PRODUCTIVITY, MORTALITY, AND POPULATION TRENDS OF WOLVES IN NORTHEASTERN MINNESOTA

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Abstract.—Population parameters, mortality causes, and mechanisms of a population decline were studied in wolves (*Canis lupus lycaon*) from 1968 to 1976 in the Superior National Forest. The main method was aerial radio-tracking of 129 wolves and their packmates. Due to a decline in white-tailed deer (*Odocoileus virginianus*), the wolf population decreased during most of the study. Average annual productivity varied from 1.5 to 3.3 pups per litter, and annual mortality rates from 7 to 65 percent. Malnutrition and intraspecific strife accounted equally for 58 percent of the mortality; human causes accounted for the remainder. As wolf numbers began to decline, pup starvation became apparent, followed by lower pup production, and then by increased intraspecific strife. At higher densities, adult pack wolves were the most secure members of the population, but as the population declined, they became the least secure because of intraspecific strife.

The determination of population trends and an assessment of the rates and causes of mortality are necessary to understand the population dynamics and ecology of any species. However, direct data on mortality have always been difficult to obtain for most mammals, so indirect methods of deducing this information from age ratios and population trends generally have been used. Wolf studies are no exception (Mech, 1970).

The technique of radio-tracking (Cochran and Lord, 1963) has increased the chances of obtaining direct information on mammal mortality by allowing investigators to determine when study animals die, and then, through autopsy and reading field signs, learning causes of death (Mech, 1967; Mech et al., 1968; Schladweiler and Tester, 1972). Furthermore, radio-tracking applied to a population can also facilitate the collecting of data on population trends. The present population and mortality study of wolves was based on this technique.

Study Area

This study was part of an ongoing, long-range investigation being conducted in the Superior National Forest and surrounding regions of northeastern Minnesota (92°W longitude, 48°N latitude), an area described by Stenlund (1955) and Mech and Frenzel (1971). The most intensive work was done in the central one quarter of the Forest, referred to as the "core" (Fig. 1). The data for this paper were collected from January 1967 through March 1976.

Until October 1970, hunting and trapping of wolves was legal in the Superior National Forest throughout the year. Thereafter, these activities were illegal on the 7,680 square kilometers (km) of federal land within the Forest boundary. However, legal taking on the rest of the land and poaching on federal areas continued. The Endangered Species Act of 1973 prohibited killing wolves anywhere in Minnesota after August 1974; since then, poaching decreased but was still evident.

Human-caused mortality of wolves, legal or illegal, is greatly influenced by accessibility (Weise et al., 1975; Robinson and Smith, 1977). Approximately half the study area is relatively inaccessible, so even with an open season on wolves, hunting and trapping directly influenced only part of the wolf population studied.

The primary prey of wolves in northeastern Minnesota is white-tailed deer, and this is supplemented by moose (*Alces alces*) and beavers (*Castor canadensis*) (Stenlund, 1955; Mech and Frenzel, 1971; Frenzel, 1974; Van Ballenberghe et al., 1975). However, from winter 1968–69 through 1973–74, deer numbers suffered a serious decline, from which they had not recovered by 1976 (Mech and Karns, 1977). In the eastern half of the core study area, deer have been non-existent, at least in winter, since 1972 (Hoskinson and Mech, 1976; Mech and Karns, 1977). Along

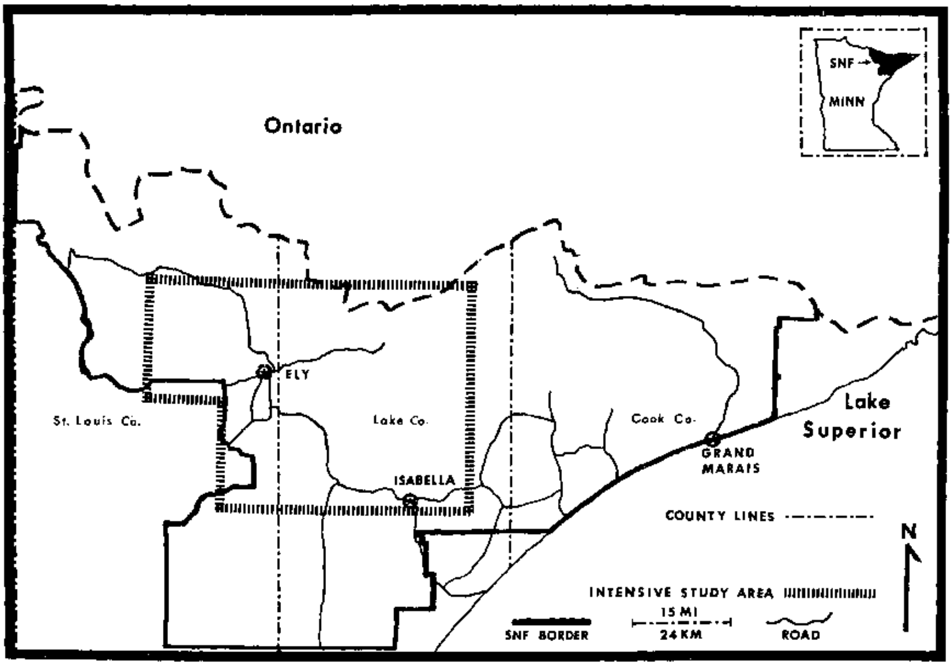

FIG. 1.—The Superior National Forest and intensive study area.

the edges of the core area deer numbers also dropped, to about 0.7 per square km in 1976 along the south edge (Floyd, personal communication).

Wolf packs inhabited all of the study area throughout most of this investigation, in an apparently saturated population with a density of about one wolf per 26 square km in 1972 (Mech, 1973). Each pack occupied a territory of from 125 to 310 square km (Mech, 1972, 1974), with territories maintained at least partly by scent-marking (Peters and Mech, 1975).

After deer began to decline, some packs started trespassing into the territories of others to obtain prey (Mech, 1972, 1976, unpublished). This usually took place in winter, and greatly increased the chances of encounters between packs.

METHODS

Beginning in November 1968, wolves were live-trapped, anesthetized, ear-tagged, radio-collared, and radio-tracked from the air and the ground (Mech and Frenzel, 1971; Mech, 1974). No wolves less than 4 months old were captured. Radios generally functioned for at least 9 months but sometimes lasted over 3 years. Attempts were made to recapture animals and replace collars each year. Most of the wolves were radio-tracked at least once each week throughout the year, usually twice per week, and often daily during winter. Approximately 2,400 hours of flying, more than half of it during winter, were used to obtain the data in this study.

Minimum and maximum natality rates were obtained using several methods. In some cases, adult female wolves were live-trapped within a few weeks after bearing pups, and the number of active teats indicated the maximum number of nursing pups. On other occasions, pups were observed from the air during mid-summer with radio-tagged adults. Live-trapping was conducted from September through November, when pups are still distinguishable on the basis of tooth replacement or canine length (Van Ballenberghe and Mech, 1975), and the number captured per pack was used as an indication of the minimum number produced. Lastly, estimates of the maximum number of pups surviving were deduced from the maximum pack sizes observed during December when all the surviving pups generally traveled with the adults (Mech, unpublished). In these cases, I assumed that packs contained the alpha or breeding pair (Mech, 1970, unpublished), plus whatever other radioed yearlings or adults were present as well as pups. For example, if a pack of seven was observed, and a yearling member was radioed, I could assume that not more than four pups survived to that time.

When a radio signal inexplicably failed to move for an inordinate period, or when other circumstances warranted (such as failure to observe the animal or tracks in snow after several days), a ground check was made. Whenever possible, carcasses found were taken to the University of Minnesota Veterinary Diagnostic Clinic for a thorough autopsy.

A message including the investigator's name and phone number, and "please call collect—REWARD" was molded into the radio-collar. Thus, even after the transmitter expired, hunters and trappers often reported killing tagged animals. A copy of Rutter and Pimlott's (1968) "World of the Wolf" was given as a reward, along with reprints about the research and a history of the animal killed. This technique even fostered the reporting of two illegal captures through an intermediary.

A few times animals were taken legally or illegally, and the functioning collars removed and discarded, or the ear-tags mailed in anonymously. In such instances, I could deduce only that the mortality was human-caused, but I could not determine the specific manner. In some cases, detective work by a conservation officer or consultation with the local "grapevine" led to carcasses or revelations about the manner of taking. Despite this, the figures on human-caused mortality must be considered as minimums.

Annual mortality rates of the population of radioed wolves were calculated from the mortality data. For this, two types of data were considered separately. One type was based on animals found dead while their transmitters were operating. This type represented all causes of mortality, although it may have slightly underrepresented human-caused mortality because people sometimes deliberately damaged the radio-collars, which may have prevented discovery of some deaths. Nevertheless, broken collars often continued to transmit after being discarded, so that, in such cases, human-caused deaths still could be recorded.

The second type of mortality data was based on reported deaths of radioed animals after their radios had expired. Such data represent only human-caused mortality. However, an estimate could be made of the number of wolves with expired radios dying from all causes, based on the number reported killed by humans. This estimate assumed that the proportion of mortality causes was the same for wolves dying while their radios transmitted ("active transmitters") as those dying after their radios expired. The percentage of human-caused deaths out of total deaths of wolves with transmitting radios was determined. This percentage was then applied to the annual number of reported human-caused deaths of wolves with expired radios, and an estimate was obtained of total annual mortality (human-caused and natural) for wolves with expired radios. These figures were then added to those obtained from mortality of wolves with active transmitters, and an estimated annual mortality figure resulted.

To calculate annual mortality rates, the estimated annual mortality was converted to a percentage of the number of wolves wearing active and expired radios. However, this number changed each year as additional wolves were radioed and as radioed wolves died. Nevertheless a range of wolves wearing radios in the population could be determined for each year. The minimum such number for any given year (for example, 1972) was the cumulative number of wolves radioed through the previous year (1971) minus the estimated number that had died through the previous year (1971). The maximum number of wolves wearing radios for the given year was the cumulative number radioed through that year (1972) minus the estimated number that had died through the previous year (1971). Most wolves were radio-tagged in autumn, so the annual mortality rate was based on a population of radioed animals intermediate between the minimum and maximum.

The rates derived as above are not true annual mortality rates because they are based on wolves radioed at a minimum age of 4 months. Therefore, the rates do not provide information about mortality between birth and the age of 4 months.

Data on wolf population trends in the core study area have been gathered since winter 1966–67 and are based on mean pack size (Mech and Frenzel, 1971; Mech 1973). From winters 1966–67 through 1969–70, most data on pack size were collected by aerial observation of non-radioed packs, supplemented by observations of a few radio-tagged packs in 1968–69 and 1969–70. It was much more difficult and less efficient to locate non-radioed packs, so there were fewer observations of them.

After winter 1969–70, however, enough packs were radioed to form the primary basis for the population index. From December through April each winter, whenever radioed wolves were aerially located, they and their associates were counted. Generally, pack sizes remained constant

TABLE 1.—*Sex and social affiliation*[1] *of radioed wolves studied.*

Year	Pack Members		Peripheral[2]		Lone Wolves		Unknown		Total
	Males	Female	Male	Female	Male	Female	Male	Female	
1968	–	–	–	–	1	1	–	–	2
1969	3	2	–	–	3	2	–	1	11
1970	7	3	–	–	1	2	1	–	14
1971	3	9	–	1	2	1	4	–	20
1972	12	8	–	1	–	2	–	2	25
1973	11	4	–	1	2	2	1	–	21
1974	8	7	–	1	2	1	–	1	20
1975	8	5	–	–	1	1	1	–	16
Total	52	38	–	4	12	12	7	4	129

[1] Pertains to capture date only because affiliation sometimes changed during the study.
[2] Live in territory of pack but do not socialize with pack members.

from week to week for any given winter, although they tended to decrease gradually over winter into spring. The highest count for each pack during December through February was considered the winter pack size, and the maximum number during March and April was regarded as the spring size (Mech, 1973). To supplement data from radioed packs, aerial counts were made of adjacent non-radioed packs.

To relate the results of the two methods, two indices were calculated. One covers the longer period (winters 1966–67 through 1975–76) and uses only one mean pack-size for each year, rather than a separate one for winter and spring. This increased the total number of packs used for the index each year, because many non-radioed packs were observed only in winter or spring. When both winter and spring figures were obtained for a pack, an intermediate figure was used for this index, if they differed. This approach provided a gross index to the population size for a particular year, somewhere between the winter and spring size.

The second index, utilizing the more detailed radio-tracking data, covers winters 1970–71 through 1975–76 and provides a more refined view of the population trend by showing both winter and spring figures. Both this refined index and the gross index were plotted on the same graph to demonstrate their relationship (Fig. 2). Generally the two show the same trend, lending confidence to the gross index for 1966–67 through 1969–70.

Mean pack size itself is not necessarily an accurate index to population size. For example, the mean size of 10 packs in a given area could equal that for eight packs, but the total population would be greater in the former case. This problem must be considered because one pack may usurp the territory of another, or new packs may form. Therefore, I adjusted mean pack size according to the known number of packs in the area when the study began. For example, when one pack was killed off and its territory usurped by another, the mean pack size after that was calculated using the original number of packs in the population. Or, when a new pack formed, the members were included in the index, but the pack itself was not considered part of the divisor in computing mean pack size. This does not negate the claim by Rausch (1967) that pack size is an index to population size, but it does increase the accuracy of the index.

RESULTS

Some 129 wolves were radio-tagged (Table 1); 17 were reradioed, a few of them two or three times, and one of them four times (Mech, 1977). At first capture, 91 (71 percent) of these animals were members of 18 contiguous packs; 26 (20 percent) were lone wolves; the remainder were of unknown affiliation. The average number of locations per wolf was 72 (range, 0 to 724). An average of six packs (range two to eight) were radioed per winter.

The radioed population of wolves generally ranged over an area about 110 by 110 km, but dispersers and nomads traveled a composite range some 320 km by 320 km, which included southern Ontario. Such travels often took dispersing and nomadic wolves into more accessible areas than in which they originated.

TABLE 2.—*Number of wolves*[1] *in each of the study packs and percent change each year. Data taken in mid-winter.*

Pack	1966–67	1967–68	1968–69	1969–70	1970–71	1971–72	1972–73	1973–74	1974–75	1975–76
Glenmore L.	6.0	—	8.0	—	—	10.0	8.0	—	—	—
Newton L.	6.0	6.0	8.0	11.0	7.0	7.0	6.0	—	—	—
Pagami L.	6.0	—	—	—	6.0	4.0	4.5[2]	5.5[2]	6.0[2]	3.0[2]
Greenstone L.	—	—	4.0	—	5.0	3.5				
Ensign L. (A)	7.0	—	—	—	11.0	12.0	7.5	4.5	2.5	2.0
(B)								3.0[3]	—	—
Thomas L.	5.0	5.0	6.0	—	6.0	5.0	3.5	—[4]	—[4]	—[4]
Quadga L.	—	—	—	—	6.0	4.5	2.0	3.0	5.5	5.5
Harris L.	—	—	5.0	4.0	7.5	2.5	4.0	2.5	2.0	5.0
Jackpine	—	—	—	5.5	6.5	7.5	6.5	8.0	—	—
Maniwaki L.	8.0	6.0	8.5	14.0	7.0	8.0	6.0	—	9.0	12.0
Timber L.	—	—	—	8.0	—	7.5	7.0	—	—	—
Sumpet L.	—	—	—	—	—	—	—	9.0	3.0	1.0
Knife L.	—	—	11.0	—	—	8.0	—	—	—	—
Canadian Pt.	6.5	—	—	9.0	—	4.0	—	—	—	—
Wind L.	—	—	6.0	—	4.0	—	—	6.0	2.0	8.5
Birch L.	6.0	—	—	—	—	—	6.0	—	—	—
Sawbill	—	—	6.0	—	2.5	4.0	4.0	5.5	3.0	8.0
Perch L.	—	—	—	—	—	—	—	2.0[3]	4.0[3]	3.5
Total wolves	50.5	17.0	62.5	51.5	68.5	87.5	65.0	49.0	39.0	50.5
No. of packs	8	3	9	6	11	14	13	10	10	10
Mean pack size (adjusted)	6.3	5.7	6.9	8.6	6.2	6.3	5.0	4.9	3.9	5.1
Change	—	−10%	+21%	+25%	−28%	+2%	−21%	−2%	−20%	+31%

[1] Many of these figures represent intermediate values between early winter and spring observations of the same pack (see Table 3).
[2] Because this pack occupied an area where previously there were two packs, it is counted as two packs in determining mean adjusted pack size.
[3] Because this pack did not exist when the study began, but formed later, it is not counted as a pack in determining mean adjusted pack size, even though its members are counted in the population.
[4] Because this pack existed when the study began, but was destroyed later, it is still counted as a pack in determining the mean adjusted pack size.

TABLE 3.—*Number of wolves in each pack in early winter (W) and spring (S) each year, and seasonal changes in the population.*

	1970–71		1971–72		1972–73		1973–74		1974–75		1975–76	
	W	S	W	S	W	S	W	S	W	S	W	S
Glenmore L.	–	–	12	8	12	4	–	–	–	–	–	–
Newton L.	7	7	7	7	6	–	–	–	–	–	–	–
Pagami L.	6	6	5	3	6[1]	3[1]	6[1]	–	7[1]	5[1]	3[1]	–
Greenstone L.	5	5	4	3								
Ensign L. (A)	–	11	15	9	10	5	5	4	3	2	2	2
(B)						3[2]	3[2]	–	–	–	–	–
Thomas L.	–	6	5	5	7	0[3]	–[3]	–[3]	–[3]	–[3]	–[3]	–[3]
Quadga L.	6	6	5	4	2	2	3	3	6	5	6	5
Harris L.	9	6	3	2	4	4	4	2	2	2	5	5
Jackpine	7	6	9	6	7	6	10	3	–	–	–	–
Maniwaki L.	7	–	9	7	9	3	–	–	9	9	13	11
Timber L.	–	–	8[4]	7[4]	7	–	–	–	–	–	–	–
Sumpet L.	–	–	–	–	–	–	9	–	–	3	2	0
Wind L.	–	4	–	–	–	–	6	–	2	2	9	8
Sawbill	3	2	5	3	4	–	6	5	3	3	9	7
Perch L.	–	–	–	–	–	–	2[2]	2[2]	5[2]	3[2]	6[2]	5[2]
Total	50	59	87	64	74	30	54	19	37	34	55	43
No. packs	8	10	12	12	12	9	10	6	9	10	10	8
Mean no. wolves/pack	6.3	5.9	7.3	5.3	6.1	3.3	5.4	3.2	4.1	3.4	5.5	5.4
Change												
Winter to winter			+16%		−16%		−11%		−24%		+34%	
Winter to spring		−6%		−27%		−46%		−41%		−17%		−2%
Spring to winter			+24%		+15%		+64%		+28%		+62%	
Spring to spring				−10%		−38%		−3%		+6%		+59%

[1] Because this pack occupied an area where previously there were two packs, it is counted as two packs in determining mean adjusted pack size.
[2] Because this pack did not exist when the study began, but formed later, it is not counted as a pack in determining mean adjusted pack size, even though its members are counted in the population.
[3] Because this pack existed when the study began, but was destroyed later, it is still counted as a pack in determining the mean adjusted pack size.
[4] Data from Van Ballenberghe et al. (1975).

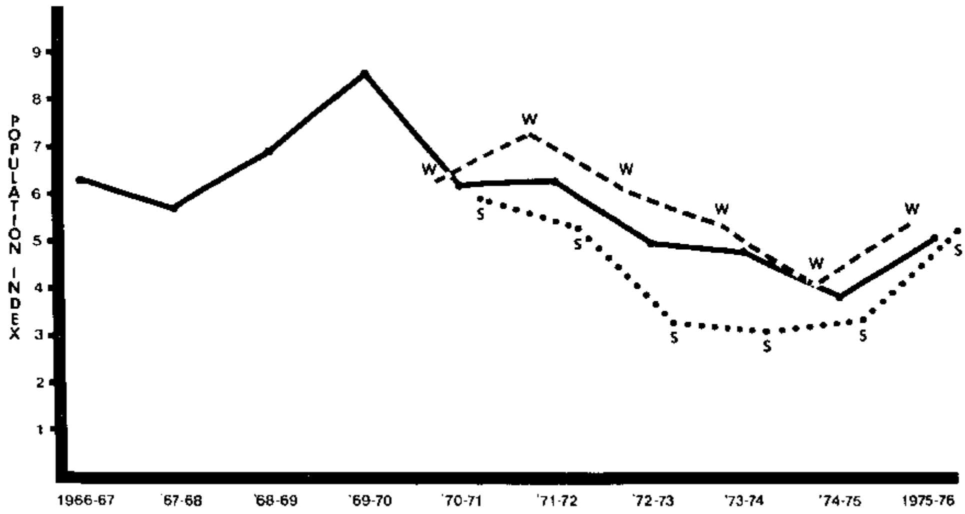

FIG. 2.—Wolf population trend in the intensive study area. Population index is the adjusted mean pack size. Solid line represents trend based on pack size observations made throughout winter and averaged for mid-winter, whereas dashed line is based on such observations for early winter, and dotted line for spring.

Population Trend

Observations of an average of 9.5 packs per year (three to 14) were available for determining mean pack size (Table 2). For the winter versus spring index from 1970–71 through 1975–76, data were available from an average of 9.7 packs per year (six to 12), most of them radioed (Table 3). Radioed packs were observed 3,800 times from December through April, which represents about 63 percent of the times the packs were located during these months.

From 1966–67 through 1968–69, the wolf population in the study area appeared relatively stable (Fig. 2). A year after the severe winter of 1968–69 in which unusual numbers of deer fell prey to wolves, and surplus killing (Kruuk, 1972) was documented (Mech and Frenzel, 1971), wolf numbers increased 32 percent compared to the mean of the previous 3 years. However, the deer never recovered from their loss in 1968–69, and their numbers generally declined drastically (Mech and Karns, 1977). The wolf population dropped to its previous level in 1970–71 and continued downward until in winter 1974–75 it was 40 percent below its 1966–67 through 1968–69 mean and 55 percent less than its peak in 1969–70 (Fig. 2). From 1974–75 to 1975–76, however, the population increased by 31 percent.

Comparison of the winter and spring wolf population indices from 1970–71 through 1975–76 provides insight into the seasonal distribution of the changes in numbers (Table 3). Increases of 15 to 64 percent from spring to the following winter were apparent each year, resulting from reproductive gains.

The winter to spring changes were always decreases. Although there is probably some overwintering loss to packs, the magnitude of the winter to spring loss increased each year from 6 percent in 1970–71 to a peak of 46 percent in winter 1972–73 (Table 3, Fig. 2). These overwinter losses were both to mortality and dispersal (Mech, unpublished). As a result, beginning in winter 1971–72, the net loss in pack members from winter to winter averaged 17 percent through 1974–75.

The spring to spring changes in the population index paralleled those of the annual winter changes (Fig. 2), except that they were more variable. They were down 10 percent and 38 percent, changed little, and then took an upturn (Table 3).

TABLE 4.—*Litter size data for wolf packs observed in mid-summer. (Figures in parentheses represent means if packs that produced no pups are excluded.)*

	Year	Pack	Maximum pups observed[1]	No. of active nipples[2]	Maximum pups surviving[3]
	1972	Harris L.	2	4	2
	1972	Jackpine	4	–	5
Mean	1972		3.0	4.0	3.5
	1973	Harris L.	2	–	2
	1973	Jackpine	6	–	5
	1973	Birch L.	2	3	–
Mean	1973		3.3	3.0	3.5
	1974	Harris L.	Did not den		–
	1974	Jackpine	Did not den		–
	1974	Sumpet L.	3	–	1
	1974	Perch L.	4	–	4
	1974	Birch L.	2	2	–
	1974	Sawbill	Did not den		–
Mean	1974		1.5 (3.0)	(2.0)	1.0 (2.5)
	1975	Harris L.	2	–	3
	1975	Jackpine	Did not den		–
	1975	Quadga L.	2	–	3
	1975	Maniwaki L.	5	–	6
	1975	Perch L.	3	–	3
	1975	Wind L.	5	–	7
Mean	1975		2.9 (3.4)	–	3.3 (4.4)
Mean			2.5 (3.2)	(3.0)	2.9 (3.7)

[1] June through August.
[2] On wolves captured May through July.
[3] To December (7 months of age); underlined figures represent knowns.

During winter 1975–76 the wolf population trend suddenly changed, with numbers increasing 34 percent from the previous winter (Table 3, Fig. 2). Of greater significance was the incorporation of this gain into the spring breeding population, which increased 59 percent from the previous spring.

The reason for the upswing in wolf numbers is unclear. Although the deer herd apparently stopped declining by winter 1974–75 (Mech and Karns, 1977), it does not seem to have increased enough to have allowed so strong a wolf population recovery. One possible factor was a striking increase in 1975 in beavers (Karns, pers. comm.). This could have allowed higher survival of wolf pups to winter. However, it could not fully explain the increase in spring to spring numbers, because beavers are unavailable from December through March. Furthermore, no increased reliance on moose was noticed in winter 1975–76. Thus, it is possible that deer may have increased more than casual observations indicated.

Productivity

In no case did I determine actual natality rates, because this would require disturbing dens and thus possibly reducing pup survival. Nevertheless, I did obtain insight into natality and/or early pup survival for up to six packs per year from 1972 through 1975. The mean values for June through August ranged from 1.5 to 3.3 pups per litter per year if packs that did not produce pups were included, and from 3.0 to 3.4 per litter with these pairs excluded (Table 4). Three females captured from May through July in 1972, 1973, and 1974 had 4, 5, and 2 active nipples.

These values are lower than those from most other areas (Mech, 1970) as well as from the same area in 1948–1952, when eight litters averaged 6.4 pups (Stenlund,

TABLE 5.—*Mortality data for wolves with functioning radio-collars.*

Wolf no.	Data at capture					Data at death			
	Sex	Date	Age	Weight (kg)	Social class[1]	Date	Age	Weight (kg)	Cause of death
1073	M	11/26/69	Pup	25	Member, Jackpine Pack	1/3/70	Pup	29	Shot
2207	M	10/5/70	Ad	31	Loner	3/22/71	Ad	25	Toxoplasmosis, Malnutrition, Parasitism
2211	M	10/12/70	Ad	34	Loner	1/—/71	Ad	—	Intraspecific strife
2213	M	10/17/70	Pup	17	Member, Jackpine Pack	10/—/70	Pup	20	Shot
2217	F	10/17/70	Pup	11	Member, Jackpine Pack	10/—/70	Pup	13	Shot
2221	F	10/22/70	Pup	18	Member, Harris L. Pack	7/—/71	Ad	—	Capture-related?
2256	F	2/23/71	Ad	31	Alpha, new pack	7/—/71	Ad	—	Unknown—natural
2260	F	5/6/71	Ad	30	Subordinate, Brimson Pack	12/—/71	Ad	32	Intraspecific strife
2401	M	10/6/71	Ad	30	Unknown	11/—/71	Ad	21	Capture-related?
2409	M	10/13/71	Ad	34	Unknown	12/—/71	Ad	—	Shot
2415	F	10/16/71	Ad	38	Member, Newton L. Pack	10/—/72	Ad	—	Unknown
2421	M	10/29/71	Ad	40	Loner	12/—/71	Ad	—	Unknown
2423	F	11/4/71	Pup	13	Member, Sawbill Pack	12/—/71	Pup	—	Malnutrition
2427	F	11/4/71	Ad	27	Unknown	11/—/71	Ad	—	Unknown
2429	M	11/5/71	Ad	34	Member, Maniwaki L. Pack	11/—/72	Ad	—	Unknown
2431	F	5/12/72	Ad	31	Subordinate, Ensign L. Pack[1]	11/25/72	Ad	30	Shot
2437	F	6/11/72	Ad	28	Unknown	10/—/72	Ad	—	Unknown
2441	F	6/26/72	Ad	27	Peripheral, Newton L. Pack[1]	1/30/73	Ad	38	Shot
2464	M	10/3/72	Pup	16	Member, Greenstone-Pagami Pack	11/28/72	Pup	—	Unknown
2468	F	10/8/72	Pup	13	Member, Quadga L. Pack	10/28/72	Pup	11	Malnutrition
2474	M	10/12/72	Pup	9	Member, Quadga L. Pack	10/21/72	Pup	—	Malnutrition
2487	F	10/9/72	Ad	25	Unknown	11/—/72	Ad	15	Capture-related?
2491	F	10/9/72	Ad	24	Alpha, Quadga L. Pack	12/12/74	Ad	27	Intraspecific strife
2493	F	10/17/72	Ad	26	Loner	4/—/73	Ad	30	Road-killed
5055	F	5/26/72	Ad	31	Alpha, Birch L. Pack	7/—/73	Ad	—	Capture-related?
5059	M	7/10/73	Ad	35	Alpha, Ensign L. Pack	3/—/74	Ad	37	Intraspecific strife
5065	M	9/21/73	Pup	11	Member, Jackpine Pack	11/—/73	Pup	15	Snared
5083	M	10/12/73	Pup	14	Member, Quadga L. Pack	11/—/73	Pup	17	Malnutrition
5089	F	10/18/73	Pup	11	Member, Quadga L. Pack	11/—/73	Pup	10	Malnutrition
5135	F	8/19/74	Ad	21	Alpha, Sand L. Pack	12/19/74	Ad	—	Intraspecific strife
5180	F	10/2/74	Ad	20	Alpha, Sumpet L. Pack	1/28/76	Ad	31	Intraspecific strife
5189	M	10/13/74	Pup	21	Member, Maniwaki L. Pack	11/—/75	Ad	—	Caught in rock-crevice
5193	M	3/11/75	Ad	42	Member, Ensign L. Pack[1]	8/—/75	Ad	—	Shot
5403	M	8/23/75	Ad	32	Unknown	9/—/75	Ad	—	Capture-related?
5417	F	10/20/75	Pup	18	Member, Maniwaki L. Pack	2/6/76	Pup	—	Human-caused, while trespassing

[1] Social class at death was the same as at capture for all wolves except 2431 and 5193 which had dispersed and were lone wolves at death, and 2441 which had dispersed and was alpha female of a new pair at death.

TABLE 6.—*Summary of mortality data from wolves killed by humans after radios expired.*

Wolf no.	Data at capture: Sex	Date	Age	Weight (kg)	Social class	Data at death[1]: Date	Weight (kg)	Cause of death	Social class
1059	F	1/22/69	Ad	—	Member, Harris L. Pack	1/10/70	30	Trapped	Member, Harris L. Pack
1075	M	11/27/69	Pup	21	Member, Jackpine Pack	10/7/70	23	Trapped[2,3]	Member, Jackpine Pack
2202	F	5/9/70	Ad	39	Unknown	3/25/71	36	Trapped	Dispersed
2204	F	5/13/70	Ad	25	Loner	5/23/72	25	Trapped	Dispersed and alpha of new pack
2215	M	10/17/70	Ad	31	Member, Jackpine Pack	2/15/74	27	Trapped	Subordinate, Jackpine Pack
2225	M	10/28/70	Ad	27	Member, Sawbill Pack	2/14/73	38	Trapped	Dispersed, new pack
2254	F	10/31/70	Ad	24	Unknown	12/28/71	—	Human-caused	Unknown
2266	M	6/5/71	Ad	37	Loner	7/27/72	39	Shot	Alpha of new pair
2411	M	10/15/71	Pup	22	Member, Pagami L. Pack	10/22/72	24	Trapped	Dispersed
2413	M	10/15/71	Ad	30	Loner	11/5/72	29	Shot	Loner
2417	F	10/17/71	Pup	26	Member, Glenmore L. Pack	1/27/73	38	Trapped	Dispersed
2489	M	10/9/72	Pup	18	Member, Harris L. Pack	11/15/74	—	Trapped	Dispersed
2499	M	5/5/73	Ad	33	Alpha, Harris L. Pack	1/10/74	—	Trapped	Alpha of Harris L. Pack, tres-passing
5087	F	10/17/73	Ad	30	Loner	2/9/74	—	Road-kill[3]	Loner

[1] All these wolves were yearlings or adults at death.
[2] Because of my intervention, this animal, which would have been killed, was released; nevertheless it should be considered as a mortality.
[3] Radio functioning but I did not learn of mortality by signal.

TABLE 7.—*Summary of causes of death of wolves with active radios.*

Cause of death	1970	1971	1972	1973	1974	1975	1976	Total	Percent[1]	
Shot	3	1	1	1	–	1	–	7	29	
Snared	–	–	–	1	–	–	1[2]	2	8	41
Road-killed	–	–	–	1	–	–	–	1	4	
Malnutrition	–	2	2	2	–	–	–	6	25	
Intraspecific strife	–	2	–	–	3[3]	–	1[3]	6	25	
Accident	–	–	–	–	–	1	–	1	4	58
Unknown natural	–	1	–	–	–	–	–	1	4	
Unknown	–	2	4	–	–	–	–	6	–	
Total	3	8	7	5	3	2	2	30	99	

[1] Excluding unknown.
[2] Unknown human-caused, but probably snared or trapped.
[3] An additional non-radioed member of a radioed wolf pack was also killed by intraspecific strife during these years.

1955). The present wolf population was subject to considerable nutritional stress as indicated by malnutrition in the pups that did survive (Van Ballenberghe and Mech, 1975; Seal et al., 1975; Mech, 1977). Malnutrition affected the pups of 1971, 1972, and 1973, and foreshadowed the more extreme consequences reported here. By 1974 the mean litter size in mid-summer had dropped to 1.5 (Table 4). This was one of the main causes of the low wolf numbers in winter 1974 (Fig. 2). Another unusual trait of this population was the production of a disproportionate number of male pups, a tendency that apparently peaked in 1972 (Mech, 1975).

Mech (1977) tried to relate pup production and survival in one wolf pack to the estimated food consumed per wolf the previous winter. He found that an intake of less than about 3.2 kilograms (kg) of food per wolf per day during winter was followed by low pup production and/or survival. However, 1975 was an exception, because the estimated consumption per day in winter 1974–75 was only 1.8 kg yet three pups survived into winter 1975–76. A high density of beavers (Karns, pers. comm.) and snowshoe hares (*Lepus americanus*) during summer 1975 (Mech, unpublished) may have made the difference in pup survival in this case.

Causes of Mortality

Thirty wolves were found dead of non-capture-related causes while their radios were still transmitting (Table 5). Another 14 were reported killed by humans after the wolves' transmitters had expired (Table 6).

Of the 30 wolves, 24 were found dead from known causes; 14 (58 percent) of these 24 died from natural causes, and the remainder from human causes (Table 7). Shooting was more important in the study area itself, and trapping was more important outside the core study area. Of the 10 wolves known to have been trapped, eight were out of their packs' territories when caught, and most were at least 16 km away. Immediately east of my core study area in a more accessible place, shooting and trapping of wolves were the main mortality factors, and road-kills constituted a third important cause of death (Van Ballenberghe et al., 1975).

Of the natural mortality, malnutrition and intraspecific strife accounted for all but one wolf, which fell into a deep rock crevice. Malnutrition took place before 1974 and involved primarily pups (Van Ballenberghe and Mech, 1975; Seal et al., 1975; Mech, 1977). Malnutrition constituted 25 percent of all mortality from known causes and 43 percent of the natural mortality (Table 7). Intraspecific strife mostly involved adult pack members and was the primary natural mortality factor for adults (Table 5); it accounted for another 25 percent of the mortality from known causes as well as 43 percent of the natural deaths. The details of intraspecific encounters will be reported elsewhere.

TABLE 8.—*Distribution of mortality[1] among wolves of different known social classes from 1969 through 1975.*

	Pack members[2]											
	Pups			Adults			New pairs			Loners		
Years	Radioed	Died	Percent	Radioed	Died	Percent	Radioed	Died	Percent	Radioed	Died	Percent
1969–1973	35	10	29	27	5	18	6	5	71	29	10	34
1974–1975	13	0	0	13	5	38	4	0	0	13	3	23

[1] Excludes possible capture-related death.
[2] Including peripheral animals.

Although sample sizes are too small for a definitive conclusion, human-caused mortality seems to have decreased considerably after 1973. Of seven animals that died after 1973 with active radios, only two (29 percent) were killed by humans, whereas of 17 deaths in 1973 or before, eight (47 percent) were human-caused (Table 7).

A trend away from malnutrition and toward intraspecific strife as a cause of mortality is evident (Table 7). This trend is probably explained by two factors—(1) the decreased natality or early pup survival (Table 6), which reduces the number of pups competing for the dwindling food resource, and (2) increased trespassing (Mech, unpublished), which raises the chances of interpack contact. Besides the six radioed wolves found dead from intraspecific strife, two wolf-killed, non-radioed members of radioed packs that fought were also found in 1974 and early 1976. (Because these wolves were not radioed, their deaths cannot be included with those of the radioed wolves without biasing the results.)

Social Distribution of Mortality

Several differences were apparent in the distribution of mortality among various social classes of wolves as well as between two periods of the study. The periods, 1969 through 1973 and 1974–75, cover two phases in the wolf population trend, a phase of rapid decline and a recovery phase (Fig. 2). During the earlier period, adult pack wolves had the lowest mortality rate, followed by pups at least 5 months old, lone wolves, and members of newly formed pairs. The mortality rate of the last class was about four times higher than that of adult pack members (Table 8).

During 1974 and 1975, mortality of newly formed pairs and of pups aged at least 5 months dropped to zero; however, mortality of adult pack members doubled (Table 8).

TABLE 9.—*Derivation of annual mortality rates.*

			No. of radioed wolves dead					Mortality rate (percent)	
Year	No. of wolves radioed	Cumulative number	With active radios	With expired radios	Total estimated	Cumulative number	Radioed wolves surviving	Range	Median
1968	2	2	–	– –	–	–	2	–	
1969	11	13	–	– –	–	–	13	–	
1970	14	27	3	(1)[1] 3[2]	6[3]	6	13[4]–27[5]	22–46	34
1971	20	47	10	(2) 7	17	23	21[4]–41[5]	41–81	61
1972	25	72	8	(4) 13	21	44	24[4]–49[5]	43–88	65
1973	21	93	6	(2) 7	13	57	28[4]–49[5]	27–46	36
1974	20	113	3	(4) 13	16	73	36[4]–56[5]	29–44	36
1975	16	129	3	– –	3	76	40[4]–56[5]	5–8	7

[1] Known.
[2] Estimated, see "methods."
[3] With active radio plus estimated number with expired radios.
[4] Minimum radioed sample, derived by subtracting column 7 of previous year from column 3 of previous year.
[5] Maximum radioed sample, derived by subtracting column 7 of previous year from column 3 of present year.

TABLE 10.—*Estimated annual productivity of wolf packs.*

Pack	Litter sizes each year					
	1970	1971	1972	1973	1974	1975
Glenmore L.	–	1–10	2–10	–	–	–
Newton L.	0–5	0–5	0–4	–	–	–
Pagami L.	0–4	1–3	1–4	0–4	0–5	0–1
Greenstone L.	0–3	0–2				
Ensign L.—A	–	0–13	0–7	0–2	0	0
B	–	0	–	–	–	–
Thomas L.	–	0–3	0–5			
Quadga L.	2–4	–	2	3	2–3	2–3
Harris L.	4–7	–	2	1–2	0	3
Jackpine	7	–	4–5	6	0	0
Maniwaki L.	0–5	0–7	0–7	–	3–7	6
Timber L.	1–2[1]	0–6	0–5	–	–	–
Sumpet L.	–	–	–	2–7	3	0
Wind L.	–	–	–	0–4	0	7
Birch L.	–	–	–	2	2	0–2
Sawbill	–	–	–	1–4	0	6
Perch L.					4	3
No. pups	14–37	2–49	11–51	15–34	14–24	27–32
No. packs	4–8	2–8	6–11	6–9	10–11	9–11
Mean annual increase	3.5–4.6	1.0–6.2	1.8–4.6	2.5–3.8	1.4–2.2	3.0

[1] From Van Ballenberghe et al., 1975.

This was the period when natality or early pup survival was lowest (Table 4) and, thus, pup competition was least. The wolf population was also lowest at this time (Fig. 2), and legal protection had reduced human hunting and trapping. Probably the latter factor was responsible for the high survival of the four newly formed pairs, each of which had colonized accessible areas with a history of wolf trapping. The doubling of the adult pack member mortality rate is attributable to the increased trespassing discussed earlier.

Mortality Rates

Annual estimated mortality rates of the radioed wolves varied from 65 percent in 1972 to 7 percent in 1975 (Table 9). These estimates are crude, because of small sample sizes and uncertainty about the precise number of radioed wolves with expired transmitters still in the population. Nevertheless, when applied to the independently derived population estimates and productivity data for a given year (Table 10), the calculated mortality rates yield population estimates for following years that compare favorably with those actually found (Table 11). This lends credence to the mortality rate estimates as well as to the estimated productivity and population indices. Mortality rates for wolves from 1969 through early 1972, immediately east of my core area were estimated at 10 to 40 percent and were thought to be conservative (Van Ballenberghe et al., 1975). A 41 percent annual mortality of wolves by human causes, including aerial hunting (now prohibited) was estimated for 1948 to 1950 in the present study area (Stenlund, 1955).

The highest mortality rates were found when the wolf population was high but declining in 1971 and 1972. By 1973, the population had dropped (Fig. 2), and productivity was also decreasing (Table 10). Thus, even with much lower mortality rates in 1973 and 1974, the population continued declining due to insufficient productivity to compensate for the 36 percent mortality (Tables 9, 10). The turnaround in population trend from winter 1974–75 to 1975–76 was anticipated by a somewhat higher productivity (Table 10) and much lower mortality in 1975 (Table 9).

TABLE 11.—*Method of predicting annual mean pack size, and comparison of prediction with actual values.*

Method of predicting and comparison with actual values	1970	1971	1972	1973	1974	1975
Mean spring pack size[1]	8.0	5.9	5.3	3.3	3.2	3.4
Mean annual increase[2]	+3.5–4.6	+1.0–6.2	+1.8–4.6	+2.5–3.8	+1.4–2.2	+3.0
Mean summer pack size	11.5–12.6	6.9–12.1	7.1–9.9	5.8–7.1	4.6–5.4	6.4
Annual mortality[3]	×.34	×.61	×.65	×.36	×.36	×.07
Annual loss	−3.9–4.3	−4.2–7.4	−4.6–6.4	−2.1–2.6	−1.7–1.9	−0.4
Predicted next spring mean pack size[4]	7.1–8.7	0.0–7.9	0.7–5.2	3.2–5.0	2.7–3.7	6.0
Median predicted mean pack size	7.9	4.0	3.0	4.1	3.2	6.0
Actual next spring mean pack size[2]	5.9	5.3	3.3	3.2	3.4	5.4
Difference between actual and predicted values	34%	25%	9%	28%	6%	11%

[1] From Table 3, except 1970 figure which is estimated from Fig. 2.
[2] From Table 10.
[3] From Table 9.
[4] Range represents result of subtracting maximum loss from minimum pack size and minimum loss from maximum pack size.

Discussion and Conclusions

The results of this study help identify the proximate causes of wolf population decline attributable ultimately to a substantial reduction in its primary prey (Mech and Karns, 1977). Before the decline in wolf numbers, the population appeared saturated. Each territory was occupied (Mech, 1973), mean midwinter pack size was 5.7 to 8.6 (Table 2), lone wolves constituted a relatively high percentage of the population (Table 1), productivity was comparatively low but adequate to maintain the population (Table 10), and a preponderance of male pups were produced and/or surviving the first few months of life (Mech, 1975).

As deer numbers dropped after winter 1968–69, the first noticeable symptom of problems in the wolf population was found in the pups. From 1969 through 1972, 33 to 91 percent of the pups captured in autumn were at least 20 percent underweight (Van Ballenberghe and Mech, 1975). Many of those animals, especially those from 1972, showed highly deviant blood profiles, particularly with parameters related to malnutrition (Seal et al., 1975). In 1973, the percent male pups captured increased to 83, after having remained between 56 and 70 percent from 1969 through 1972 (Mech, 1975).

Malnutrition, which had not been observed previously, suddenly constituted 30 percent of the wolf mortality from 1971 to 1973 (Table 7). An estimated 65 percent of the radioed wolves perished from various causes in 1972 (Table 9).

Meanwhile, a decrease in productivity became apparent, especially by 1974. Almost half of the 11 packs for which data were obtained that year were known or thought to have produced no pups (Table 10), and the mean midsummer litter size was 1.5 (Table 4). Mean midwinter pack size the following winter dropped to 3.9 (Table 2). By that time the proportion of lone wolves captured, which should be a rough measure of the proportion in the population, had dropped from over 40 percent in 1969 to about 6 percent in 1975 (Table 1). On the other hand, those loners that did exist survived longer, especially the ones able to find a mate and a vacant territory (Table 8). Although this greater survival may have been due partly to increased legal protection, the effect of decreased competition due to lowered wolf numbers probably also was important.

Despite these substantial changes to basic population parameters, this was still not enough to bring the wolf population to where it could survive on the available prey.

The remaining wolves had to increase their territory size and resort to trespassing into other pack territories to try to obtain sufficient food (Mech, 1977). The result was yet another mortality factor, intraspecific strife. In 1974 and 1975, 100 percent of the wolf mortality discovered in the core study area was a result of wolves killing other wolves (Table 7).

Mortality from intraspecific strife may have profoundly different consequences from the other factors reducing the wolf population. Malnutrition affects young animals almost exclusively (Table 5), while helping preserve established breeders by reducing competition. This was also demonstrated in the analysis of a 6-year history of the Harris Lake Pack from this study area. Weights, survival, and blood data indicated that the healthiest of the eight pack members for which data were available were the alpha animals (Mech, 1977). Population reduction by malnutrition and decreased productivity tends to preserve breeding members of the population. Whenever prey biomass increases sufficiently, the breeders can quickly repopulate the area with little change in the frequency of genotypes.

Intraspecific strife, because it usually affects alpha animals (Table 5), would have substantially the opposite effect. Not only would the genotypes of the losers in intraspecific conflicts be selected against, but some other genotype (for example, that of the winner) would be the selective agent. This process could quickly change the gene frequency in the population, and perhaps result in an increase in a genotype more capable of coping with lowered prey densities.

Because the subject of this study is on the U.S. Secretary of the Interior's list of Endangered Species and, consequently, is of considerable interest to the lay public, it is necessary to emphasize a few qualifications to this study. The results apply only to the core study area in the Superior National Forest, not to the entire Forest nor all of Minnesota. There is evidence that outside the study area deer and wolf numbers are higher than reported herein, and that elsewhere in the state wolf numbers are increasing.

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