 1 short yearling for October–May period and 6.0 occurrences of fetus or fawn with assumed weights of 64, 35, and 2.3 kg (Erickson et al. 1961). June–July calculations based on 55.0 occurrences of adults (including yearlings) and 220.2 occurrences of fawns with assumed weights of 64 and 10 kg (Cowan and Wood 1955, Murphy and Korschgen 1970, Robbins and Moen 1975). August–September calculations based on estimated kill age ratio of 1 adult : 2.33 fawns (i.e., a ratio intermediate between 1:9.0 in June–July and 1:1 in winter) with weights of 64 and 20 kg. Fawn weight is for 85-day-old fawn born 7 June (Cowan and Wood 1955, Robbins and Moen 1975).

² April–May calculations based on assumed “adult” age ratio eaten of 2.8 adult : 1.4 long yearling : 1 short yearling (Berg 1975) and 4.3 occurrences of calves, with weights of 360, 270, 160, and 15 kg (Peterson 1974). June–July calculations based on 6.9 occurrences of adults (including yearlings) and 6.6 of calves with weights of 360, 200, and 26 kg (Peterson 1974). Assume ½ of “adults” were yearlings (Berg 1975). August–September calculations based on same “adult” : calf ratio as calculated for June–July (i.e., 1:1.5). Assume ½ of “adults” were yearlings (Berg 1975). Weights used for adult, yearling, and calf were 360, 240, and 70 kg, respectively (Peterson 1974).

³ Assuming weight of 1.2 kg.

⁴ Based on weight of 10.0 kg (Longley and Moyle 1963), assuming most beavers eaten are dispersing yearlings.

⁵ Based on 0.9 occurrences of adult cattle, 5.4 of calf, and 6.9 of adult or calf; 1.0 occurrence of goat; and 2.0 occurrences of hog, using assumed weights of 400, 25, 50, and 50 kg, respectively (Spector 1956).

⁶ Based on 0.1 occurrence of fox squirrel, 1.6 occurrences of woodchuck, and 1.6 occurrences of smaller rodents, with assumed weights of 0.9, 3.0, and .03 kg, respectively (Burt and Grossenheider 1964).

⁷ Based on total of 9.1 occurrences of prey ranging in size from grasshoppers to wolf and categorized as birds, carnivores, insects, and unidentified small mammals. Weights used were arbitrary depending on species composition of food category. Figures for number of individuals eaten are exclusive of insects.

⁸ Not distinguishable. Assume figures above not altered significantly by omission of this datum from calculations.

variation reflects to some extent the annual variation in time of year represented in collections (Table 11). The proportions of summer and winter scats in the collection did not differ appreciably between years, except for 1976, when more winter scats were included. During 1974–1976 an inverse relationship existed between occurrence of deer and moose in scats. Collection of fewer scats containing deer during 1974 and 1976 relative to 1975 probably is explained by a greater proportion of scats for 1974 and 1976 having been collected at a time of year when greatest consumption of moose occurred.

Moose was the second most important food during both winter and summer (Tables 9, 10). The estimated biomass of moose eaten in summer was 1.3 times greater than in winter, and the number of individuals eaten in summer was probably about 1.5 times that in winter. Per-

centage relative estimated bulk of moose in summer scats was highest in the April–May subsample (20.0), but especially high in May (32.5). Estimated biomass ratio for the 3 summer periods was 1.00:0.15:0.06, whereas the numbers ratio was 1.00:0.25:0.08. Consumption of moose biomass probably was greater than of deer biomass in April–May. Although consumption of moose peaked in May, it generally was higher from March through June than during the remainder of the year.

The distribution of scats that contained moose indicated it was eaten by all packs in the study area, being found in 6.0 to 23.1 percent of scats assignable to specific packs. Those figures were highest for packs with ranges generally in the western half of the Forest where the moose density was higher. Occurrence of moose in scats collected at dens and rendezvous

TABLE 11.—PREY REPRESENTED IN 960 WOLF SCATS FROM THE BELTRAMI ISLAND STATE FOREST, MINNESOTA, 1972–1976, SUMMARIZED BY YEAR OF COLLECTION WITH ESTIMATED BIOMASS AND NUMBERS OF PREY (CALCULATED ACCORDING TO FLOYD ET AL. 1978)

Food	No. scats:	% Relative estimated bulk					Combined years (960)	Approximate % of animal biomass ¹	Ratio of no. individuals in diet ² (combined years)
		1972 (12)	1973 (191)	1974 (231)	1975 (252)	1976 (274)			
Deer		66.7	69.6	74.2	82.1	74.0	75.3	67.0	1.00
Moose		5.0	8.6	11.3	7.1	12.9	9.8	26.6	0.06
Hare		27.5	7.7	3.6	2.0	0.7	3.6	0.7	0.32
Beaver		0	1.0	3.4	2.6	3.2	2.5	0.6	0.03
Livestock		0	5.1	1.9	0	3.3	2.4	4.3	0.01
Fruit		0	4.8	0.5	3.1	0	1.9	—	—
Small rodents		0	0.2	1.4	0.4	0.8	0.7	0.1	0.06
Other		0.8	1.5	1.4	1.5	0.7	1.2	0.7	0.07
Deer or moose ³		0	1.5	2.3	1.2	4.3	2.6	—	—

¹ Obtained by taking the mean of the biomass eaten/100 scats for each food category for winter and summer.

² Obtained by taking the mean of the number individuals eaten/100 scats for winter and summer.

³ Not distinguishable.

sites differed considerably between packs, ranging from 2.2 percent relative estimated bulk at the second den of the Clear River Pack in 1975 to 26.7 percent at the Faunce Pack's 1973 rendezvous site.

Approximately 40 percent of the moose remains found in scats from May through July were of calf. Occurrences of adult outnumbered those of calf for that period every year except 1973. In April–May, the estimated biomass ratio of fetus/calf: older moose was 1:64.6, and the estimated ratio of individuals was 1:3.3. Thus, the elevated occurrence of moose in scats during April–May was not primarily the result of consumption of neonates. The calf: adult numbers ratio in June–July was approximately 1:0.7, and the biomass ratio was 1:7.8. Analyses of scats from other areas suggest relatively heavier exploitation of calves in summer than do our findings (Mech 1966, 1970; Shelton 1966, unpublished doctoral dissertation, Purdue University, West Lafayette, Indiana; Pimlott et al. 1969; Byman 1972, unpublished master's thesis, University of Minnesota, Minneapolis, Minnesota; Frenzel 1974; Peterson 1977).

Berg (1975) reported a high rate of natural mortality in moose from northwestern Minnesota during the study period. This was due in calves primarily to ex-

posure in severe weather in conjunction with heavy winter tick *Dermacentor albipictus* infestations and in adults to cerebrospinal nematodiasis *Parelaphostrongylus tenuis* and liver flukes *Fascioloides magna*. Mortality peaked in late winter and spring, which was when most moose remains appeared in wolf scats. Therefore, it is likely that the moose eaten by wolves either were scavenged or were severely weakened individuals when killed.

Our calculations indicate that deer and moose composed at least 94 percent of the animal biomass eaten by wolves in the Forest (Table 11). That figure is slightly low because a few scats that contained either deer or moose (indistinguishable) were not considered in the calculations (Tables 9, 10).

Snowshoe hare *Lepus americanus* was eaten frequently year round, ranking second only to deer in number of individuals eaten. Nonetheless, this food composed less than 1 percent of the total animal biomass consumed. Occurrence of hare in scats declined annually throughout the study (Table 11). Hare pellet counts conducted by the Minnesota Department of Natural Resources indicated a steady decline in the local hare population from 1972 to 1976 (W. E. Berg, pers. comm.).

Beaver was found in scats from April to

July (and possibly August), but was not an important food (Table 10). Occurrence in April–May was higher than in June–July ($\chi^2 = 23.3$, $P < 0.005$). Because muskrat *Ondatra zibethicus* hair is very similar to beaver hair, some muskrat remains possibly were classified as beaver.

Beaver was not more common in scats collected at rendezvous sites than elsewhere ($\chi^2 = 1.02$, $P > 0.05$), in contrast to findings by Theberge et al. (1978) in Algonquin Park, Ontario. Relatively few scats were collected in late summer and autumn when consumption of beaver was highest in northeastern Minnesota (Byman, unpublished thesis, Frenzel 1974). Therefore, this food might have been underrepresented in our collection. Nonetheless, beaver apparently is a less important food in the Forest than in northeastern Minnesota. Use of this food has increased dramatically in southern Ontario, related to a decline in white-tailed deer populations (Voigt et al. 1976, Theberge et al. 1978).

Species of livestock found in scats and their respective percentage relative estimated bulks were cattle *Bos taurus*, 1.9; swine *Sus scrofa*, 0.3; and goat *Capra hircus*, 0.2. In most cases we were unable to distinguish adults and juveniles of those species by their hair. A relatively high proportion of scats composed of livestock (5.6 of 23.1 occurrences) could not be assigned to season, but likely were deposited in late winter or early summer. Because these were excluded from biomass and numbers calculations, the consumption of livestock indicated for both seasons may be slightly low (Tables 9, 10). An opposite effect would have resulted if the livestock was scavenged, because our calculations assumed the availability of intact carcasses. Occurrence of livestock in April–May scats was greater than during June–September ($\chi^2 = 5.63$, $P < 0.025$). Predation on livestock is given additional attention later.

Fruit occurred in scats in July, August and September. Identifiable fruit items included blueberries *Vaccinium* sp. and strawberries *Fragaria* sp. Occurrence of

fruit in scats collected at rendezvous sites was greater than in those collected elsewhere ($\chi^2 = 5.73$, $P < 0.025$), suggesting that this food was eaten primarily by pups. Van Ballenberghe et al. (1975) reported a high incidence of fruit in scats from rendezvous sites in northeastern Minnesota. Annual variation in occurrence of this food in scats from the Forest reflected yearly differences in number of scats collected at rendezvous sites.

Small rodents identified in scats were bog lemming *Synaptomys* sp., fox squirrel *Sciurus niger*, jumping mouse *Zapus hudsonius*, meadow vole *Microtus pennsylvanicus*, white-footed mice *Peromyscus* sp., and woodchuck *Marmota monax*. Most of the biomass of that insignificant food category was of woodchucks, which were available only in summer. Other miscellaneous items were black bear *Ursus americanus*, striped skunk *Mephitis mephitis*, unidentified *Canis*, and wolf. Birds represented were black-capped chickadee *Parus atricapillus*, unidentified grouse, mallard duck *Anas platyrhynchos*, duck egg shells, song sparrow *Melospiza melodia*, and unidentified warbler. Insects and unidentified mammal remains made up the remainder of scat contents. Grass, not digestible by wolves, was not considered food in the analyses, although it may be ingested intentionally.

In summary, the scat analyses identified deer and moose as the predominant foods of wolves in the Beltrami Island State Forest, with moose most important in spring. Beaver and moose appeared to be eaten less in the study area than in northeastern Minnesota, and deer fawns were highly important from mid-June at least until August.

Aerial Observation of Deer and Moose Eaten

Remains of 106 deer and moose that had been killed, or at least eaten, by wolves were observed during aerial radiotracking and searches for wolf sign. Carcasses were suspected to be present at 17 additional locations because of the

presence of ravens *Corvus corax*, magpies *Pica pica*, or bald eagles *Haliaeetus leucocephalus*. Evidence of predation on smaller animals was not obtainable by aerial observation. Of deer and moose seen near instrumented wolves, 71 percent were observed from December through March when permanent snow-cover and absence of leaves on deciduous vegetation facilitated aerial viewing.

Of the 106 "kills," 88 could be identified with a reasonable degree of certainty. Deer comprised 65 (74%) of these, and another 13 (15%) probably were deer. Eight definitely were moose, and 2 more probably were. Thus the observed ratio of deer to moose carcasses was approximately 8:1, compared with a ratio of 17:1 calculated from scat data. The ratio of deer to moose in the population was 14–21:1. The observed ratio probably was biased in favor of moose because of their greater size and increased observability. Also, distribution of moose in the study area generally corresponded to the more open habitat types and deciduous vegetation where aerial observation of prey animals was easiest. In any event, aerial observations complemented the scat analysis in showing that moose was an important food during the study.

In other areas, wolves rarely prey on adult moose when white-tailed deer are present (Peterson 1955, Stenlund 1955, Pimlott et al. 1969, Mech and Frenzel 1971, Kolenosky 1972, Mech 1977a). Therefore, the proportion of moose among cervid carcasses seen near wolves in the Forest was unusually high especially in view of the abundance of deer. Because the moose population in the Forest is known to have a high rate of natural mortality (Berg 1975), it appears likely that most moose eaten by wolves there were scavenged.

Sixty-one (78%) of the 78 deer kills were observed in winter (October–March); several were clearly small deer suspected to be fawns. At least 2 of 17 summer (April–September) observations were of fawns. The small size of fawns and the extent of utilization of their car-

cases in summer reduces their probability of being observed, so their relative frequency of observation by no means reflects the extent to which they are preyed on by wolves in summer. Three moose carcasses were seen near wolves in August and 1 in May. Winter observations of moose carcasses consisted of 1 in October, 3 in November, 1 in December, and 1 in March; however, some appeared to have been dead a long time prior to the date of observation.

Distribution of dead moose generally corresponded to areas of highest moose density in the Forest (W. E. Berg, pers. comm.). Five of the 10 "kills" seen were near the territory of Peet's Pack. Six of the 10 moose were in areas of marsh with scattered willows, whereas the other 4 were in coniferous vegetation. Six were found within a few meters of the drainage ditches along section lines in most of their areas of highest density.

Among 92 deer kills, unidentified kills, and suspected kills (the latter 2 categories probably were deer also), 57 were in pure or mixed coniferous vegetation. Forty-five (80%) of 57 located in December–March were in conifers, whereas only 12 (34%) of 35 seen in April–November were in coniferous cover. Such seasonal difference in basic cover type associated with kills was highly significant ($\chi^2 = 18.34$, $P < 0.005$). Nine deer kills and 1 suspected kill were located in close association with ditches or streams.

No chase of deer or moose was witnessed. On 1 April 1976, 2 wolves (Morehouse Pair) were observed as they finished killing a large adult deer that already had been brought to the ground. On several occasions a wolf was observed standing over a deer that apparently had been killed just minutes before. It was not unusual to see wolves and deer or moose within short distances of each other, but giving no indication that either was aware of the other's presence. Such observations were more common in habitats characterized by dense willows, alder, or aspen where visibility at ground level is poor.

TABLE 12.—ESTIMATED MINIMUM KILL RATES AND FOOD CONSUMPTION RATES OF WOLVES IN WINTER, BELTRAMI ISLAND STATE FOREST, MINNESOTA, 1972–1977

Social unit	Winter of study	Number locations	Number kills ¹ observed	Number locations per kill	Estimated number kills per winter ²	Group size in midwinter	Kg per wolf per day
Clear River	1972–1973	29	1	29.0	4.1	4	0.5
	1974–1975	32	5	6.4	19.0	6	1.5
	1975–1976	19	1	19.0	6.3	3	1.0
Winner/Thief Lake	1973–1974	15	0	—	—	2	—
	1974–1975	22	3	7.3	16.4	2	3.7
	1975–1976	28	1	28.0	4.3	2	1.0
	1976–1977	1	0	—	—	?	—
Faunce (original)	1972–1973	4	0	—	—	3	—
	1973–1974	22	2	11.0	10.9	3	1.6
	1974–1975	14	1	14.0	8.6	3	1.3
Faunce (new)	1974–1975	12	2	6.0	20.0	2	4.5
	1975–1976	29	5	5.8	20.7	3	3.1
	1976–1977	5	0	—	—	?	—
Peet's	1974–1975	23	3	7.7	15.6	6	1.2
	1975–1976	35	9	3.9	30.8	6	2.3
Rapid River	1974–1975	28	5	5.6	21.4	5	2.0
	1975–1976	35	2 (4) ³	17.5 (8.75) ³	6.9 (13.7) ³	7	0.9
Bankton	1975–1976	38	9	4.2	28.6	4	3.3
	1976–1977	12	3	4.0	30.0	6	5.0
Vacuum	1975–1976	34	4	8.5	14.1	7	0.9
	1976–1977	3	1	3.0	—	?	—
Baudette River	1975–1976	21	0	—	—	3	—
Hogsback	1975–1976	12	3	4.0	30.0	2	6.8
Morehouse	1975–1976	24	5	4.8	25.0	2	5.7
Waskish	1975–1976	22	3	7.3	16.4	2	3.7
Malcolm	1974–1975	14	3	4.7	25.3	2	5.7
Northome	1975–1976	6	0	—	—	2	—
No. 5141 ⁴	1974–1975	7	0	—	—	1	—
No. 5143 ⁴	1974–1975	13	0	—	—	1	—
No. 5171 ⁴	1975–1976	15	2	7.5	16.0	1	7.3

¹ Suspected kills included and assumed to be deer.

² Projected number kills in 120-day period (December–March).

³ One kill was moose—probably calf, treated as equivalent of 3 deer (Mech 1977a).

⁴ As a lone wolf.

Kill Rates in Winter

The absolute number of deer and moose killed by instrumented wolves was not determined because study animals were not relocated daily. However, it was possible to estimate the kill rates during winter (defined here as December–March) by using information obtained during aerial telemetry work (Mech 1977a). The number of daily re-

locations per kill observed was determined for December–March. When projected to the total 120-day period, those figures gave estimates of the minimum number of kills made during winter. Suspected kills were included, but the total number of deer and moose still should be considered minimal because we undoubtedly missed seeing some kills.

Estimated winter kill rates for 7 packs (3+ wolves) over 13 pack winters ranged

from 4.1 to 30.0 and averaged 17.2 kills per winter (Table 12). The Baudette River Pack was not included in this computation because no kills were seen at 21 locations of the group. When the pack kill rate is computed as: $120 \text{ days}/(\Sigma \text{ all pack locations}/\Sigma \text{ all pack kills})$, the resulting figure is 14.5 kills per pack per winter.

The estimated rate of kills for the Clear River Pack seems unrealistically low compared to other groups of comparable size and in view of the number of deer and deer tracks we saw in their territory. The area included more coniferous cover than some others, so perhaps several kills were not seen. Three of 17 kills discovered incidentally during ground work were within the Clear River Pack's territory.

Among 6 pairs followed for 7 pair winters, the estimated kill rate ranged from 4.3 to 30.0 and averaged 19.6 per winter. Combining data for pairs, i.e., $120 \text{ days}/\Sigma \text{ pair locations}/\Sigma \text{ pair kills}$, produced a figure of 16.0 kills per pair per winter.

Only 2 lone wolves, 5141 and 5171, were followed during winter. Data were insufficient for comparing their kill rates to those of packs and pairs.

Most data on kill rates were obtained during winters 1974–1975 and 1975–1976. The mean number of aerially determined locations per kill was 7.5 and 7.2 for those winters, based on 165 and 318 locations. Snow conditions probably were more favorable for wolves in 1974–1975. Instrumented wolves were observed at 58 percent of their winter locations in 1974–1975 and 78 percent in 1975–1976. Assuming that success rate at seeing wolves is directly proportional to that of seeing any kills nearby, it is likely that more of the total kills present were seen in 1975–1976. Therefore, the difference in kill rates for the 2 years may have been greater than indicated by the figures. Only 1 kill was seen at 33 locations in 1972–1973; 2 were seen at 37 in 1973–1974; and 4 were seen at 22 in 1976–1977.

Breakdown of kill rate by winter month revealed a peak in February. The num-

bers of kills seen per 100 relocations in December, January, February, and March were 11.9, 17.6, 18.6, and 15.4, respectively. In the Superior National Forest, Mech (1977a) reported a peak in kill rate by the Harris Lake Pack from mid-February to mid-March, at which time 14.7 kills were seen per 100 relocations.

Kill-rate estimates were divided by number of individuals in social units to estimate mean minimum winter (December–March) consumption of deer per wolf. When pack size was known to decrease over winter, the midwinter size was used. Moose (only 1; the others were observed outside the December–March period) were converted to an equivalent number of deer (Mech 1977a:70), so figures represent deer-sized kills. Unidentified and suspected kills were assumed to be deer. The estimated number of kills made per wolf per winter varied greatly from 1.0 to 16.0. The mean rate for pack members over 13 pack winters was 3.7, whereas the mean rate for pair members over 7 pair winters was 9.8.

If it is assumed that the average deer provides about 54.5 kg of food (Mech 1977a:70), the estimated mean minimum consumption rate would be 345 kg (range = 27–872 kg) per wolf per winter. This converts to 2.9 kg (range = 0.2–7.3 kg) per wolf per day. The average minimum daily rate for members of packs and pairs would be 1.63 kg and 4.45 kg, respectively. These figures are similar to those from previous reports of wild and captive wolves (Mech 1966, 1977a; Mech and Frenzel 1971; Kolenosky 1972; Kuyt 1972; Haber 1977, unpublished doctoral dissertation, University of British Columbia, Vancouver, British Columbia) except that our figures cover a wider range (0.2–7.3 kg vs. 1.1–6.4 kg). Mech (1970) concluded that 1.7 kg per day probably is the minimum maintenance requirement of wolves in the wild.

The difference in kill rates per wolf between packs and pairs is sufficient to indicate a real disparity in food intake. Such a finding is surprising because it implies that pairs are more efficient than

packs at hunting deer. Moreover, it suggests a low optimum group size in the Forest, if the optimum group size is one that maximizes energy returns to individuals (Nudds 1978). In the Superior National Forest, single wolves and pairs had a higher kill rate per wolf than a pack of 5, but this might have been atypical because of unusual snow conditions favoring wolves (Mech and Frenzel 1971). Snow conditions probably were not responsible for that result in our study. The finding of a higher kill rate per wolf in pairs would in part be explained if pairs spent a greater proportion of their time at kills (because it took longer for a pair to consume a carcass), and thus a higher percentage of their total kills was observed. However, it probably also reflects the sharing of food by adult pack members with their pups, which probably do not contribute substantially to the kill rate.

Again, it must be emphasized that estimates of kill rates and food consumption represent minimum values, because kills at some locations undoubtedly went unobserved. Estimates of food consumption would be low if some of the unidentified and suspected kills were moose rather than deer. Because scat analyses indicated that deer and moose composed all but a small fraction of the total food biomass in winter, noncervid prey in the diet would add little to the estimates provided.

Distribution of Kills in Relation to Edge of Territories

Killing of deer along territory edges in northeastern Minnesota is thought to be extreme and unusual behavior to which wolf packs resort only when desperate (Hoskinson and Mech 1976; Mech 1977a,c); Nelson and Mech 1981). The presumed reason for the reluctance to make kills near the edge of territories is greater probability of interpack contact there (Mech 1977c). We examined distribution of kills in relation to territory edges to determine whether the same

phenomenon existed in the Beltrami Island State Forest where the prey density was higher and the wolf density lower.

Each territory that was reasonably well defined by locations of instrumented wolves was divided into a "center" and "edge." The edge consisted of a strip 1 km wide inside the boundary of each territory. This distance was selected because Peters and Mech (1975) and Mech (1977a,c) suggested that a shared or overlap zone of about 2 km existed between packs in the Superior National Forest. When boundaries were known to shift during the study, they were redrawn as accurately as data permitted. Locations of kills were superimposed on the territories.

Significantly more kills per area were observed within the centers of territories than within the 1-km edge ($\chi^2 = 4.919$, $P < 0.05$). Only 8 (10%) of 78 kills were within the edge, which comprised 21.1 percent of the total area considered. Even with the edge of territories defined as a 2-km strip (i.e., 4 km of overlap), significantly more kills per area were made within the center ($\chi^2 = 9.129$, $P < 0.005$). In that case the edge comprised 40.5 percent of the total area. Inclusion of suspected kills produced similar results.

Altogether, 18 kills and 3 suspected kills fell within a 2-km edge. Sixteen were located in areas where (1) no pack was thought to exist beyond the edge of the territory even though suitable habitat was present, (2) there was a wide marsh just beyond the edge, or (3) farmland bordered the edge. Only 5 of 21 kills within edges were situated across from the territory of another wolf pack. Those data suggest that the existence of neighboring packs had a major influence on patterns of territory use and distribution of kills.

There was an apparent relationship between age of social groups and distribution of kills. No tendency to avoid making kills at the edge was apparent among newly formed groups (e.g., Faunce Pack in early 1975 after 5115 and 5141 paired, Hogsback Pair, and Morehouse Pack). However, it was more difficult to deter-

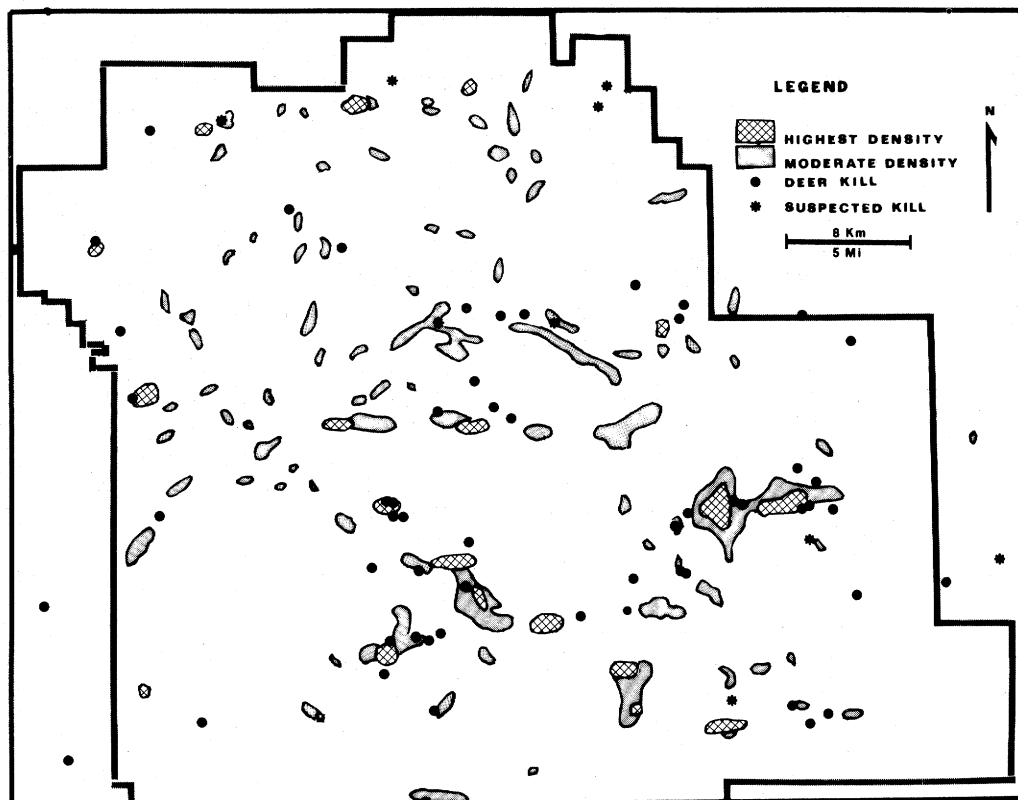


FIG. 34. Distribution of deer kills and suspected kills observed during December–March in the Beltrami Island State Forest in relation to high and moderate density wintering areas. Wintering areas identified primarily by E. Clem, Minnesota Department of Natural Resources.

mine from telemetry data where the territory was for new groups, which may wander somewhat before settling into a definite area. From winter 1973–1974 to winter 1974–1975, the Faunce Pack which may have been composed of 3 sub-adult littermates, made kills over an area of 880 km² during a period when their movements suggested little avoidance of surrounding packs. Perhaps the unusual trio was unaware of traditional boundaries of its territory or was not responding normally to scent marks and howling by its neighbors (Peters and Mech 1975, Harrington and Mech 1979).

Only 2 kills by lone wolves were found within the main study area, one of which was between pack territories in an 8-km-wide tamarack swamp. The other was in a frequently used central part of the Vac-

uum Pack's territory. It may be significant that that kill, a deer fawn, was dragged about 50 m from a logging road into dense brush before being consumed.

Distribution of Deer Kills in Relation to Deer Distribution

Kills were widely distributed during April–November, but little is known about the summer distribution of deer in the study area.

Distribution of deer kills observed in the Forest in December–March was compared to known deer wintering areas. For this analysis, we included 9 locations where unidentified kills were seen and 9 locations of suspected kills. Deer wintering areas were identified over the past 20 years, primarily by Everett Clem,

Minnesota Department of Natural Resources. Some of the same yards were examined from 1949 to 1956 by Minnesota Department of Conservation crews (Erickson et al. 1961). Supplementary and supporting data were obtained during this study. These observations verified that most wintering areas, particularly major ones, were still used.

Approximately 119 km² of the study area were identified as deer wintering areas, within which 27.5 km² and 91.5 km² were classified as areas of high and moderate concentration, respectively (Fig. 34). During mid to late winter, the few areas of high concentration probably contained a large proportion of the deer in the study area, especially in winters of heavy snow accumulation.

However, of 67 kills located during aerial tracking from December through March, only 2 (3%) were clearly within high density wintering areas, and 9 (13%) inside moderate density wintering areas. Eight were on the fringe or barely outside high density areas, and 7 were at the edge of moderate density areas. Thus, 41 kills were found outside of even moderate density areas.

The low number of deer kills found inside the major wintering areas and the substantial number near the perimeter and outside of the areas was surprising. This finding must be viewed with caution because of uncertainty about (1) the exact boundaries of deer yards, (2) the relative importance of concentration areas, and (3) the degree of deer concentration during winters of the study. However, it is significant that E. Clem (pers. comm.) concluded independently from several winters of observations in the study area that wolf packs generally hunted and killed deer on the fringe of wintering yards, whereas deer in the interior of yards were relatively safe.

Laramie and White (1964) thought that does and fawns enter wintering yards earlier and that fringes of yards are occupied by small groups of adult males. Predation on wintering deer in Ontario was heaviest along the edge of a main

wintering area where small pockets of deer occurred (Kolenosky 1972). Heavier predation along the edge was believed responsible for the greater percentage of adult male deer in his sample. If this conclusion is correct, it might help to explain why other researchers have reported more adult males than females killed by wolves in winter (Stenlund 1955, Pimlott et al. 1969, Mech and Frenzel 1971, Mech and Karns 1977). Certainly, more research is needed on the hunting patterns of wolves at deer yards and the distribution of sexes at those sites, but the data from the present study support the hypothesis that winter yarding and the spatial organization of deer function as antiwolf defenses (Nelson and Mech 1981).

Major wintering areas usually were not situated along edges of wolf pack territories as they are in the central Superior National Forest (Hoskinson and Mech 1976, Mech 1977c, Rogers et al. 1980, Nelson and Mech 1981). A noteworthy exception was the Oaks yard, which was between territories of Peet's Pack and the Rapid River Pack. Both packs appeared to avoid the yard. Among 121 radio fixes for the 2 packs in December–March, only 1 location (Peet's Pack) was at the yard. However, female 5111, apparently drifting alone at the time, was killed by another wolf (wolves?) there in March 1974, and 3 deer kills were found within 0.4 km of her carcass. Neither Peet's Pack nor the Rapid River Pack was instrumented before summer 1974; one or both of those groups could have been using the Oaks yard at the time. Lone female 5141 visited the area in February 1975, and lone male 5109 was shot by a deer hunter there in November 1973.

The occurrence of major deer wintering areas along edges of territories probably is the result of special circumstances not present in the Forest during this study: wolf territories must be stable over long periods, and the deer population must have been highly exploited by wolves in the centers of their territories. In view of the changes in territorial

TABLE 13.—SEX AND AGE OF 48 DEER KILLED BY WOLVES IN THE BELTRAMI ISLAND STATE FOREST, MINNESOTA, 1972–1977

Sex	Age															Unaged adults ¹	Total	\bar{x} Age ²	
	Fawn	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	11+	12+	13+	14+				15+
Male	8	1	0	1	0	1	2	0	1	1	3	0	0	0	0	0	1	19	7.3
Female	2	1	0	2	0	0	1	1	0	0	0	1	1	0	1	1	1	12	8.5
Unknown	11	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	4	16	—

¹ Age to year could not be determined because of insufficient remains.

² Excluding fawns.

boundaries during this study and the abundance of deer in the Forest, the presence of most major deer yards along boundaries of wolf pack territories would have been an unexpected finding.

Age, Sex, and Condition of Deer and Moose Examined

Kills that had been seen from the air often were difficult to reach for examination. Nevertheless, remains of 54 deer killed by wolves were examined between January 1975 and May 1976. All but 4 were killed during winter. Failure to locate skull and mandible precluded determination of sex and age of several deer; yet, sex of 31 and age (to year) of 42 were determined (Table 13). Six deer could be classified only as “adults.”

The age structure of the 42 deer killed by wolves during winters 1974–1975 and 1975–1976 was significantly different from a sample killed by hunters from the same general area during those years (Kolmogorov-Smirnov, $P < 0.05$) (Fig. 35). The latter sample was assumed to approximate the age composition of the population at large. Fawns composed a greater proportion of the sample killed by wolves than the one killed by hunters ($\chi^2 = 5.638$, $P < 0.01$). That age cohort composed 51 percent of deer killed by wolves in winter and 44 percent of the total sample. Because fawns usually are more completely consumed than adults, they may have been subject to a collection bias. Therefore, 51 percent probably is a conservative figure. Even so, this is the highest percentage of fawns yet

found in a sample of white-tailed deer killed by wolves in winter. Previously reported figures from Minnesota and southern Ontario range from 17 to 30 percent (Stenlund 1955, Pimlott et al. 1969, Mech and Frenzel 1971, Kolenosky 1972, Mech and Karns 1977).

The mean age of adult deer killed by wolves was 7.6 years (7.3 for 10 males; 8.5 for 9 females), compared with 3.3 years for adults killed by hunters (3.4 for 114 males; 3.7 for 123 females). The mean age of adult deer killed by wolves in the Forest was greater than the mean age (5.5 years) of adults killed by wolves from the Superior National Forest in the collection of Mech and Frenzel (1971) ($t = 2.213$, $P < 0.05$). Comparison of samples killed by hunters from the 2 areas revealed a younger adult population in northwestern Minnesota (Kolmogorov-Smirnov, $P < 0.05$). Thus, selection of fawns and old adults appeared to be particularly strong in the Beltrami Island State Forest. A higher and more productive deer population probably allowed wolves to be more selective for individuals that were easiest to capture.

Examination of the combined 1974 and 1975 samples of adult deer killed by hunters revealed a difference in age structure of the sexes (Kolmogorov-Smirnov, $P < 0.05$), which may have been related to the hunter harvest. Generally, the female group included older animals. This may in part explain the higher mean age of females among adults killed by wolves. If fawns are included, the mean age of all males killed by wolves was 4.28 years, compared to 7.05 for females.

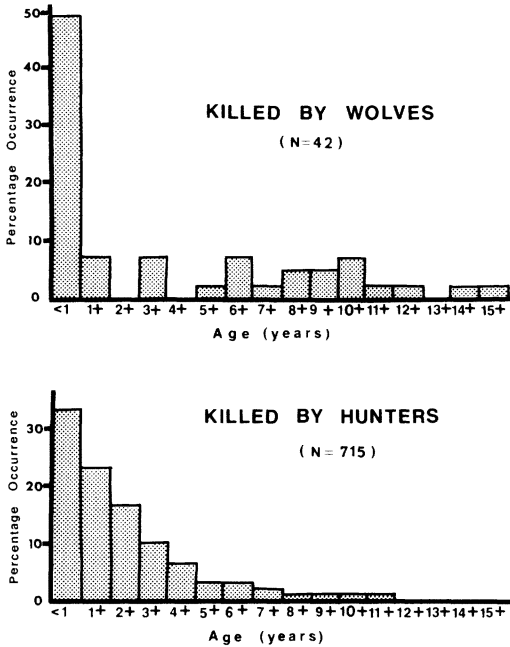


FIG. 35. Age composition of deer killed by wolves and by hunters in the study area, winters of 1974–1975 and 1975–1976.

Because of more complete consumption of fawns, we were able to determine the sex of only 10, 8 males and 2 females, which was significantly different from the 114:123 sex-ratio of fawns in the sample killed by hunters ($\chi^2 = 3.904$, $P < 0.05$). That result is contrary to findings of differential predation on female fawns in the Superior National Forest (Stenlund 1955, Mech and Frenzel 1971, Mech and Karns 1977).

The sex-ratio among adult deer killed by wolves was 11 males:10 females, which was not significantly different from the 377:338 ratio recorded for adult deer taken by hunters during the same period ($\chi^2 = 0.056$, $P > 0.1$). In the studies cited above, there was differential predation on adult males.

Femur marrow from 39 deer killed by wolves in winter was examined as an index of general physical condition (Cheatum 1949, Bischoff 1954). Percentage fat content (dry weight/wet weight $\times 100$) of 29 samples was determined in the laboratory, and fat content of another 10 sam-

ples was estimated by visual inspection (Peterson 1977:30). There was no evidence of serious fat reduction in most samples, suggesting malnutrition was not an important factor in deaths of most deer. Among 29 samples examined in the laboratory, the mean fat content was 91 (73–99) percent for adults and 82 (33–99) percent for fawns. Four deer whose marrow fat was considered low were all fawns, 3 of which were killed in March and 1 in early April. Although fawns probably are weakened more than adults by a negative energy balance in late winter, a monthly breakdown of age ratios in the winter kill revealed no apparent increase in percentage of fawns in the kill in late winter.

A total of 123 legs representing 45 deer was examined grossly for abnormalities or pathological conditions. Hoof abnormalities were noted in limbs of 4 (9%) individuals. Two of those deer of unknown sex and age had crossed hooves, a 3-year-old male had an exceptionally long dewclaw, and the halves of a hoof from a 3-year-old female were asymmetrical in size. The incidence of hoof abnormalities in the deer population at large is unknown; no sample killed by hunters was available for comparison. Mech and Frenzel (1971) reported lower limb pathology in 6.7 percent of a sample killed by wolves from northeastern Minnesota, compared to 0.8 percent of a sample killed by hunters.

Minor periodontitis (assumed *Actinomyces* sp.) was found in mandibles from a 7-year-old female and a 10-year-old male deer; an advanced case was found in a 9-year-old male. An unusual tooth wear pattern was noted in an 11-year-old female. These cases represent 11 percent of deer examined. Mech and Frenzel (1971) reported dental and jaw abnormalities in 9.8 percent of deer examined, compared with 2.3 percent of their sample killed by hunters.

The only moose examined was a female calf. Remains of that individual were discovered a few hours after it had been consumed by the noninstrumented

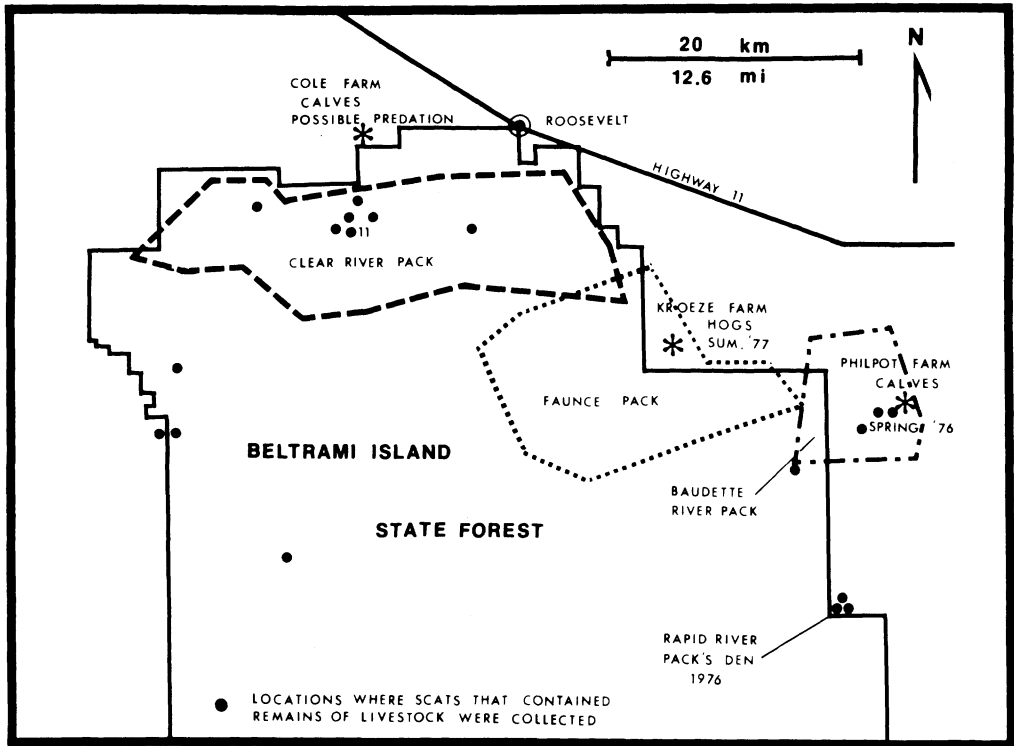


FIG. 36. Locations of wolf scats that contained livestock remains and sites of 1 possible and 2 known cases of predation on livestock (*) by study packs in the Beltrami Island State Forest.

Moose River Pack in mid-March 1976. Femur marrow gave no indication that malnutrition contributed to the calf's death.

Consumption of carcasses usually was complete, with only rumen contents, skin, and scattered parts of the skeleton remaining at kill sites. Five deer were not completely consumed. Four of these were killed in late March or early April, suggesting wolves were having little difficulty killing at that time (Mech and Frenzel 1971). The other deer, killed in early January, was located near a frequently traveled road, so human activity may have contributed to its premature abandonment. No cases of surplus killing (Kruuk 1972) were noted during the study.

Domestic Animals as Food

The potential of wolves as livestock predators is well documented (Young

and Goldman 1944). Major types of livestock available to wolves in the study area were cattle, sheep, and hogs at a ratio of approximately 23:6:1. Most sheep were located west of the study area in Roseau and Marshall counties, which rank 1 and 2 among Minnesota counties in sheep production (Minnesota Crop and Livestock Reporting Service 1976). Cattle and sheep were confined with virtual impunity from predation from about November to April or May, at which time they were released to graze. Turkeys were produced on open range in summer, primarily west of the Forest. The part of the primary study area with the greatest apparent potential for predation on livestock was along the north, northeast, and northwest edges of the Forest. Livestock are produced on most of the many small farms there, and the transition from forest to farmland is relatively sharp. Territories of radiocollared packs

extended to the edge of forest cover there.

Remains of Livestock in Scats

Effort expended in scat collecting was greatest within the northern part of the Forest. For example, 282 of the 960 (29.4%) scats were from the range of the Clear River Pack. Therefore, the content of those scats was of considerable interest in evaluating the extent to which wolves living in the Forest fed on domestic species.

Twenty-nine of 960 (3.0%) scats contained remains of livestock, primarily cattle (Fig. 36). The majority of these scats were collected in summer near the edge of the Forest. Seventeen were from the northern part of the Forest within the territory of the Clear River Pack, and 11 of those were collected near a den or rendezvous site. Most scats composed of livestock were collected in 1973 and 1976, but some were obtained also in 1974 (Table 11). Thus, the scats did not indicate an increase in consumption of livestock by wolves in the Forest associated with the increase in wolf density. Estimates of livestock biomass and numbers represented by these scats were given under scat analyses (Tables 9, 10).

In only 1 case could we conclude that remains of livestock in scats represented animals actually killed by wolves. Five fresh scats collected from a road within the Baudette River Pack's range in spring 1976 contained hair from Hereford calves that likely were killed (Fig. 36). While trapping for the group in May, we found tracks indicating periodic entry into a pasture at the Philpot farm near the eastern edge of the group's known range. Six small Hereford calves were reported killed and eaten by wolves there in April and May. The Baudette River Pack probably killed the calves and fed them to their pups. The pups were thought to be at a den only 2–3 km from the farm.

Three scats collected at the Rapid River Pack's 1976 den contained black hair identified as cattle. That den was 6 km

from the nearest farm. Livestock producers in that area were unaware of any losses.

Goat hair was found in 2 scats from the Clear River Pack's range. A few goats were available to the pack at the edge of its range, but no losses to wolves were known to occur there.

Some of the Clear River Pack's scats that contained remains of cattle could have been from animals killed at a farm at the northern edge of the Forest. Calf losses were reported there at the Cole farm during summers of 1973–1976, and wolves were thought by the farmer to be responsible (Fig. 36). However, instrumented wolves were relocated no closer than about 3 km of the farm.

Four of the scats from the Clear River Pack's range were composed of hog hairs, and 3 contained Hereford cow or calf and hog hairs together. The only farmer who raised hogs near the range of the Clear River Pack knew of no losses to wolves in recent years. The presence of remains from more than 1 livestock species within a single scat suggested the foods might have been obtained as carrion at a disposal site. Two such scats collected in 1973 contained a paper match and a small burned stick both of which could have been ingested at a disposal site. Furthermore, at least 1 and possibly 2 of the scats composed of hog and cattle remains together were deposited in winter when closely confined domestic animals rarely are available to wolves. Two scats composed of hog hairs were collected within the Winner Pair's range near the western edge of the Forest, but nearby hog producers were certain no losses to wolves had occurred.

Some livestock carrion was available to wolves at the forest-farmland interface. When farmers were asked how they disposed of dead livestock, the most common response was that carcasses were dragged to the edge of a pasture or into the woods. Remains of butchered animals also were left at those sites. A few trappers in the study area were known to use parts of livestock carcasses as bait.

TABLE 14.—CONFIRMED (C) AND PROBABLE (P) CASES OF WOLF PREDATION ON LIVESTOCK IN AND AROUND THE STUDY AREA, BELTRAMI ISLAND STATE FOREST, MINNESOTA, 1973–1977. CASE NUMBER IS CROSS-REFERENCED WITH FIG. 37

Case no.	Farm	Date	Losses	Type of social unit involved (when known)/remarks
1 (C)	Sikorski	Jul 1977	12+ sheep	Noninstrumented pack
2 (C)	Lorenson	Aug 1976	39 turkeys	—
3 (C)	Frenzel	Oct 1976	6 calves, 6–7 sheep, 2 cows wounded	Thief Lake Pack
4 (P)	Cervin	Each year for past several	calves	—
5 (C)	Olson	summer 1972, Jun 1973	2 sheep, 2 sheep	Farmer trapped wolf at carcass in 1973
6 (C)	Solberg	Jun 1973	1 calf	On another date wolf seen stalking calf
7 (P)	Losse	Summer 1976	30 lambs, 15 adult sheep	Coyotes probably involved also
8 (P)	Rinkenberger	Aug–Sep 1976	194+ turkeys	Probably a pack Coyotes involved also
9 (C)	Phillipe	May–Jun 1973	8–9 sheep	Wolf frequented farm for 3 months before being trapped
10 (C)	Hegstad	Summer 1976	136 kg calf	Single wolf
11 (P)	Cole	Spring 1977	30 lambs, 5 ewes	Coyotes probably involved also
12 (P)	Cole	1973–1976	“few” calves	Wolves frequently seen with cattle
13 (C)	Kroeze	Summer 1977	1 calf, 1 227-kg sow	Faunce Pack
14 (C)	Philpot	Apr–May 1976	6 small calves	Baudette River Pack
15 (P)	Avery	Summer 1977	1 calf	Probably lone wolf
16 (P)	Lott	Summer 1977	Up to 47 calves	Coyotes involved also
17 (C)	O’Neil	Summer 1975	Up to 26 calves, 11 heifers	Probably a pack
18 (C)	Hasbargan	Summer 1977	Up to 13 calves	Noninstrumented pack
19 (C)	LeClaire	Aug 1976	15 geese	Lone dispersing wolf ¹
20 (C)	Halama	May 1977	1 calf	—
21 (C)	Leonhardt	Summer 1976	1 cow	—
22 (C)	Lindquist	Summer 1976	3–4 newborn calves	Noninstrumented pack

¹ Radiocollared yearling male (W. E. Berg, pers. comm.).

Also, bear hunters sometimes used carcasses of domestic animals at baiting stations.

On several occasions, we were informed of sheep losses to coyotes or

wolves. These generally were so far from ranges of the study packs that it is unlikely they were involved. Furthermore, no sheep remains were found in 960 scats collected inside the Forest.

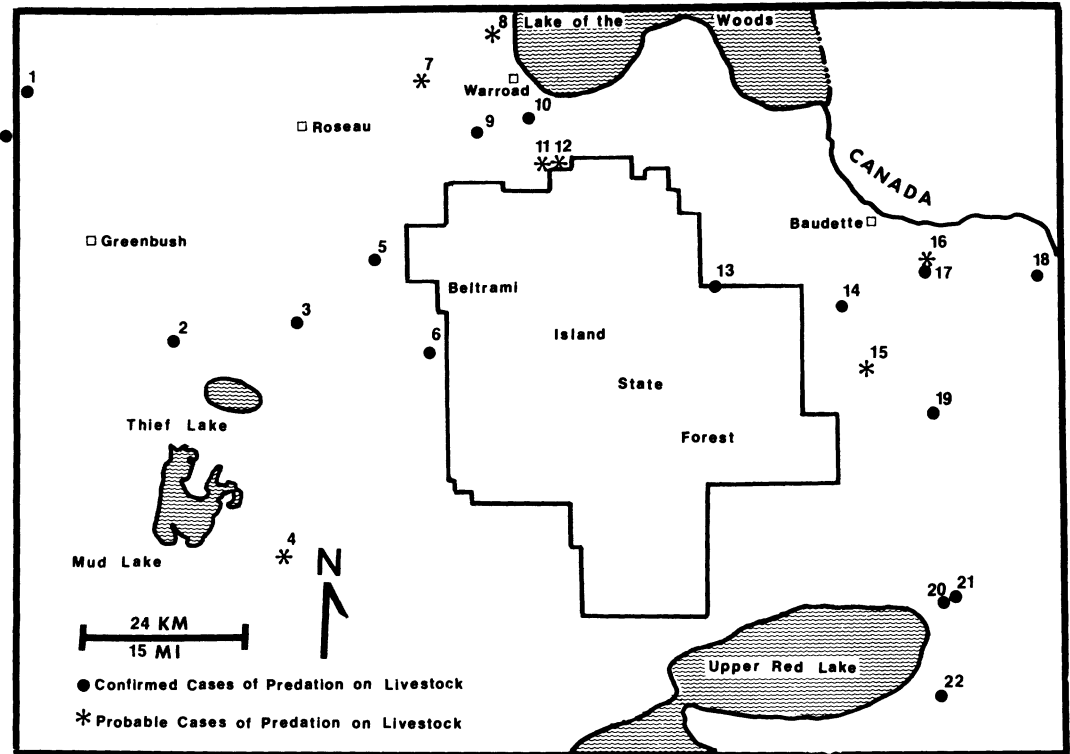


FIG. 37. Distribution of confirmed and probable cases of wolf predation on livestock in part of northwestern Minnesota, 1973-1977. Case numbers refer to Table 14.

In summary, analysis of scats from the Forest indicated that livestock was of little importance in the diets of resident wolves, except perhaps locally during summer. Natural prey predominated in scats, even in areas where domestic animals were available. Much of the livestock in scats probably was eaten as carrion.

Other Indications of Predation or Scavenging on Livestock

Instrumented wolves and their associates in the study area occasionally were located near farmland, but seldom close to livestock, never in a pasture, and rarely close to farm buildings. In the few cases where wolves were radiolocated at the edge of the Forest and close to livestock, we questioned the farmers about possi-

ble losses at the time, but learned of none. Instrumented wolves conceivably could have made forays into farmland to prey on livestock at night when not being monitored. However, the scarcity of complaints from farmers living near the edge of the Forest indicated they rarely, if ever, did so.

The Faunce Pack evidently preyed on livestock at the Kroeze farm (see Fig. 36) in summer 1977, after fieldwork ended. A federal trapper captured adult male 5115, another adult or yearling male, and a pup at that farm in August (case #13 in Table 14, Fig. 37). The trapper found scats containing hog hair on Forest roads near the farm, and one of the captured wolves regurgitated hog hair. There was no evidence that the Faunce Pack preyed on livestock while it was being monitored from 1973 to 1976.

The Thief Lake Pack was alleged to have preyed on livestock in 1976 (case #3 in Table 14, Fig. 37). That group's territory was about 25 km west of the Forest and virtually surrounded by farmland. In October, wolves killed 6 Hereford calves and 6 or 7 sheep at the Frenzel farm, which was within 1–2 km of the pack's known range. An adult wolf and 6 pups reportedly were seen near the farm. The Thief Lake Pack probably was the only pack in the area, and included 6 or 7 pups in late summer when fieldwork was terminated. In July 1977, a federal trapper captured 2 pups, which probably were from the Thief Lake Pack, after a farmer complained of sheep losses about 10 km northwest of their known range. The pups were captured near the pack's 1976 den, which was about 15 km from the farm. Thus, the evidence in this case is scanty, and the pack may or may not have been involved in this incident. That pack may have had ample natural prey within its small range in winter but not in summer. A major deer yard was within the range, with a minimum of 80 deer being observed there in March 1976. However, much of the Thief Lake Pack's range was marsh, so many of the deer at the yard probably had summer ranges within surrounding broken farmland.

Wolf 840, as a yearling male with the Clear River Pack, was found near an adult sheep he may have killed in October 1975. The sheep was about 1.1 km within forest cover and at least 5.5 km from the nearest farm with sheep. Perhaps this animal strayed into the Forest (as occasionally happens in this area); or, the carcass could have been dumped by a farmer and scavenged by the wolf. After the carcass was examined, 840 returned and consumed about 90 percent of it.

On 11 October 1975, the Rapid River Pack was observed near the edge of its range resting a few meters from the periphery of a field. A dead cow was lying at the edge of the field about 0.4 km away. The cow, which had not been scavenged, apparently had been dragged to

the site by a tractor. A check of the carcass on 16 October revealed the wolves had not fed from it before leaving the area.

During dispersal through farmland, female 5173 was found on 25 September 1976 within a small grove of aspens into which a cow or horse carcass recently had been dragged. Bones at the site indicated previous disposal of animals there.

Female 5145, after dispersing south-eastward about 61 km and settling in the Armstrong Creek area northwest of Northome, was near cattle at 4 of 5 locations between 20 July and 2 September 1976. Two of those fixes were within 0.1 km of a herd, yet the owner claimed that no losses occurred that summer. A small Hereford calf was killed in August 1976 within the known range of 5145, but coyotes rather than wolves were thought responsible. A cow and a calf reportedly were killed by a wolf (wolves?) at a farm located just south of 5145's known range, so she and associates could have been involved. We learned of several other possible incidents of wolf predation in that general area. However, discussions with local farmers suggested most of them involved coyotes.

The Red Lake State Forest, into which male 840 and his mate settled in winter and spring 1976, was close to livestock on all sides. In September 1976, 840 was located across a road from a flock of domestic turkeys, but we were unable to confirm any losses there. Three or 4 newborn Hereford calves were killed by wolves at a farm in that general area in July 1976 (case #22 in Table 14, Fig. 37). Two wolf pups were captured at the farm and an adult female was captured nearby by a federal trapper. These wolves could have been from 840's pack; however, the location was about 10.5 km east of any of the radio fixes of 840 that summer.

Additional information and insight into the incidence of wolf predation on livestock were obtained from livestock producers. Approximately 65 producers located both adjacent to the Forest and in

other parts of Lake-of-the-Woods, Roseau, Beltrami, Marshall, and Koochiching counties were contacted in person or by telephone. Forty of those were rumored to have suffered losses or had reported losses. The U.S. Fish and Wildlife Service's Animal Damage Control Division contributed information on complaints received and investigated in the area from 1974 to 1977, after it began a program of selective trapping and removal of problem wolves. Documentation of wolf depredations was difficult. Even in cases considered confirmed, the evidence usually was somewhat circumstantial. Most documentable cases of predation on livestock in the area probably were brought to our attention. Confirmed cases usually were well publicized, often including local newspaper coverage.

Including cases already mentioned in which study packs were involved, we learned of 15 "confirmed" and 7 "probable" incidents in which wolves killed domestic animals in a 5,500-km² area (Table 14, Fig. 37). Depredation occurred in a variety of circumstances on a variety of domestic species. Packs were involved in a minimum of 6 incidents, and lone wolves or single pack members were implicated in 6. All but 2 or 3 incidents, including the ones in which packs were involved, occurred near expanses of undeveloped land that appeared capable of supporting wolves.

Preliminary findings in Alberta (R. R. Bjorge, pers. comm.) and observations by the U.S. Fish and Wildlife Service in Minnesota (R. Wetzal, pers. comm.) suggested that cattle are more likely to be preyed on in woodland than in open pasture. This probably was true in our study area, although not clearly indicated by the data. Sites of predation reported here ranged from open pasture a few meters from farm buildings to remote wooded pasture. Minnesota wolves probably are more likely to kill in wooded habitat where they are accustomed to hunting, and animals killed there would be less likely to be found and reported.

Selectivity for calves over larger cattle

was evident, as was suggested by some of the accounts given by Young and Goldman (1944). It was not clear whether more lambs than adult sheep were killed, although such a pattern was evident in cases in which coyotes were implicated.

There apparently was an increase in livestock losses in northwestern Minnesota during the study associated with the increase in wolf density. The complaint rate increased from 1974 to 1976, but this was at least partially the result of increased public awareness of the federal wolf removal program.

Several farmers repeatedly observed timber wolves with their cattle without losses occurring. One farmer observed a wolf kill a deer in open pasture within a herd of cattle. Such observations suggest either that some wolves do not initially recognize domestic animals as prey or that they prefer to prey on native herbivores, perhaps because of their past experience or of size relationships.

Most farmers contacted who had not already reported losses did not believe they had lost any animals to wolves during the study. This number included 13 producers who had raised cattle near the boundary of the Forest for several years. A few said they suspected predation on a few lambs or calves that were missing, but did not know whether timber wolves or coyotes were responsible.

Coyotes were found to be involved in at least 18 (45%) of 40 reports of presumed wolf predation on livestock received and investigated by the Animal Damage Control Division and ourselves in this area from 1973 through 1977. Only reports of timber wolf predation had been solicited, and many reports in which coyotes were involved were first screened out. Therefore, the 40 reports mentioned above are not a representative sample of losses to wild *Canis*. The total percentage of livestock loss (especially sheep) to coyotes probably was much higher. One of 2 coyotes radiotracked during this study preyed intensively on calves and sheep. Our observations and those of local state personnel suggested

that losses from coyotes were mistakenly attributed to timber wolves more often than vice versa.

Losses of sheep to coyotes were commonplace in northwestern Minnesota. We learned of single-season losses of up to 100 individuals by some farmers. Persons interviewed agreed unanimously that sheep production in this area has declined drastically over the past several years because heavy losses from an increasing "wolf" (coyote) population had forced most producers out of the business. This trend appears to be part of a general trend being experienced over much of the western U.S. (Terrill 1977, Sterner and Shumake 1978).

In view of all available information, it seems that wolf predation on livestock was uncommon in the study area. Wolves living short distances from livestock generally relied on natural prey. That conclusion agrees with the findings of R. R. Bjorge (pers. comm.), who has found a low level of predation on cattle on grazing leases in the Peace River region of Alberta where wolves and cattle coexisted from May to October. Losses of livestock can have a severe economic impact on individual farmers, but the majority of producers in northwestern Minnesota were little affected by the presence of wolves.

Problems Related to the Perception of Wolves as Livestock Predators

A substantial problem in gathering information through interaction with local persons was the widespread confusion on the taxonomy and nomenclature of wild *Canis*. Coyotes appeared to be abundant in all parts of northwestern Minnesota where livestock is produced. Large numbers of coyotes are shot and trapped annually. Most residents of the area use the term "wolf" in referring to both *Canis lupus* and *C. latrans*. The term "brush wolf" often is applied to *C. latrans*, but frequently the "brush" is dropped, and both species are referred to merely as "wolves." The distinction between the 2

species seemed of little importance from the local perspective. Almost all persons interviewed acknowledged 2 kinds of wolves, based on size, but about 20 percent admitted they might not be able to distinguish between them. When wolves were given legal protection in 1974 many residents of the area assumed coyotes were protected too.

Because of the above problem, a report of "wolves" killing livestock might involve either wolves or coyotes, and depredations by the 2 species proved to be inseparable problems. Accounts of "wolf" predation occasionally were published in local newspapers. We determined that some, probably most, involved coyotes. Persons who read such stories from outside northern Minnesota likely would conclude that timber wolves were involved and gain a distorted impression of their importance as predators of domestic animals. The public's view of wolves as livestock predators was obscured and in all probability was highly distorted because these 2 species often were not distinguished.

Many livestock producers in northwestern Minnesota allow their herds and flocks to graze and give birth in woodland or pasture interspersed with forest and brush. Cattle may receive little surveillance during the summer and not be counted until assembled in autumn. "Wolves" often are assumed responsible for deaths of individuals that cannot be found, especially if "wolves" or their tracks have been seen near the herd or if neighbors have experienced losses. An extreme example of such a case was a farmer who turned out 31 pregnant cows in spring but found only 5 calves with the herd in autumn. No doubt wolves or other predators were responsible for the disappearance of some animals; however, other causes of mortality also should be considered (Henne 1977, R. R. Bjorge, pers. comm.).

SUMMARY AND CONCLUSIONS

Population dynamics, movements, and feeding ecology of wolves were studied

in northwestern Minnesota from August 1972 through March 1977. The study was conducted mainly within the 2,700-km² Beltrami Island State Forest near the western edge of the primary range of the wolf in Minnesota. Farmland is located immediately west, north, and northeast of the Forest, and livestock on those farms were potential prey for wolves. Wolves in the Forest are vulnerable to persecution by humans. They were unprotected until the Endangered Species Act of 1973 provided total legal protection beginning in August 1974.

Thirty-nine wolves (22 adults and 17 pups) were captured, and 35 were radio-collared from 1972 through 1976. One was instrumented 3 times, and 5 were collared twice. Sixteen social units (packs and pairs) were monitored for periods of a few days to 4 years. Instrumented wolves were relocated by aircraft on 2,295 occasions and were observed 850 times.

Population density was low at first but increased substantially during the study. The increase was best documented from winter 1974–1975 to winter 1975–1976 when the minimum winter population increased from 38 to 58 wolves. Size of social units in winter ranged from 2 to 9 and averaged 4.3 (5.3 with pairs excluded). At least 8 of 13 social units present in mid-1976 had formed during the study.

Size of 15 litters of established packs averaged 4.6 pups, and 5 litters of newly formed pairs averaged 4.1. Pup production within the Forest increased from a minimum of 16 in summer 1974 to at least 40 in 1976. Of 14 pups instrumented in mid to late summer, 8 survived until December and 6 until the following spring.

Mortality decreased during the study. Humans were a major cause of mortality, accounting for the deaths of at least 4 of 5 instrumented wolves that died before protection, and for 4 to 6 of 12 deaths thereafter. Recruitment of young wolves into the population exceeded mortality after legal protection. The reduction in human-related mortality that resulted

from legal protection was the apparent cause of the population increase.

A high rate of dispersal of young wolves from packs was documented. Eight instrumented wolves left their packs; all but 1 appeared to be nonbreeders, and at least 3 were yearlings. Prior to 1977 there were no known cases of instrumented wolves staying with their pack past breeding age unless they became breeders after the death of alpha animals. Dispersal peaked in autumn. Most wolves paired within a few days of leaving their packs. At least 3 or 4 dispersers settled within the Forest and were involved in formation of new packs. In 5 cases, wolves emigrated from 20 to 390 km from the Forest. A yearling female returned to the Forest after traveling 138 km away. Three wolves that left the Forest helped form new packs in peripheral areas outside. Three of 5 lone wolves captured within the Forest paired, and 2 of them formed packs. Noninstrumented lone wolves were accepted into packs in at least 1, and possibly 3, cases.

Lone wolves and newly formed pairs avoided pack territories both before and during the increase in density. Two processes of pair formation were noted: (1) 2 lone wolves joined and traveled together until a potential territory was found, or (2) a lone wolf settled in an area not used by a pack or between pack territories and remained there until joined by another lone wolf of the opposite sex. The edges of parental territories were colonized in at least 3 instances.

Before the increase in density, territories were larger than in northeastern Minnesota where densities were higher. At that time, some parts of the Forest either were not used or were rarely visited by packs, and newly formed pairs had little difficulty finding an area to colonize. New packs occupied smaller territories than original ones, and the average territory size decreased as the population increased. Several boundary shifts occurred, and all but one original territory compressed as newly formed

pairs established territories between existing ones or at the edge of the Forest. By 1976, the space available to new social units was relatively limited, more dispersers appeared to be leaving the Forest, and intraspecific strife possibly became a significant mortality factor. The rate of population increase may have slowed then due to territoriality; however, supporting data are inconclusive.

There was evidence of breeding from 2 February until 3 March. Alpha females first became sedentary at dens from 13 March to 26 April. Pups were moved from natal dens from 2 June to 12–16 July.

Subordinate pack members differed considerably in their association with their pack during summer. Some frequented the edge of their territories or traveled just outside. Alpha males, alpha females, and some subordinates also ranged over most of their territories in summer, while returning periodically to their homesites. Most packs became nomadic again in late September or early October; transition to the nomadic phase usually was a gradual process. Packs traveled extensively and often were found at the edge of their territories in late September, October and November. In general, packs covered more area in winter than in summer.

Deer and moose composed an estimated 94 percent of the animal biomass eaten by wolves in the Forest (based on analyses of 960 scats), with deer alone composing about 67 percent. Consumption of moose peaked in spring, at a time of high natural mortality. Deer fawns were highly important from mid-May until at least August, during which period the estimated ratio of fawns to adults eaten was 9:1. During winter, the mean minimum daily rate of food consumption was 1.63 kg for pack members and 4.45 kg for members of pairs.

Remains of at least 65 deer and 8 moose eaten by wolves were observed near instrumented wolves. Remains of 54 deer killed by wolves were examined, 50

of which were killed in winter. Fawns composed a greater portion of deer killed in winter (51%) than found in other studies elsewhere. Mean age of adult deer in the sample was 7.6 years. The findings supported the hypothesis that strong selection of fawns and old adults will occur if deer are abundant.

Significantly more kills were found within centers of wolf pack territories than at edges. Among 67 deer kills located during aerial tracking from December through March, only 11 were within deer wintering areas; 15 were at the edges of wintering areas.

Territories of at least 5 packs bordered farmland where livestock was produced, yet wolves living within the Forest rarely preyed on livestock. Only 2 such cases were confirmed; both occurred after the wolf population had increased. Remains of livestock were found in 29 (3%) of 960 wolf scats collected within the Forest, primarily near the northern edge. Most of those scats apparently were from livestock carrion.

An instrumented pack 30 km west of the Forest killed livestock at least once in 1976. From 1973 through 1977, a minimum of 15 confirmed, and 7 probable, cases of wolves killing livestock (primarily cattle) occurred in a 5,500-km² area east, north, and west of the Forest. Coyotes were more important predators of livestock than were wolves in the study area. Coyotes and wolves often were not distinguished by the public, and the term "wolf" was applied to both. This problem led to a distorted public impression of the importance of wolves as livestock predators.

The wolf population in the Forest apparently had been held at a low density by persecution from humans prior to about 1974, but responded rapidly when mortality was reduced by complete legal protection. Therefore, at least when prey is abundant, legal protection can be an effective management tool in reducing mortality of wolf populations and allowing an increase in population density to

occur. Moreover, the reproductive potential of wolves is sufficiently high for the increase to be rapid.

This study provided new information on the dynamics of a recolonizing wolf population and provided insight regarding the importance of dispersal, pair formation, establishment of new territories, and compression of existing territories in an increasing population. Wolves that were approaching breeding age appeared to be following a strategy of early dispersal and formation of new social units rather than attempting to breed within their natal packs.

The combination of low density and reduced persecution allowed lone and dispersing wolves an unusually high degree of reproductive success during the study. Also, the abundance of vulnerable deer and moose carrion undoubtedly expedited the success of colonizing wolves. This was evidenced by the preponderance of fawns and old adult deer in the diet, the appearance of moose in the diet in spring, and the high kill rate per wolf by pairs. Our data supported the hypothesis of Packard and Mech (1980) that young wolves should disperse from their packs when population density is low and food is abundant, at least when mortality is not excessive. Because young wolves generally were following that breeding strategy, the population increase occurred by way of increased numbers of social units more tightly packed into the available habitat, rather than by way of increased size of existing social units and a static spatial organization of those units.

The high rate of dispersal found during this study indicates that maturing wolves possessed the behavioral flexibility to follow the optimum breeding strategy. That, in turn, suggests that subordinates were able to gather information on the potential for colonization outside, or at the edge of, the territories of their natal packs. In fact, some of the subordinates followed during this study appeared to be exploring areas at the perimeter or outside the parental territory in summer

during the pack's sedentary phase. Information obtained during these movements probably influenced their decision on whether to disperse or remain with their pack.

Edges of parental territories appeared to be preferred sites for colonization, possibly because such areas were already familiar to dispersers. In addition, breeding pack members might be more tolerant of their own progeny attempting to colonize at the edge of their territory than of unrelated wolves, so long as food is abundant. Under the conditions present in the Forest during this study, breeding pack members might maximize their genetic fitness by tolerating colonization of the edge of their territory by their offspring.

The results of this study do not support the hypothesis of Rausch (1967) that pack size is positively correlated with population density. The average size of social units in the Forest did not increase during the early phase of the population increase. Instead it declined temporarily as new groups (initially pairs) became established. While wolf populations are increasing, the size of even the existing reproducing packs will not change much initially because of a high rate of dispersal. Some increase in pack size might have occurred after completion of our study if the breeding strategy of yearlings changed with the increase in density and thus more remained with their packs past minimal breeding age (Packard and Mech 1980). However, it is clear that group size alone would not have been an adequate index of density in the Forest during this study.

Finally, our research demonstrated that the Beltrami Island State Forest is capable of supporting substantial numbers of wolves despite being located at the edge of the species' range and near considerable human activity. The finding of an increasing wolf population in northwestern Minnesota contrasts with results of recent studies in northeastern Minnesota and southern Ontario where wolf numbers have declined in recent years

because of declining deer populations (Mech 1977b, Mech and Karns 1977, Theberge and Strickland 1978). Therefore, the Forest is now of greater importance as habitat for the wolf in Minnesota than it has been in the past. Apparently, a substantial density of wolves can exist there with minimal conflict with agricultural interests. Whether that will remain true in the future is, of course, unknown.

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