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Role of the WOLF in a DEER decline in the SUPERIOR NATIONAL FOREST

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NORTH CENTRAL FOREST EXPERIMENT STATION • FOREST SERVICE, U.S. DEPARTMENT OF AGRICULTURE

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ROLE OF THE WOLF IN A DEER DECLINE IN THE SUPERIOR NATIONAL FOREST

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The objectives of this paper are (1) to document a severe decline in the numbers of white-tailed deer *(Odocoileus virginianus)* in the Superior National Forest of Minnesota from winter 1968-69 through winter 1974-75, (2) to discuss the probable causes of the decline, and (3) to assess the role of the wolf *(Canis lupus)* in the decline.

Changes in the deer population in this region are important for several reasons. First, a high percentage of campers in the Superior National Forest regard observing deer as an important part of their outdoor experience (Lime and Cushwa 1969). Second, local residents and sportsmen from several urban areas spend considerable time hunting deer in the Superior National Forest. Third, deer form the primary prey of the eastern timber wolf *(Canis lupus lycaon)* in the area (Stenlund 1955, Mech and Frenzel 1971), an animal on the Secretary of the Interior's list of Endangered Species.

THE STUDY AREA

The Superior National Forest, in Cook, Lake, and St. Louis Counties of northeastern Minnesota encompasses some 10,752 km^2 (4,200 mi^2) (figs. 1 and 2). At about 92° W longitude and 48° N latitude, it lies in the northern 20 percent of the deer's natural range (Hall and Kelson 1959). Winter temperatures of -40 C (-40 F) and lower are not unusual, and average snow depths range from 50 to 75 cm (20 to 30 in) (Mech and Frenzel 1971).

Predominant trees in the Superior National Forest before the advent of logging and subsequent fires consisted of balsam fir *(Abies balsamea)*, black spruce *(Picea mariana)*, white spruce *(Picea glauca)*, white-cedar *(Thuja occidentalis)*, jack pine *(Pinus banksiana)*, white pine *(Pinus strobus)*, and red pine *(Pinus resinosa)*. Extensive stands of white birch *(Betula papyrifera)* and aspen *(Populus tremuloides)* developed after widespread logging and fires, and matured, with succession advancing to conifers. Currently about 18 percent of the Superior National Forest is composed of virgin forest, mostly conifers (Heinselman 1973), located primarily in the Boundary Waters Canoe Area, in the northern third of the Superior National Forest.

Although deer inhabited almost all regions of the Superior National Forest during the present century, their densities were highest in recently burned or cutover areas and low in virgin forests (S. Olson 1938, Stenlund 1955).

During winter, deer in the Superior National Forest concentrate primarily in three major winter yards: (1) two strips about 1.6 km (1 mi) wide and 29 km (18 mi) long, adjacent to Lake Superior along the southeast edge of the Forest, called the Jonvick Yard and the Brule River Yard, (2) a more diffuse stretch of variable width from the east end of Lake Vermilion east-northeasterly through Mud Creek, just north of Shagawa Lake to Ely, along both sides of Fall Lake, the Fernberg Road, and northeasterly along Moose Lake and a chain of lakes through Knife Lake, a total length of about 72 km (45 mi), and (3) two strips about 1.6 km (1 mi) wide and 6.4 to 9.6 km (4 to 6 mi) long just north of the Gunflint Trail in the northeast edge of the Forest (fig. 2).

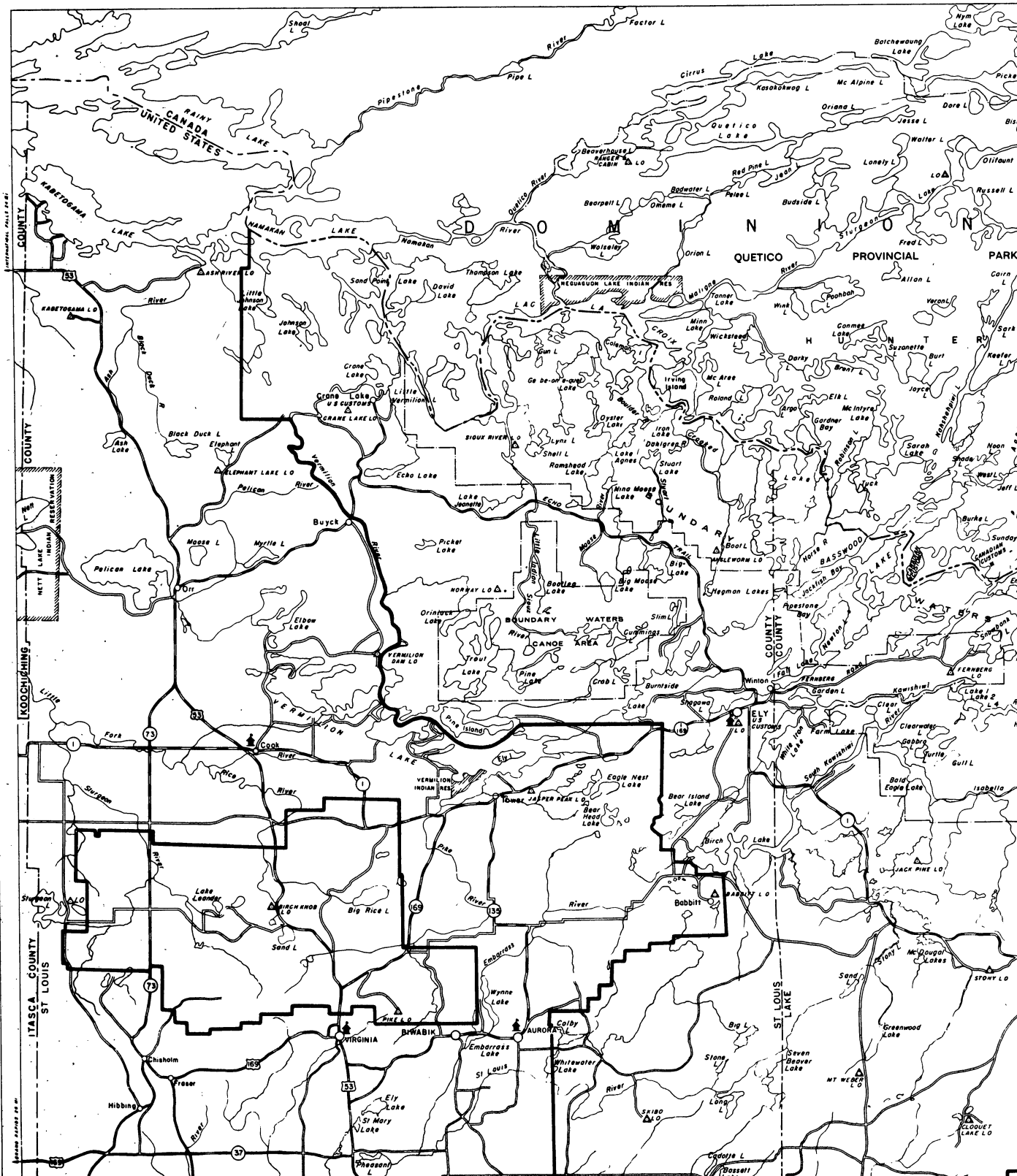
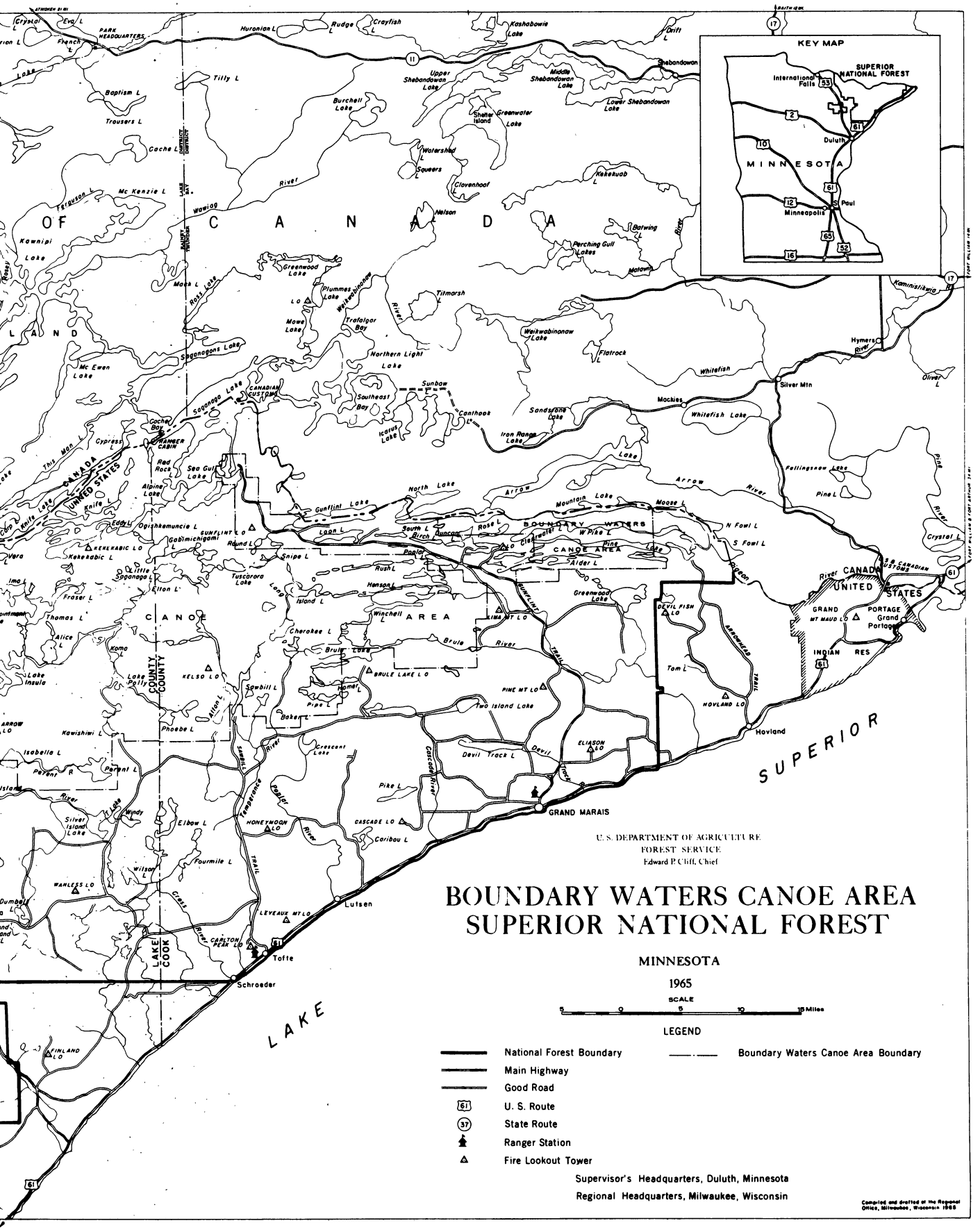


Figure 1. – *Map of the study area.*



U. S. DEPARTMENT OF AGRICULTURE
FOREST SERVICE
Edward P. Cliff, Chief

BOUNDARY WATERS CANOE AREA
SUPERIOR NATIONAL FOREST

MINNESOTA

1965

SCALE
5 0 5 10 15 Miles

LEGEND

- National Forest Boundary
- Boundary Waters Canoe Area Boundary
- Main Highway
- Good Road
- 61 U. S. Route
- 37 State Route
- Ranger Station
- Fire Lookout Tower

Supervisor's Headquarters, Duluth, Minnesota
Regional Headquarters, Milwaukee, Wisconsin

Compiled and drafted at the Regional Office, Milwaukee, Wisconsin 1965

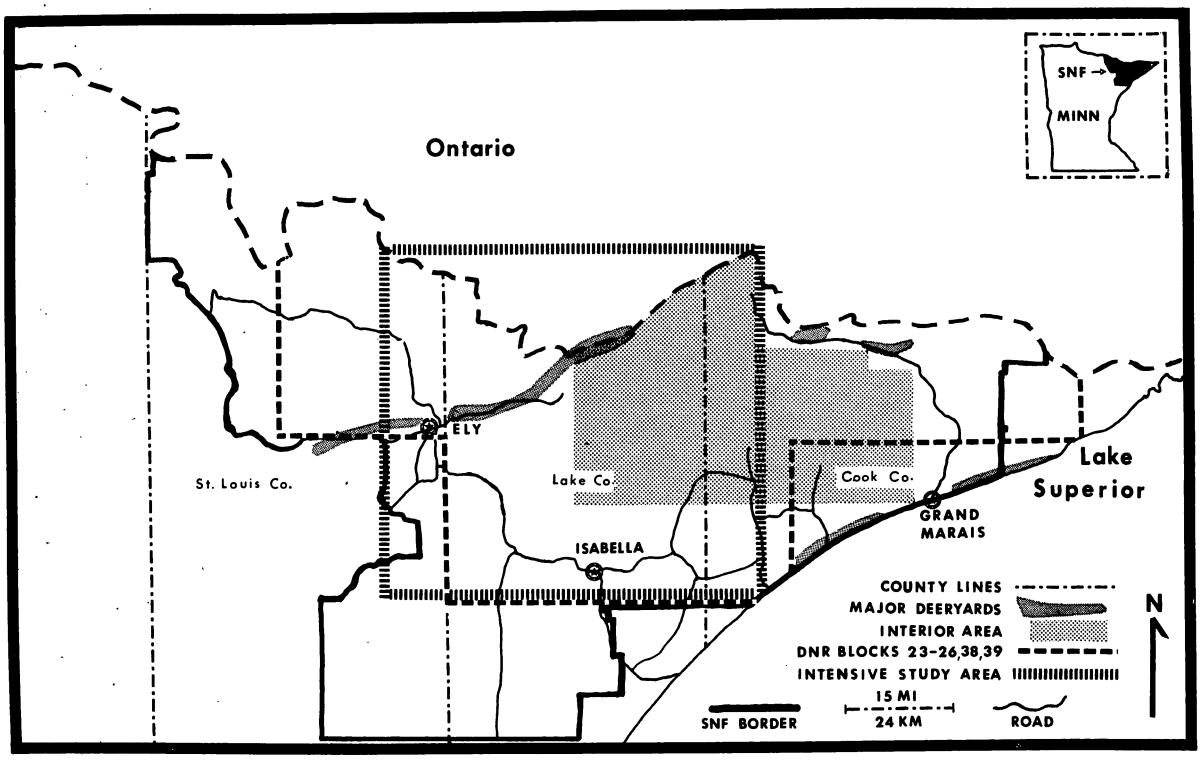


Figure 2. — *The intensive study area in the Superior National Forest. Minnesota Department of Natural Resources Grid Blocks 23-26, 38 and 39 are deer-harvest blocks in which the deer-age-structure sample is considered to best represent deer from the wilderness area. Blocks 14, 15, 22, 37, 50, and 51 lie immediately west, south, and east of the wilderness blocks and are considered to represent the accessible region best.*

The Lake Superior and Fernberg yards are about 96 km (60 mi) apart. In between, yarding also takes place in small, scattered "pockets" near lake shores and in conifer swamps, and in a few yards of up to about 5 km^2 (2 mi^2). Most of the region between the major concentration areas is relatively inaccessible wilderness, to be referred to as the "Interior Area" (fig. 2), consisting of about 3,072 km^2 (1,200 mi^2). Depending on snow and weather conditions, deer begin to concentrate in late fall and early winter and disperse again about April. Movements to yarding areas extended as far as 40 km (25 mi) (H. Olson 1938, Hoskinson and Mech 1976,[1,2]).

Sport hunting of deer is inconsequential in the Interior Area due to the area's inaccessibility. Roads are nonexistent through much of the Interior, and where they do exist in the Boundary Waters Canoe Area, they are closed to mechanized vehicles. Newly formed ice during deer hunting season (November) restricts travel by boat and snowmobile. Deer hunting occurs west, south, and east of the Interior Area, but most of it is restricted to relatively narrow strips along roads, trails, and waterways. The general distribution of hunter-killed deer along the western edge of this area was documented by Mech and Frenzel (1971).

Wolves in the study area prey primarily on deer, supplementing their diet with beaver *(Castor canadensis)* from March through November, and with moose *(Alces alces)* (Frenzel 1974, Van Ballenberghe and Mech 1975,[3]). In inaccessible areas, the wolf is the primary agent of deer mortality (Stenlund 1955, Mech and

[1] *Nelson, M. W. 1977. Migration and social organization of white-tailed deer in northeastern Minnesota. Unpublished M.S. thesis, University of Minnesota, St. Paul, Minnesota.*

[2] *Karns, P. D. Unpublished data on file at Minnesota Department of Natural Resources, Grand Rapids, Minnesota.*

[3] *Mech, L. D. Unpublished data on file at North Central Forest Experiment Station, St. Paul, Minnesota.*

Frenzel 1971). Along roads in the region bordering the wilderness area, hunting by humans constitutes another important mortality factor.

Wolf control programs by the Minnesota Conservation Department (now the Minnesota Department of Natural Resources) ceased in 1950. Wolf bounties were terminated in 1965, and wolves were protected by the USDA Forest Service on Federal lands within the Superior National Forest beginning in October 1970. In much of the Interior Area, inaccessibility prevented any significant reduction of wolves even before. However packs along the west, south, and east edges of the Interior Area were subject to moderate hunting and trapping pressure. This pressure continued illegally but in reduced amounts after 1970. Wolves were legally protected throughout Minnesota in August 1974 by the Federal Endangered Species Act of 1973.

The wolf population in the Superior National Forest was estimated to be saturated at about one wolf per 25.6 km^2 (10 mi^2) in winter 1971-72 (Mech 1973), with the population organized into pack territories of 125 to 310 km^2 (48 to 120 mi^2) (Mech 1974) and nomadic lone wolves (Mech 1972). From 1972 to 1975, wolves declined about 40 percent in an area of about 2,560 km^2 (1,000 mi^2) in and near the Interior Area (Mech 1977b). Evidence was found there of pup malnutrition (Van Ballenberghe and Mech 1975, Seal *et al.* 1975), disproportionate production and survival of male pups (Mech 1975), decreased litter sizes, and increased intraspecific strife (Mech 1977a, 1977b).

METHODS

We employed several methods to obtain the data presented here. From winter 1966-67 through winter 1974-75, the senior author and his assistant used light aircraft to survey the study area for wolf-killed deer and from 1968-69 through 1974-75 to radio-track wolves (Mech and Frenzel 1971, Mech 1974). Such flights allowed incidental observations of deer and their sign many times each year throughout an intensive study area just east of Ely (fig. 2). Other parts of the Forest were visited often but less regularly. Although only incidental notes were kept on deer seen in earlier years, all deer observed during winters 1972-73, 1973-74, and 1974-75 were noted. During February and March 1972 through 1975, a total of 9 flights involving 17 hours were made deliberately to search for deer and deer sign in the intensive study area. These flights followed all the major waterways and other lowland areas where deer generally yarded in previous years.

In addition, the junior author collected data on (1) the winter severity index [WSI] (Verme 1968) from 1967-68 through 1974-75; (2) fawn:doe ratios and fawn sex ratios in the hunter harvest from 1955 through 1973 (no data for 1971 when the season was closed, or 1974 when only bucks were legal); (3) age structures of hunter-killed does in 1972 and 1973 and of bucks in 1974. The age-structure data were based on jaws and incisors left by hunters at compulsory registration stations and aged according to incisor sectioning (Gilbert 1966,[4]).

Residents who have maintained artificial feeding stations in the Jonvick deeryard were interviewed via telephone regarding the number of deer using their stations each year.

To determine the potential effects of various factors in the deer decline, we used a modeling approach. The basic model involved only the female population and was composed of three empirical parameters: the annual fawn:doe ratios, the annual fawn sex ratios, and an annual wolf population index derived from Mech (1977b). The following assumptions were made: (1) the deer population was relatively stable from 1967 to 1968, (2) therefore, the annual mortality in the herd in 1967 approximated the annual increment, (3) most of the deer dying in the Interior Area were killed by wolves or utilized by them, and (4) annual changes in the wolf population resulted in proportional changes in the annual take of deer by wolves.

In projecting with the above model, we tested the effect of various changes in these assumptions, along with variations in the empirical parameters.

A separate approach to modeling the wolf-deer system in the Interior and surrounding region (DNR Grid Blocks 23 to 26, 38, and 39) (fig. 2) was to adapt the Minnesota Department of Natural Resource's deer population management model (SNOPOP) to allow wolf and deer populations to interact in accordance with the WSI, with estimated wolf consumption rates, and with the wolf population trend.

[4] *Kuehn, D. W. 1970. An evaluation of the wear method as a criterion for aging white-tailed deer. M.S. thesis, University of Minnesota, St. Paul, Minnesota.*

RESULTS
The Deer Decline

Approximately 1,500 hours of flying were logged during the nine winters of this study, and 454 wolf-killed deer were located, including 142 actually examined by Mech and Frenzel (1971) and 71 examined during the present study. Because the entire study area was repeatedly surveyed each winter, the information obtained can be used to determine changes in deer distribution during the 9-year period.

Of special interest is the eastern half of the study area, including the northern half of Lake County and most of Cook County, much of which composes the relatively inaccessible Interior Area. Unpublished records (Minnesota Department of Natural Resources files) showed that deer inhabited all or part of this area in the 1930's in high densities (fig. 3). Stenlund (1955) then documented the continued existence of deer in the area from 1948 to 1952 (fig. 4). Our own data, including those from Mech and Frenzel (1971), show that deer still wintered in at least the western part of the Interior Area from winter 1966 through winter 1970 (fig. 5).

During the following five winters, however, the usual measures of deer distribution, i.e., wolf kills (figs. 6 and 7) and aerial observations of deer (fig. 8), indicated that the wintering deer population in the Interior Area was depleted.

Although the decline of deer was most dramatic in the Interior Area, deer also decreased outside the Area. This was clearest for winter 1972-73 in two areas: (1) west of Kekekabic and Alice Lakes, and (2) around Bald Eagle Lake, just west of the Interior Area. In the first area, numbers of deer wintered and were killed during at least the previous 6 years, but no deer or kills were found in 1972-73, 1973-74, and 1974-75 (figs. 6, 7, and 8). In the second area, only a few kills and deer were located during 1972-73 and 1973-74 (figs. 6, 7, and 8). This was true even though five radioed wolf packs used the region (Mech 1973), and many kills had been found there during previous winters (fig. 5).

In addition to the loss of deer in these two areas and the Interior Area, several other local concentrations of deer present in earlier years were much reduced or absent in winter 1972-73 (figs. 5, 6, 7, and 8).

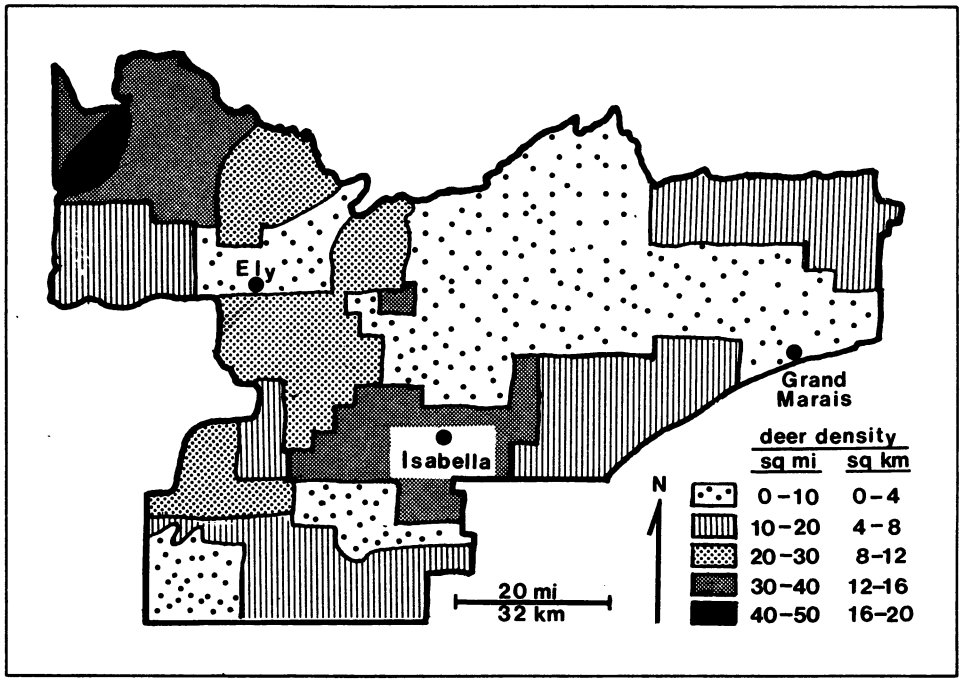


Figure 3. – *Estimated deer densities in the Superior National Forest in 1936, based on extrapolations from deer drives (Minnesota Department of Natural Resources files). Data indicate that areas supporting 0.4 to 4 deer per square kilometer (1 to 10/mi^2) probably had closer to 4 deer/km^2.*

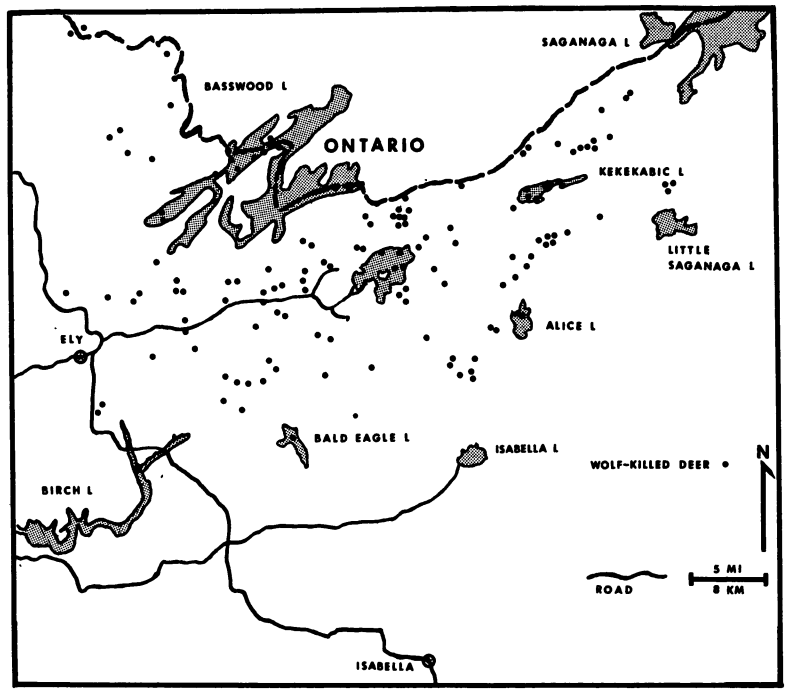


Figure 4. – *Distribution of wolf-killed deer in the intensive study area (fig. 2), 1948 to 1952, reported by Stenlund (1955). No kills were found in the southern half of this region because Stenlund did not include it in his study.*

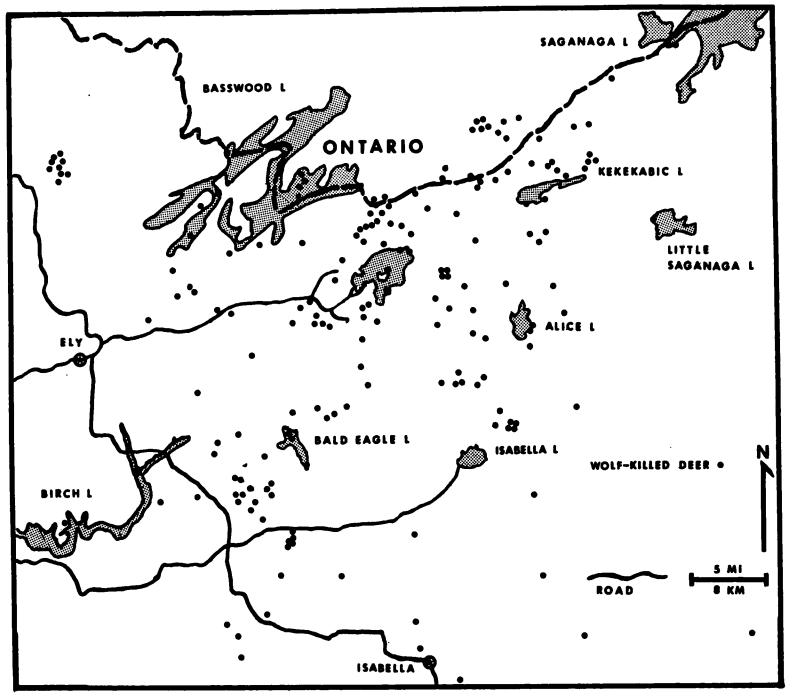


Figure 5. – *Distribution of wolf-killed deer found in the intensive study area (fig. 2) from winter 1965-66 through 1969-70, including those reported by Mech and Frenzel (1971).*

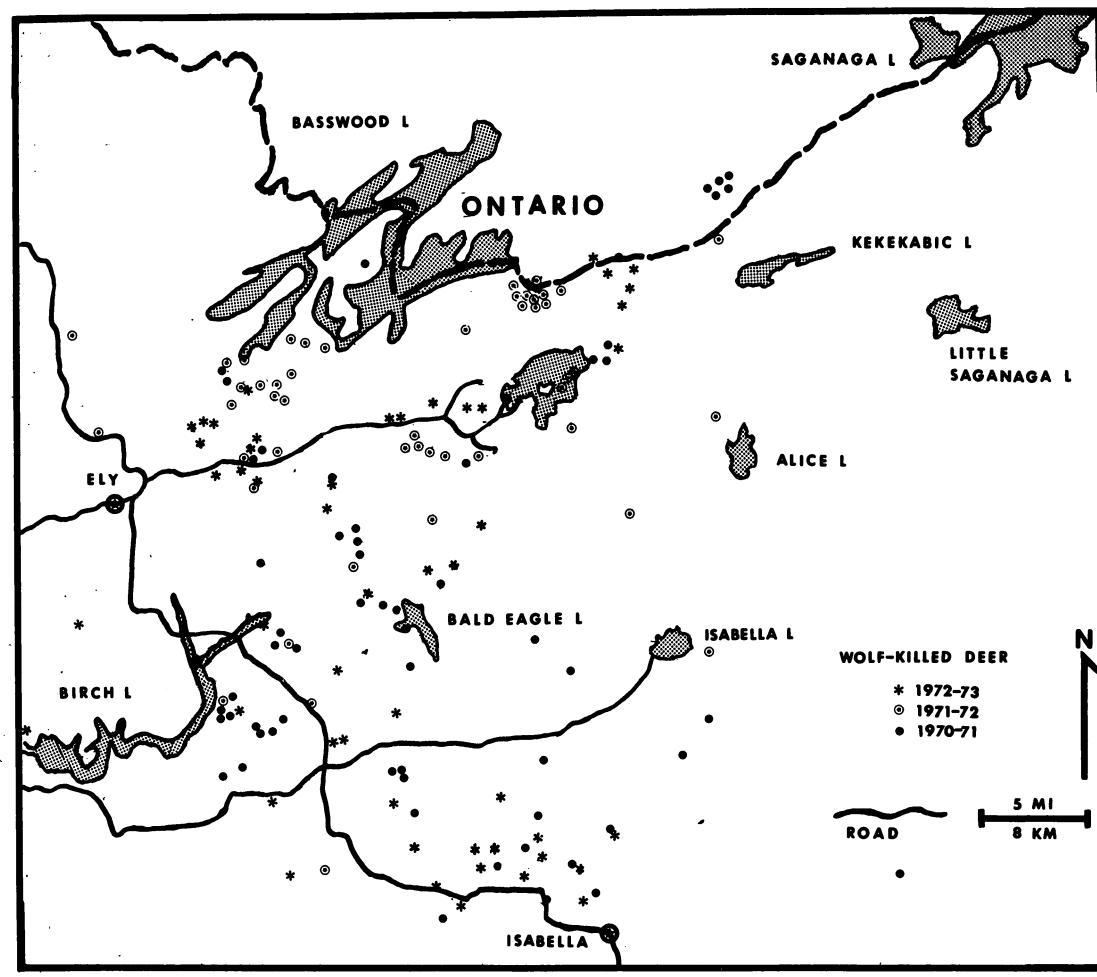


Figure 6. – *Distribution of wolf-killed deer found in the intensive study area (fig. 2) from winter 1970-71 through 1972-73.*

The total loss of the deer populations described above could not be attributed to a shift of these animals into other wintering areas. During the same period, deer populations were greatly reduced in the Fernberg Yard east of Ely (fig. 2), and the remaining deer wintered almost exclusively in the Garden Lake portion of the Yard about 10 km (6 mi) northeast of Ely. This Yard constituted only a tiny fraction of the original concentration area (fig. 2).

In the Jonvick Yard along the eastern edge of the Superior National Forest, the number of overwintering deer also dropped. Local residents who regularly fed deer there during winter were unanimous in their opinions about the trend in the deer population. They stated that deer numbers in their feeding areas had remained stable through most of the decade preceding winter 1968-69 but that thereafter they had steadily declined. The estimated numbers of deer visiting feeding stations in winter 1973-74 were 51 to 73 percent less than in winter 1968-69 (table 1). Pellet counts conducted in the Jonvick Yard in 1959, 1973, and 1976 estimated the overwintering deer population as 55, 45, and 39/km^2 (140, 116, and 101/mi^2).[2]

Table 1. – *Results of interviews with Lake Superior Deeryard residents (Lutsen, Minnesota) who regularly feed deer*

Resident	Maximum number of deer using yard		Decrease
	1968 to 1969	1973 to 1974	
			Percent
Earl Funk	82	40	51
Arnold Peters	81	22	73
Curtis Truman	45	20	56

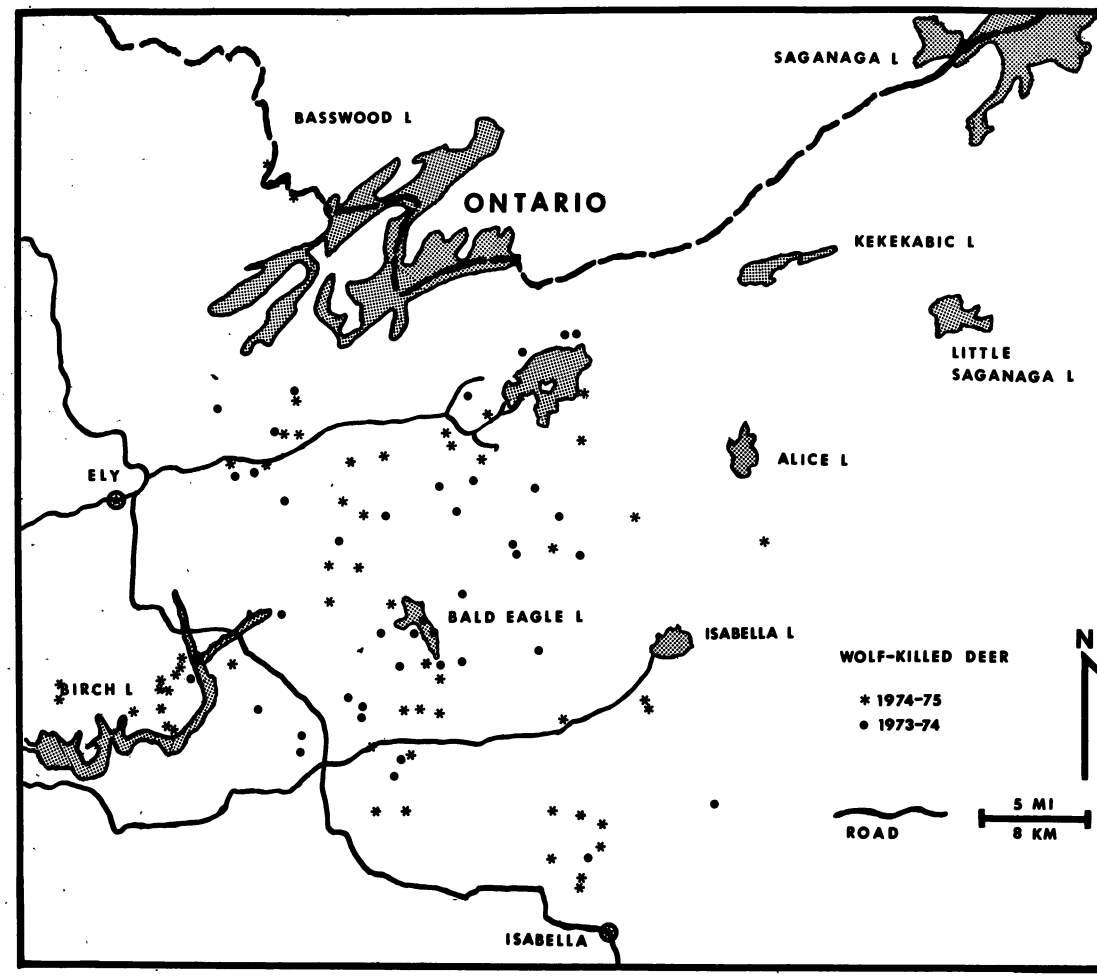


Figure 7. – *Distribution of wolf-killed deer found in the intensive study area (fig. 2) in winters 1973-74 and 1974-75.*

Similarly, deer numbers also declined substantially in the Brule River Yard and the Gunflint Trail Yards east of the study area.[5]

The deer decline in the Interior Area was most noticeable and best documented during winter. In summer, deer that overwintered in the Garden Lake portion of the Fernberg Yard migrated toward the Interior (Hoskinson and Mech 1976,[1,2]), and the same trend took place in the Jonvick Yard (H. Olson 1938,[1]). Thus instead of the absolute lack of deer noticeable throughout most of that region in winter, summer data indicated only extremely low deer densities. For example, in May 1973 the senior author found tracks of deer in only five locations during a 46-km (29-mi) hike of old logging roads in the Interior.

Although the deer decline was absolute in the Interior Area of the Superior National Forest, it took place to some degree throughout northeastern Minnesota, and in the entire Great Lakes Region. Whereas the hunter harvest for Minnesota had fluctuated between 95,000 and 127,000 from 1959 through 1968, it dropped from 103,000 in 1968 to 68,000 in 1969 (Gunvalson 1971). The hunting season was then reduced from the usual 9 days in northern Minnesota to 2 in 1970, and 45,000 deer were killed. The season was closed statewide in 1971.

[5] *Personal communication with W. J. Peterson.*

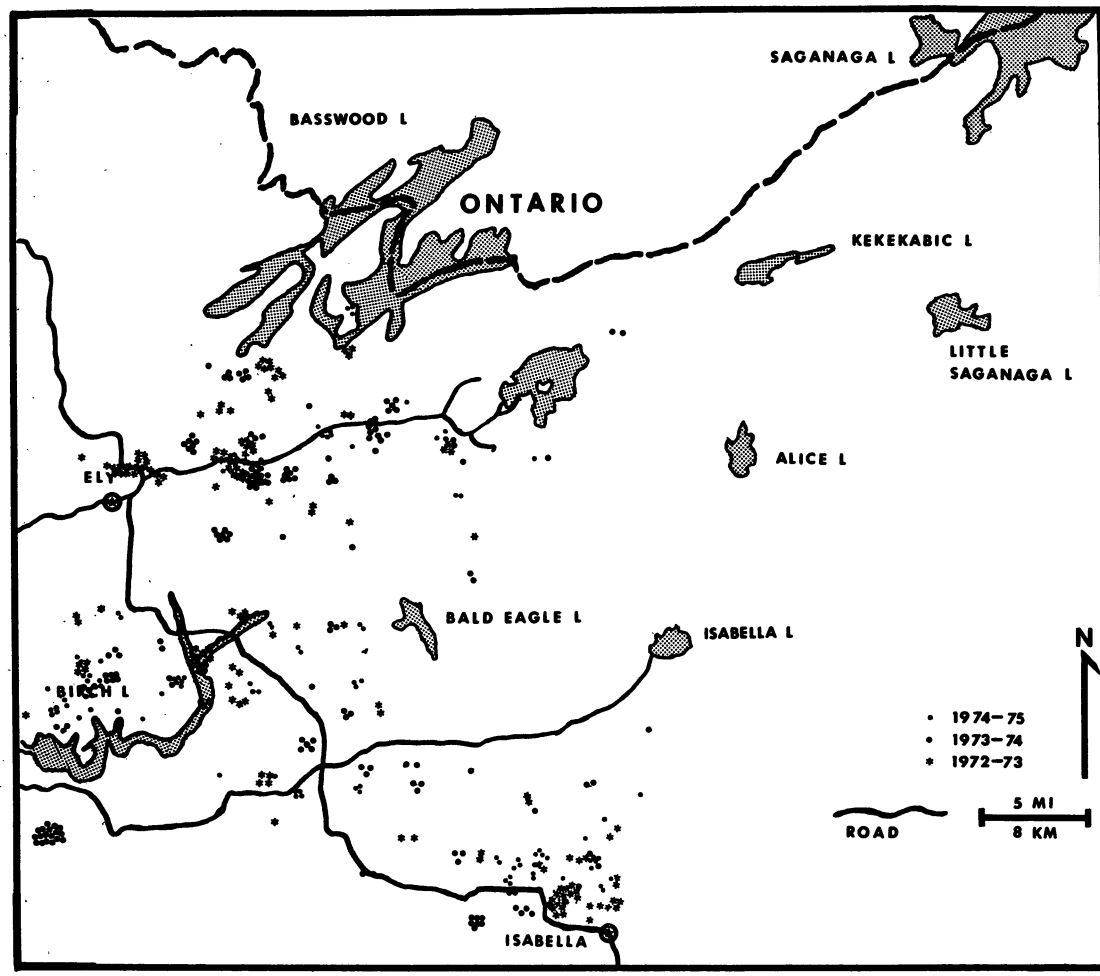


Figure 8. – *Distribution of deer and deer sign observed in the intensive study area (fig. 2) during winters 1972-73 through 1974-75.*

In the study area during 1972 and 1973, the deer season was opened for 2 to 5 days during a 30-day "hunter's choice" framework. Hunters could take deer of either sex and any age before 1974; in 1974, the harvest was restricted to "bucks-only". The hunter kill per 2.6 km^2 (1 mi^2) averaged only 0.83 deer of both sexes in 1973 in the accessible perimeter of the wilderness. In 1974, it averaged 0.54 antlered bucks there. In the wilderness, the hunter harvest averaged 0.25 deer of both sexes in 1973 and 0.13 antlered bucks in 1974.

In central Ontario, indications are that deer declined between 1966 and 1972 (Voigt *et al.* 1976). In both Wisconsin[6] and northern Michigan[7], deer numbers also declined until 1972. However in both States, they then increased each year thereafter.

Winter Severity Index

All but two winters from 1954-55 through 1963-64 were mild in northeastern Minnesota, but from 1964-65 through 1971-72, seven of the eight were rated as severe, and one as moderate (table 2). Verme's (1968) Winter Severity Index (WSI) measured at Isabella (fig. 2) varied from 157 to 270 from 1967-68 through 1971-72, and then dropped to 94 in 1972-73 (table 2), for a 6-yr mean of 177. This was much higher than the means of 112 to 145 for the same years from six other stations in northern Minnesota outside the study area (Agassiz National Wildlife Refuge, Aitkin, Grand Rapids, Togo,

[6] *Personal communication with B. E. Kohn and K. R. McCaffery.*

[7] *Personal communication with R. E. Bailey.*

Norris Camp, and Mille Lacs Wildlife Management Area). A WSI of 100 is sufficiently severe under Minnesota conditions to result in deer mortality[2], just as Verme (1968) established for the Upper Peninsula of Michigan.

Table 2. – *Winter Severity Index and fawn production as evidenced by fall hunter-kill statistics, Lake and Cook Counties, Minnesota*

Year	Winter Severity Index[1]	Fawns per 100 does
1955	Mild	111
1956	Severe	100
1957	Moderate	144
1958	Mild	128
1959	Mild	91
1960	Mild	81
1961	Mild	98
1962	Mild	91
1963	Mild	107
1964	Mild	85
1965	Moderate	71
1966	Severe	72
1967	Severe	90
1968	Severe (157)	66
1969	Severe (190)	65
1970	Severe (164)	71
1971	Severe (270)	--
1972	Severe (196)	51
1973[2]	Mild (94)	85

[1]Preceding winter; numbers in parenthesis refer to Verme's (1968) WSI, measured at Isabella, Minnesota.

[2]Season changed to bucks-only after this year.

Fawn Production and Survival

The fawn:doe ratio is an index of the relative proportion of fawns surviving until fall, and is an indicator of relative fawn production. However, this index is a ratio only. A high ratio, for example, does not necessarily mean a large fawn crop but only indicates a high proportion of fawns produced by what may be a large or small number of producing does. On the other hand, a low ratio definitely indicates a reduced fawn crop, which then may be even smaller if few does are left to produce it.

Fawn production and/or survival, based on fawn:doe ratios from the November hunter harvest, declined substantially from 1955 through 1972, both in wolf-inhabited Lake and Cook Counties and in a nearby, relatively wolf-free area (fig. 9). In Lake and Cook Counties, the fawn:doe ratio averaged 104:100 from 1955 through 1964 (table 2), but then dropped to 71:100 from 1965 through 1973. The fawn:doe ratio was probably very low in 1971, the fall following the record high WSI (table 2), but closure of the hunting season precluded its measurement.

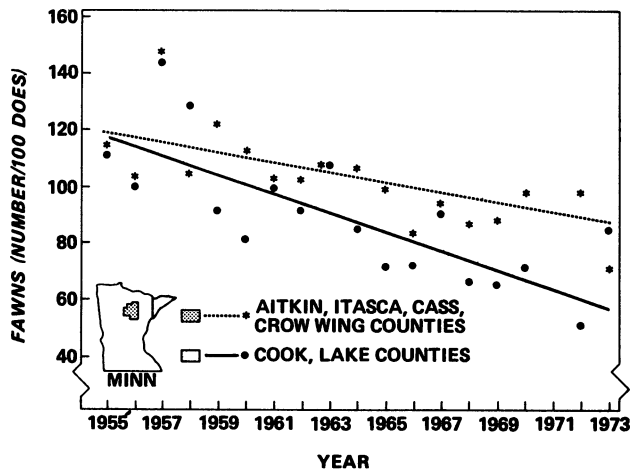


Figure 9. – *Numbers of fawns per 100 does each year in the hunter-kill from relatively wolf-free north-central, and wolf-inhabited northeast, regions of Minnesota, and regression lines for each. For the north-central region, the slope is 1.83 percent per year with a standard error of 11.92; for the northeastern region, the slope is 3.30 percent with a standard error of 15.58.*

Fawn Sex Ratio

The sex ratio of fawns in the fall hunter kill may or may not reflect the sex ratio of fawns produced. However it does generally indicate the ratio surviving to fall, assuming equal vulnerability of the sexes to hunting. From 1955 through 1970, this ratio varied from 35 to 48 percent females in the Lake and Cook County samples, and averaged 41 percent, a difference statistically different from the expected, at the 0.001 level (fig. 10). The ratio was unknown for 1971 and 1974, but in 1972 it increased to 48 percent females, and in 1973 to 52 percent.

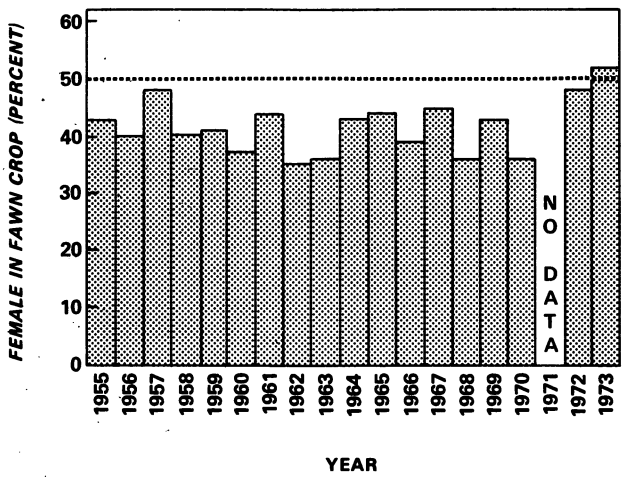


Figure 10. – *Percentage of females in the fawn crop during the hunting season (November) in Lake and Cook Counties.*

Age Structure of the Deer Herd

The age structure data from hunter-killed deer were segregated into those from a region immediately adjacent to the Interior wilderness of the Superior National Forest, and those from more accessible and settled areas adjacent to this region (fig. 2). Wolves inhabited both regions, but human exploitation was much greater in the accessible area. This was because of accessibility, and because the predators were legal quarry in most of the area. Beginning in 1970, they were legally protected in the first region.

In addition, the sample of hunter-killed deer from the more accessible area no doubt included deer primarily from around well traveled roads, active forestry plots, frontier farms, and other areas probably least frequented by wolves. Thus the "wilderness" sample represents a population of deer most influenced by wolves, and the adjacent "accessible" sample represents one that is subject similarly to most natural factors but is less influenced by wolves.

The 1972 and 1973 female age structures appeared basically similar so were combined by superimposing common year classes within each area. The age distributions of does from the wilderness and the accessible regions differed significantly (Kolmogorov-Smirnov, p=0.01). The age structure of the sample from the accessible region was generally typical of most deer populations, with each older year class composing a smaller proportion of the total (fig. 11). However, the wilderness sample was highly deficient in the 1969, 1970, 1971, and 1972 year classes.

Age-structure data were available for bucks only in 1974. In both wilderness and accessible regions, the male age structures (fig. 11) were much closer to typical than was the female age structure for the wilderness area. The 1970, 1971, and 1972 age cohorts made up a considerably greater proportion of the male populations than they did in the female population in the wilderness, although the 1969 class was disproportionately low just as in the female samples (fig. 11).

The trends seen in the various age structures were also reflected in the mean ages of the samples (table 3). The samples of the oldest deer were those from the wilderness does, with a mean age of 5.3 years in 1972 and 4.7 in 1973, excluding fawns. Does in the accessible areas had a mean age of 3.5 years. The samples of the youngest deer were those of the 1974 bucks, 2.5 years for those from the accessible area, and 2.6 for the wilderness sample. These ages were even younger than the mean ages of the samples of bucks taken in 1967 and 1968 before the drastic decline (table 3).

The above figures strongly suggest that survival was greater for male fawns than for female fawns during the decline, but that the reverse was true for adults. This difference is supported by the fact that the oldest animal in the larger sample of bucks in 1974 was only 7.5 years old, whereas the oldest doe was 10.5 years. (The above interpretations all assume that the relative vulnerability of the various age classes of deer to hunters was approximately the same in both areas.)

DISCUSSION

The severe decline of deer in the Superior National Forest raises the question as to the cause or causes of the decline. One of the most conspicuous and pertinent pieces of information available is the long range, decreasing trend in production of fawns in both northeastern and central Minnesota (fig. 9). Because these two areas differed in winter severity, hunter density, vegetation types, and habitation by wolves, some other factors seem responsible. Circumstantial evidence suggests that nutritional influences related to increasing forest maturation and succession may be the major factor.

The effect of poor nutrition and low quality range in reducing deer productivity has long been recognized. Deer on poor diets shed fewer ova (Cheatum and Severinghaus 1950), and produce fewer fawns (Verme 1965, 1969) and fawns of decreased viability (Verme

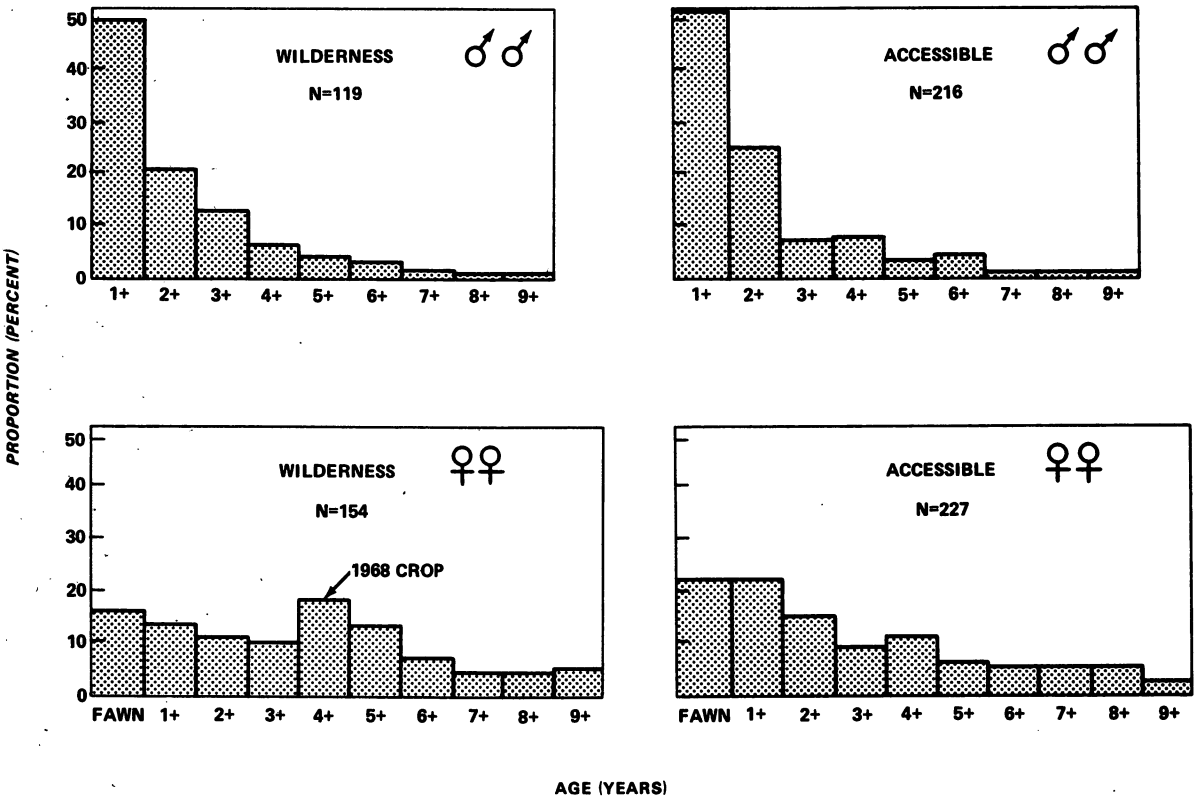


Figure 11. – *Age structures of hunter-killed does in 1972 and 1973 and bucks in 1974 from wilderness and accessible regions of the Superior National Forest (see fig. 2). No fawns are included in 1974 because it was illegal to take them during the bucks-only season.*

Table 3. – *Mean ages of hunter-killed deer in the Superior National Forest*

Years	Area	Including fawns			Excluding fawns[1]	
		Sex	Number	Mean Age	Number	Mean Age
				Years		*Years*
1967, 1968[2]	Wilderness & Accessible	M	269	2.7	215	3.3
1967, 1968[2]	Wilderness & Accessible	F	154	2.4	100	3.5
1972	Wilderness[3]	F	58	4.5	48	5.3
1972	Accessible[4]	F	118	3.3	91	4.1
1973	Wilderness	F	154	3.1	98	4.7
1973	Accessible	F	173	2.6	109	3.8
1974	Wilderness	M	---	---	119	2.6
1974	Accessible	M	---	---	216	2.5

[1]These columns are included because the bucks-only hunting season during 1974 precluded the inclusion of fawns in the sample.

[2]Mech and Frenzel (1971)

[3]Minnesota Department of Natural Resources Deer Kill Block Nos. 23, 24, 25, 26, 38, 39.

[4]Minnesota Department of Natural Resources Deer Kill Block Nos. 14, 15, 22, 37, 50, 51.

1962, 1963). In moose, it appears that such reduced viability persists as individuals grow older, thus predisposing them to wolf predation at an earlier age than usual (Peterson 1974, Peterson and Allen 1974). Furthermore, poor nutrition tends to prevent yearling does from becoming fertile (Verme 1967). Since yearlings usually form the largest age class of potential breeders in a herd, their infertility could have a substantial effect on fawn production.

An additional effect of inadequate nutrition in controlled captivity experiments is the production of a preponderance of male fawns (Verme 1965, 1967, 1969). Thus the surplus of male fawns in our hunter-kill samples from 1955 through 1970 (fig. 10) probably also is attributable to poor nutrition resulting from forest maturation. Surpluses of males can seriously decrease the breeding potential of a deer herd.

Young aspen communities less than 25 years old are considered prime deer habitat in northern Minnesota and the Great Lakes Region. Generally both the quality (Halls and Epps 1969) and the quantity (Halls and Alcaniz 1968) of deer browse decreases with advancing forest succession (Cowan *et al.* 1950). However, the aspen forests of Minnesota are maturing faster than they are being cut or burned. From 1952 to 1972 the percentage of young aspen forests dropped from 65 to 21 (Stone 1966), and the older forests were being succeeded by balsam fir (Buell and Niering 1957), which further closed the canopy. This trend led Urich[8] to conclude that "the decline of deer numbers in northern Minnesota appears to be related to loss of spring, summer and fall habitat due to forest maturity."

The deer decline during the present study, and eventually the complete loss of deer in the Interior Area, was first evident in the most extensive stand of virgin forest in the Superior National Forest, near Little Saganaga Lake. As early as 1936, this region harbored the fewest deer (fig. 3), and Stenlund (1955) wrote: "Deer numbers have remained low [in the virgin forest] for the past 30 years, and there is no reason to believe that they will increase in the future." Thus we conclude that the gradual maturation of the forests of northern Minnesota seriously contributed to the deer decline in the late 1960's.

[8] *Urich, D. L. 1973. Nutrient levels in deer and moose forage in northern Minnesota as related to site characteristics. Unpublished M.S. thesis, University of Minnesota, St. Paul, Minnesota.*

However forest maturation cannot account completely for the precipitous loss of deer and the total demise of the herd in the Interior. Deer numbers dropped even in areas of the Interior that had been extensively logged from 1940 to 1968. Furthermore, all the deer were not lost in most of north-central and northeastern Minnesota despite the trend there in increasing forest maturation. A population averaging up to 15 deer/2.6 km^2 (1 mi^2) still inhabits those regions.

A second important factor contributing to the deer decline in northeastern Minnesota and the entire Great Lakes Region, was the series of severe winters that began in 1964. The mean number of fawns per 100 does in northeastern Minnesota dropped from 104 during 1955 through 1964 to 71 during 1965 through 1973 (table 2). Even in the north-central region, where winters were consistently less extreme although still severe, the drop during the same period was from 112 to 94 fawns per 100 does.

Besides having an adverse effect on fawn production, extreme winters may directly reduce viability and survival of deer (Verme 1968). Such an effect was widely seen in the study area in February and March 1969. The WSI that winter was 190, and the snow accumulation was the deepest on record (Mech and Frenzel 1971). Surplus killing (Kruuk 1972) by wolves was conspicuous and seemed to be related both to the snow conditions and to reduced viability of the deer (Mech and Frenzel 1971). That was the last winter during which large numbers of deer were seen in the Interior and surrounding areas (figs. 5, 6, 7, and 8). Similar surplus killing of moose by wolves was observed for the first time during the same winter on nearby Isle Royale (Peterson and Allen 1974).

The series of extreme winters, combined with the deteriorating deer habitat resulting from forest maturation and succession, no doubt explains the general decline of deer throughout the Great Lakes Region. However, it does not explain why the loss of deer was total in the Interior Area and why the population did not begin to recover in northeastern Minnesota in 1972 as it did in other parts of Minnesota and in Michigan and Wisconsin.

Role of the Wolf

The main difference in deer ecology between northeastern Minnesota and other areas of the Great Lakes

Region was the presence of a high wolf population in northeastern Minnesota. Based on winter predation rates projected year-round, the estimated average annual kill by wolves is the equivalent of about 18 deer per wolf (Mech and Frenzel 1971, Kolenosky 1972). When use of other prey is considered, the annual rate is estimated at 15 deer per wolf (Mech 1971). At one wolf per 26 km^2 (10 mi^2), which approximates the density present in the Interior Area during winter 1967-68 (Mech 1977b), this amounts to an estimated annual kill by wolves of 1.5 deer per 2.6 km^2 (1 mi^2), or about 2.6 kg (5.6 lb) per wolf per day. However, under some conditions during winter, wolves can consume up to twice as much food (Mech 1966, 1977a).

Furthermore, the wolf density in the Interior Area increased to the following percentages above the 1967-68 level: 21 percent in 1968-69, 46 percent in 1969-70, 9 percent in 1970-71, and 11 percent in 1971-72 (Mech 1977b). Assuming a predation rate of one deer per 15 days per wolf, this could have meant an annual kill of as high as 4.5 adult-sized deer per 2.6 km^2 (1 mi^2) in 1969-70.

The deer density in the area during this study was not estimated by any census. Stenlund (1955) considered the average density for the entire Superior National Forest to be 9.0 deer per 2.6 km^2 (1 mi^2) in 1953, but he felt it to be less in most of the Interior.

Assuming a density as high as 9.0 deer per 2.6 km^2 (1 mi^2), a fall ratio of 100 fawns:100 does, and an even ratio of bucks to does, the annual increment to the fall deer population would be 33 percent, or 3.0 deer/2.6 km^2. With the wolf population consuming an estimated 1.5 to 4.5 adult-sized deer/2.6 km^2, these very general figures indicate that even with a relatively high deer density and annual productivity, wolves at the estimated density could consume the equivalent of an entire annual crop of deer each year.

To test the effect of an increasing wolf population interacting with a deer herd producing decreasing numbers of fawns, we applied the actual data to the simple predator-prey model described earlier. The application of the general model (table 4) yields a prediction of a deer herd declining rapidly to zero by 1972 (fig. 12). (The more sophisticated SNOPOP model yielded the same basic population trend, as discussed in Appendix A.)

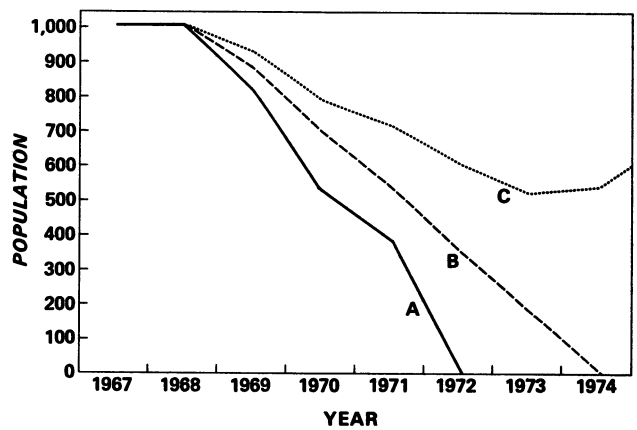


Figure 12. — *Results of model of deer population decline, assuming herd of 1,000 does in 1967 (see table 4). A = result of basic model, applying to the eastern half of the intensive study area (fig. 2); B = result assuming 15 percent less annual kill of deer; C = result assuming 25 percent less annual kill of deer.*

Table 4. — *Basic model of deer decline in the wilderness eastern half of the Superior National Forest, females only*

Year	Fall population of does	Annual increment: Fawns per 1,000 does[1]	Annual increment: Female fawns[2]	Annual increment: Female fawns	Wolf population index[3]	Annual loss: Estimated	Annual loss: Net	New population
			Percent	*Number*				
1967[4]	1,000	850	41	349	1.00	349	0	1,000
1968	1,000	660	36	238	1.21	422	184	816
1969	816	650	43	228	1.46	510	281	535
1970	535	710	36	137	1.09	380	243	292
1971	292	[5]630	[5]41	75	1.11	387	312	0

[1]From table 2. The 1967 figure is the mean of 1963-1967 rates, used to dampen effect of sampling error.

[2]From figure 9.

[3]Derived from Mech (1977b). 1.00 of this index equals 5.7 in figure 2 of Mech (1977b).

[4]The basic assumptions are that the deer population was stable from 1967 to 1968, that 100 percent of the deer mortality in the area was either caused by wolves or utilized by them as carrion, and that the annual loss of deer was proportional to the Wolf Population Index.

[5]Since no figures are available for 1971, the mean for 1968-1972 was used. This mean probably is too high because 1971 was the severest winter on record.

In applying the simple predator-prey model, we made several changes in assumptions to determine the effect that any inaccuracies in our assumptions would have on the final results. One of the most critical assumptions was that the deer population was stable from 1967 to 1968, because future mortality was based entirely on the mortality rate implicit in that assumption. The actual trend from 1967 to 1968 was unknown. However the drop in net production from 90 to 66 fawns per 100 does during those years (table 2) makes it highly probable that the population actually declined. If so, the effect on the model would be to predict depletion of the deer earlier than 1972.

Nevertheless, we tested the assumption that from 1967 to 1968 the deer herd actually increased by 10 percent. The results still predicted depletion, but by 1978 instead of 1972; by 1972 the population would have equalled about 43 percent of the 1968 herd. Furthermore, by using the mean of the fawn:doe ratios from 1963 to 1967 (85 fawns:100 does) for 1967, rather than the actual 1967 ratio (90:100), we dampened the effect any changes in population from 1967 to 1968 might have had.

Another assumption whose effect was tested was that changes in wolf density brought proportional changes in deer mortality, e.g., if wolves increased by 25 percent, so did deer mortality to wolves. To test the effect of inaccuracies in this assumption, we imposed on the model an arbitrary 15-percent decrease in calculated deer mortality for all years after 1967; the result was that the predicted year of depletion was 1975 rather than 1972 (fig. 12). Greater reductions in mortality merely caused later decimation except that reductions of 25 percent or more allowed the population to begin to recover (fig. 12). This recovery trend occurred because in 1973 fawn production returned to pre-decline levels. Thus a 25 percent reduction in annual mortality would preserve enough breeding stock to allow the increased fawn production to more than compensate for the mortality. This point will be discussed later.

In actuality, it appears that rather than deer mortality being reduced proportionally as the wolf population increased after winter 1967-68, such mortality may have increased. Frenzel (1974) found that deer made up a much higher proportion of the wolf's summer diet in the Interior Area in 1968, 1969, 1970, and 1972 (not measured in 1971) than in 1967, as indicated by scat analyses. When this trend was applied to the model, it caused the decline to become steeper and the year of depletion to be earlier than 1972.

The model was also manipulated to see what it would predict if the wolf population had remained stable from winter 1967-68 through 1971-72 instead of increasing but then had declined as it did from 1971-72 through 1974-75. (A bucks-only deer season precluded obtaining fawn production data in 1974, so we assumed that the increased fawn production found in 1973 also held for 1974.) The result was still depletion, but in 1975 instead of 1972.

Our last manipulations simulated reductions in the wolf population by various constants from year to year. Because of the assumption that changes in wolf populations brought proportional changes in deer mortality this manipulation is precisely the same as the arbitrary reductions in deer mortality described above. When the wolf population in the model was reduced by 25 percent each year, the deer population eventually began to recover (fig. 12).

All the above simulations were based on a model of the female segment of the deer population because the fawn production data were collected in numbers of fawns per 100 does. Assuming an equal ratio of bucks to does, the population decline for males would be somewhat slower because males constituted a higher percentage of the fawns than did females (fig. 10). Nevertheless the population would still disappear.

The net result of the various manipulations performed with the model was that, given all the assumptions that we believe reasonable, and the data available, the model always predicted that the deer population in the Interior Area would decline to zero. Generally this would take place by 1972. Even when the assumptions were extended moderately in directions that appear unlikely the hypothetical deer herd would still become extinct but a few years later than with the reasonable assumptions.

In actuality, deer were decimated throughout the Interior Area by winter 1972-73, after the "deer void" had enlarged in radius each winter (figs. 5, 6, and 7). By winter 1974-75, it appeared that the rate of expansion of this void had decreased and that the remnant deer population might have begun to stabilize (figs. 7 and 8).

The model demonstrates what might have happened to the wolf-deer system in the Interior Area, and puts the role of the wolf in the deer decline into sharper focus. It suggests the following hypothesis:

1. Wolf numbers were high at a time when production and/or survival of female fawns dropped markedly

because of forest maturation and a series of extreme winters.

2. Winter 1968-69, with a record snow accumulation, allowed surplus killing by wolves and a consequent increase in wolf numbers.

3. During the subsequent severe winters, then, not only did the fawn:doe ratio and percentage of female fawns remain depressed, but the basic breeding population itself was much reduced. Not only were fewer female fawns per 100 does being produced, but there were fewer does to produce them. This doubly-reduced production accelerated the decline.

4. Meanwhile the larger wolf population was exerting increased pressure on a smaller deer herd. The wolves were still killing primarily older animals and vulnerable fawns during winter (fig. 13), but no doubt they were taking much higher proportions of them than usual. Furthermore, less and less fawn recruitment was available to replace the adults killed.

5. The decreased fawn recruitment might have resulted from increased wolf predation on fawns during summer, for the percentage of fawn remains in wolf scats increased from 10 and 15 in 1967 and 1968 to 50 in 1969 and 1970 (Frenzel 1974). However, fall fawn: doe ratios in 1969 and 1970 were no lower than in 1968. Thus the ultimate factor in the poor fawn recruitment may have been the severe preceding winters, with the wolves merely preying on fawns having a poor chance of surviving anyway.

6. By 1972, deer had begun to decline in importance in the wolf's summer diet, and the use of beaver almost tripled (Frenzel 1974), just as Voigt *et al.* (1976) found during the same period in Ontario. In winter 1973-74, the consumption of moose greatly increased[3]. The change to alternate prey probably had the effect of temporarily subsidizing the wolf population and allowing it to remain larger than it could have on deer alone. This use of alternate prey also allowed the wolves to continue to exert unusual pressure on the reduced deer herd.

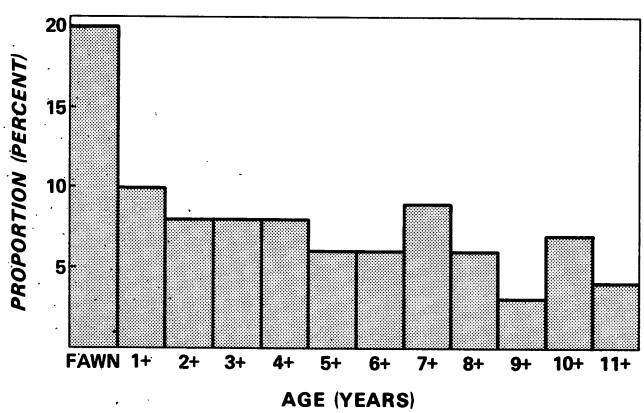


Figure 13. – *Age structure of wolf-killed deer, winters 1970-71 through 1974-75. (No doubt fawns are under-represented here because fawn carcasses are eaten so entirely that usually there are few remains.)*

7. As the prime-age deer that survived the extreme predation pressure grew older and became vulnerable, the wolves depleted their numbers (fig. 13). This fact explains the gradual loss of pockets of wintering deer in the Interior Area (figs. 6 and 7).

8. The tendency of wolves to prey disproportionately on female fawns (Stenlund 1955, Mech and Frenzel 1971) apparently was accentuated (Hoskinson and Mech 1976), thereby further decreasing the proportion of breeders in the deer population. Thus, the males showed a relatively normal age distribution, whereas the females lacked several age classes, at least in the wilderness areas where the effect of wolves was most prevalent (fig. 11). It appears, then, that with a combination of maturing vegetation, severe winters, and intensive wolf predation, it is the female fawns that are the most vulnerable members of a deer herd.

9. As the deer population rapidly diminished, the wolves became increasingly desperate and began concentrating on whatever deer they could find, even if this meant "trespassing" into the territories of other packs (Mech 1972, 1977a, 1977b). This trespassing had several effects: (1) it helped increase the radius of the deer decline outward from the Interior, (2) it put abnormal pressure on the remaining herd outside this area, and (3) it delayed any repopulating of the Interior by deer outside that might otherwise have taken place.

10. Eventually the wolves were still unable to obtain enough food. They began producing fewer young (Mech 1977a, 1977b). The pups they did produce were increasingly underweight (Van Ballenberghe and Mech 1975) and malnourished (Seal *et al.* 1975, Mech 1977a). A disproportionate number of pups were males (Mech 1975).

11. The net result was the extirpation of deer in areas of poorest habitat first. Eventually this decline spread throughout even good habitat. A desperate, declining wolf population (Mech 1977a, 1977b) then continued to exert extreme pressure on the remaining deer around the edges of the "deer void". This pressure helped enlarge the void further.

The deer population model (table 4, fig. 12), then, can be considered to apply earliest to the central Interior Area. In succeeding years, it would apply to an expanding radius around that area, especially as trespasses and migrations of wolves outside the Interior increased wolf density and predation in peripheral areas.

12. However, as the wolf population itself dropped, an estimated 32 percent from 1967-68 to 1974-75, and 55 percent from 1969-70 to 1974-75 (Mech 1977b), its effect on the deer herd diminished. This fact probably explains why the deer decline appeared to be arrested or at least greatly slowed by winter 1974-75 and deer persisted outside the Interior Area.

It is difficult to prove that wolves contributed to the deer decline rather than that they merely took advantage of it. However, several strong pieces of evidence support a hypothesis that wolves did contribute to the decline. First, although reduction of the fawn:doe ratio probably resulted from forest maturation and extreme winters, reduction of the *number* of adult does, i.e., the breeding population, is attributable to wolves. With an adequate fawn crop each year to replace the old deer killed by wolves, this loss would be of no great significance. However, when annual fawn recruitment is poor, wolves must resort to killing a higher proportion of older potential breeders which are not replaced. This doubly disastrous effect accelerates the decline. Without wolves, these older deer could live longer, and despite the loss of several fawn crops, the population could persist. Then when favorable weather again prevailed, the breeders could produce a few good fawn crops and thereby help the herd recover.

Second, comparison of the doe age distributions for the wilderness versus the accessible area indicates that the loss of the 1969-72 age classes was much more extreme in the wilderness area where wolf predation was strongest (fig. 11).

As mentioned earlier, wolves were killed much more often by humans in the accessible area thus reducing wolf predation, there. The deer age-structure sample from that area was basically normal. The sample probably represented primarily deer harvested around well used roads, farms, and other areas less affected by wolves. This region still has a remnant deer herd.

Third, wolves are known to prey disproportionately on female fawns and adult males, as discussed earlier, and comparison of the age structures of the doe and buck samples reflect this predation pattern. In the sample of does taken in 1972 and 1973 in the wilderness, the largest age class was that of 1968 (fig. 11). This age class itself was abnormally low because of the reduced production of fawns that year and the high loss of fawns the following winter (Mech and Frenzel 1971). Despite this fact, the 1969, 1970, and 1972 classes were even lower. In 1975, the 1968 class was 7 years old. Inasmuch as deer vulnerability to wolf predation increases markedly after 5 years of age (Pimlott *et al.* 1969, Mech and Frenzel 1971), many of these deer probably were dead by 1975. Meanwhile, female members of the 1969-72 crops were extremely scarce.

The age structure of the males indicated a high turnover of adult bucks, as evidenced by the relative youth of this sample compared both with the does of about the same period (fig. 11) and with the bucks of 1967 and 1968, before the decline (table 4).

Fourth, the deer herds in Michigan and Wisconsin, which underwent similar declines after the same severe winters, were well on their way to recovery by 1975—unlike those in the study area.

Fifth, a high percentage of the deer that remained adjacent to the Interior lived in narrow strips along the outer edges of wolf pack territories. This distribution of deer persisted both in summer and winter, even though summer and winter ranges were sometimes separated by more than 40 km (25 mi) (Hoskinson and Mech 1976,[1]). Wolf packs tend to kill deer along their territory edges after they have depleted the supply elsewhere in their territory and they become desperate (Mech 1977a). Many of the remaining deer living along territory edges are very old (Hoskinson and Mech 1976), demonstrating that animals that did find an area relatively secure from wolves survived longer. In the Interior Area, however, even deer populations living along territory edges were depleted.

The above facts strongly lead to the conclusion that if wolves had not inhabited the Interior of the Superior National Forest, the deer herd would not have disappeared there, the decline would not have been so drastic in the surrounding area, and any tendency for the deer population to recover would not take so long. In fact, one of the trials with the predator-prey model suggests that if the wolf population had been 25 percent lower each year, beginning in 1968, the deer population would have begun to recover by 1973 (fig. 12), as herds did elsewhere.

The conclusion that wolves were one of the main causes of the deer decline in the Superior National Forest will seem trite to many laymen. Certain local residents and many deer hunters have long maintained that wolves were "killing off all our deer". However, we believe that this paper is the first documentation of such a conclusion. Most of the literature on wolf-prey relations has shown that wolves usually do not deplete

their prey populations (Murie 1944, Stenlund 1955, Mech 1966, 1970, Pimlott *et al.* 1969, Kolenosky 1972). Furthermore, logic dictates that if a predator depletes its prey resource over a large enough area, the predator-prey system cannot persist.

The question of the effect of wolf predation on deer populations has been considered by Stenlund (1955), Pimlott (1967), and Mech (1970). However, none of these authors addressed the question of whether wolves could deplete their prey population. Rather, all discussed the ability of wolves to control their prey, and all dealt with more deer per wolf than existed in our study area during the deer decline. Mech (1971) also considered the possible role of the wolf as a competitor with human hunters in accessible areas, but he too assumed a greater ratio of deer per wolf, as is usually the case.

Both Pimlott (1967) and Mech (1970) emphasized that the greatest limiting effect of wolves probably would be through predation on young animals. However, during our study it appeared that predation on old animals was also extremely important in that it reduced the breeding population while there was insufficient fawn recruitment to replace it (fig. 13).

Conceivably the drop in the fawn:doe ratio also was attributable to wolves. However, because this decrease coincided with a series of severe winters and also took place in relatively wolf-free areas (fig. 9), the wolf's role in the fawn crop reduction perhaps was incidental. It is also conjectural how much winter wolf predation on fawns was facilitated by the severe weather during the previous year, when the fawns were fetuses, or during the fawns' first winter. Nevertheless, the apparent predisposition of wolves to take female fawns, during winter at least, and the striking scarcity of female members of the 1969 through 1972 age classes in the wilderness area (fig. 11), suggest the important effect of wolves in fawn predation also.

Because this study describes a situation contrary to most other reports, it is important to emphasize the peculiar combination of circumstances that allowed the present situation to occur. It seems safe to speculate that if the vegetation in the study area were not passing its prime as deer habitat, the mere combination of severe winters and wolf predation would not have had such an extreme result. Evidence for this contention is the fact that deer first disappeared from the region of poorest habitat—the virgin forest. No doubt better habitat would have supported a higher deer density with greater productivity. Then even with severe winters and intensive wolf predation, a larger base population would have been available to resist depletion and to begin recovery.

Or even with maturing vegetation and gradually declining productivity, plus substantial wolf predation, the deer herd probably would not have dropped so precipitously if the series of winters had not been so severe. The severe winters apparently reduced deer productivity far more drastically than the declining habitat, in addition to decreasing the general survivability of deer and increasing deer vulnerability to wolves.

From this analysis, and from the fact that deer herds so seldom disappear, we can conclude that deer populations are remarkably resilient. Only when such important factors as declining habitat, inclement weather, and intensive predation are combined for several consecutive years are local herds unable to survive. It seems significant that the only other report we can find of wolves seriously reducing their prey populations also involved the same combination of detrimental circumstances (Rausch and Hinman 1977).

Future of the Wolf-Deer System

If the disappearance of deer continues to spread throughout the Superior National Forest and northeastern Minnesota, the wolf population there must decline, just as it has already in the Interior Area (Mech 1977a, 1977b). Nevertheless, wolves will be able to survive on moose, supplemented in spring, summer, and fall by beavers, although a much lower wolf density can be expected.

However, there are some promising signs that the deer population may now be holding its own or may even be starting to recover in the study area. After the relatively mild winter of 1972 to 1973, the fawn:doe ratio in Lake and Cook Counties increased to 85, and 52 percent of the fawns were females, the highest ratios for 6 years. That was the last year in which data on such ratios could be obtained because of the bucks-only hunting season, but records of three sets of fawn triplets in the study area during summer 1974 may indicate another year of high production of fawns.

In addition, two of the heaviest fawns on record were live-trapped in the study area in 1973 (Hoskinson and Mech 1976).

Blood samples taken from 1973 through 1976 from 44 deer in the central and eastern Superior National Forest indicated they were in moderately good to excellent condition (Hoskinson and Mech 1976[9]).

The wolf population also declined substantially (Mech 1977b), which reduced the predation pressure. The survivability of the deer remaining in 1973 and 1974 was much higher than in previous years (Hoskinson and Mech 1976). A few deer apparently even began to repopulate part of the Interior Area in winter by 1974-75, although some ended up as kills (fig. 7).

On the negative side, the wolves' resistance to decline, and their ability to respond to any local or temporary availability of prey by an increase in numbers, is considerable (Mech 1977b). This ability could hinder the deer population recovery. Furthermore, the future of the deer herd also depends greatly on the vagaries of winter weather during the next few years.

Of greatest ultimate importance, of course, is the habitat problem. Without considerable increase in logging and/or fires throughout the Superior National Forest, the long-range outlook for deer is dim. Moreover, any prolonged diminution in the deer herd will very probably result in reduced wolf numbers.

Authors' Note: The wolf-deer models described in this bulletin should not be confused with the wolf-deer model publicized in late 1976 in the popular press (Schara 1976). The models, data bases, and conclusions presented herein apply only to the areas and periods described and should not be extended without sufficient corroborating data.

[9] *Seal, U. S. Manuscript in preparation at U.S. Veterans Administration Hospital, Twin Cities, Minnesota.*

APPENDIX A

The Minnesota Department of Natural Resources deer population management model (SNOPOP) was applied by the junior author to the data available for the deer and wolf population of Department of Natural Resources Grid Blocks 23-26, 38, and 39 (fig. 2) from 1971 to 1976. The model assumes an average deer density of 2.3 deer per km^2 (6 deer/1 mi^2) and a predation rate of 15 to 20 deer per wolf per year. It also uses deer age structure as indicated by the hunter kill, productivity as indicated by fetus counts of road-killed deer, and direct winter kill based on actual mortality rates found in an adjacent area and correlated with the WSI.

The model indicates that without wolf predation the deer herd would have declined very little by 1976 but that with the known wolf densities the deer population would drop to less than 0.4 deer/km^2 (1/mi^2) (fig. 14).

SNOPOP is considerably more sophisticated than the simple predator prey model presented in the text (table 4, fig. 12), but it again points out the effects of wolf predation and severe winters on the deer population of northeastern Minnesota.

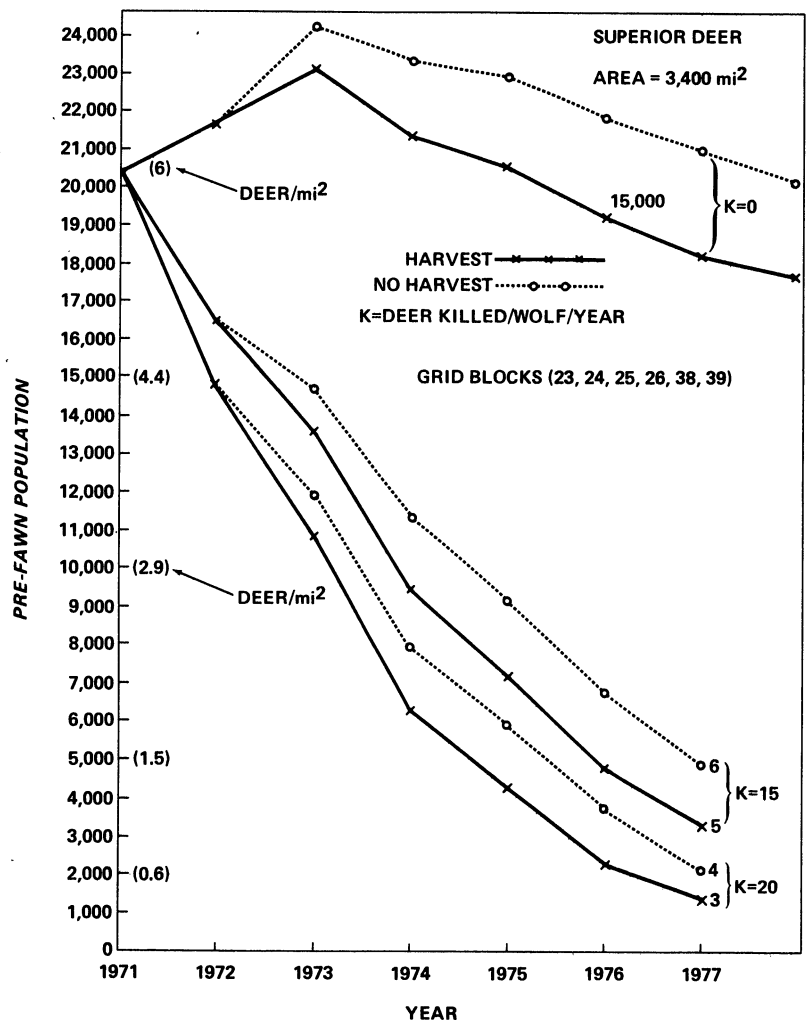


Figure 14. – *Minnesota Department of Natural Resources "SNOPOP" model of the northeastern Minnesota deer population used by the junior author to test the effect of intensive wolf predation during a period of high winter kill of deer.*

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OXFORD: 149.74 *Canis lupus*:149.6 CERVID. KEY WORDS: predation, prey, Minnesota, winter severity.

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Birds, animals and flowers are dying to tell us...no pollution, please!