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# A HISTORY AND CURRENT ESTIMATE OF WOLF DISTRIBUTION AND NUMBERS IN MINNESOTA

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The eastern timber wolf (*Canis lupus lycaon*) formerly occurred throughout most of the eastern United States and southeastern Canada, but by 1965, it inhabited only 3% of its former range in the U.S. outside of Alaska (Bailey 1978). In 1967, the eastern timber wolf was listed as "endangered" in the contiguous U.S. and was completely protected by the Federal Endangered Species Act of 1973 in August 1974. In addition, the Eastern Timber Wolf Recovery Plan was developed "for the maintenance, enhancement, and recovery of this subspecies throughout as much of its present and former range as feasible" (Bailey 1978).

Specific recovery objectives and progress toward recovery might best be assessed by reviewing historical population levels and trends (Gunson 1992). Herein, we present information on the distribution and numbers of wolves in Minnesota since 1950. We also estimate current wolf range from a survey of wolf observations made mostly by government natural resource personnel in Minnesota during winter 1988–1989 and from road and human population density and distribution data. These results are combined with wolf demographic data and estimated densities of white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*) to obtain a statewide estimate of wolf numbers in 1989.

## HISTORICAL DISTRIBUTION AND NUMBERS

### *Range Changes Through the 1940's*

Before settlement by Europeans, wolves inhabited all of Minnesota, although the eastern timber wolf probably intergraded with the buffalo wolf (*C. l. nubilus*) along the prairie-forest border (Young and Goldman 1944, Mech and Frenzel 1971). Bounty payments began in 1849, and by 1900, wolves were rare in southern and western Minnesota (Herrick 1892, Surber 1932). Wolf range decreased further between 1915 and 1941 (Young and Goldman 1944), and highest wolf densities (39 wolves/1,000 km$^2$; Olson 1938) occurred in remote areas of the northern third of the state (Surber 1932:55).

### *Numbers and Range: 1950–1952*

During 1948–1953, Stenlund (1955:19) estimated that 205–273 wolves occupied 10,620 km$^2$ of the Superior National Forest (SNF) in northeastern Minnesota (19.3–25.7 wolves/1,000 km$^2$), a density 33–51% less than that estimated by Olson (1938) there during the

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1920's and 1930's. Stenlund also extended this density to an additional 7,500 km² of adjacent wolf range and indicated that "between 300 and 400 wolves" lived in the 3 northeastern-most counties of Minnesota (18,120 km²). Stenlund (1955:13–14) did not estimate wolf numbers on the 12,960 km² of "major" wolf range (". . . timber wolves are seen occasionally, sign is relatively common, and the animals breed and raise their young in this area") he outlined in the northwest part of the state (Van Ballenberghe 1974). However, the wolf bounty rate there averaged 4.2 wolves/1,000 km², 80% of that in the northeast (Minnesota Dep. Nat. Resour. [MDNR] files, St. Paul, Minn.). If wolf density in the northwest part of the state was even half of that in the northeast (approximately 10–13 wolves/1,000 km²), then the population was perhaps 130–170. Therefore, numbers of wolves in all major range (31,080 km²) would have been at least 430–636. Some wolf packs also lived as much as 120 km south of major range (Stenlund 1955:13), and if these comprised an additional 5–10% of the population, the statewide total was perhaps 450–700.

### *Harvest, Range, and Numbers: 1953–1965*

From 122 to 252 wolves ($\bar{x}$ = 189) were submitted for bounty annually during 1953–1959 (not including the additional harvest by MDNR personnel that continued until 1956), which was less than the number submitted during 1950–1952 ($\bar{x}$ = 253; MDNR files, St. Paul, Minn.). During 1960–1965, 171–211 wolves ($\bar{x}$ = 186) were submitted for bounty annually, and, compared to 1950–1952, fewer were submitted for bounty south and west of what Stenlund (1955:13) considered major wolf range (MDNR files, St. Paul, Minn.). Based on limited, subjective interviews with state and federal biologists, Cahalane (1964) estimated that the wolf population in Minnesota in 1963 numbered 350–700 and was restricted to the northeastern-most part of the state.

### *Harvest, Range, and Numbers: 1966–1972*

Wolves still could be killed year-round after bounties were ended in 1965, and during 1966–1973, estimated annual harvest was approximately 200 (MDNR files, St. Paul, Minn.). In addition, during 1969–1974, some trappers were authorized by the new MDNR Directed Predator Control Program to kill wolves in areas of verified livestock losses (Fritts 1982:3); an average of 64 (range = 18–92) wolves were killed annually under this program (MDNR files, St. Paul, Minn.).

The statewide wolf population was first officially assessed in 1970 at the request of the MDNR Commissioner; a questionnaire survey asked MDNR game management and enforcement personnel to provide their best estimate of wolf numbers and range. Results indicated that the population numbered 750 (Leirfallom 1970, Nelson 1971), and major wolf range (38,400 km²) was somewhat larger than outlined earlier by Stenlund (1955:14). Based on the opinions of MDNR field personnel who were most knowledgeable about wolves (i.e., game managers and conservation officers), statewide wolf numbers had declined during the 1950's and early 1960's, but after the bounty was terminated, wolf numbers remained stable or increased moderately (MDNR files, St. Paul, Minn.).

The 1970 population estimate was questioned during a joint agency meeting in March 1972 (MDNR files, St. Paul, Minn.) because of its subjectivity and has remained somewhat suspect. However, we evaluated the estimate using results from an unpublished March 1972 survey (M. Nelson, MDNR files, St. Paul, Minn.). Nelson queried 42 MDNR conservation officers and 22 MDNR game managers and biologists in northern Minnesota regarding wolf distribution during 1965, the 1972 wolf population trend, and the number of wolves killed by legal harvest in 1970–1971 and 1971–1972. The survey results implied that wolf distribution in 1965 (as indicated by presence or

absence of wolves in each work area) was similar to that determined from bounty records and that wolf distribution apparently did not change substantially between 1965 and 1972. However, wolf numbers were reported to have increased in work areas of 22 of 51 (43%) respondents. MDNR conservation officers were aware of a legal wolf harvest of at least 146 in 1971 and 174 in 1972. Adding the kill by the Directed Predator Control Program in 1971 and 1972 (60 and 92 wolves, respectively; MDNR files, St. Paul, Minn.), total human-related kill was at least 206 and 266 wolves, respectively. If wolf numbers were not decreasing, then harvest mortality probably amounted to 28% or less (Fuller 1989), suggesting the wolf population numbered at least 736–950 in the early 1970's, similar to the 1970 estimate.

### *Numbers and Range: 1973–1983*

Under federal legislation, wolves were classified as an "endangered species" in 1966, and completely protected on the SNF in 1970 by supervisory decree (Van Ballenberghe 1974) and in all of Minnesota in 1974 by the revised Endangered Species Act of 1973. Wolf numbers in some areas quickly increased as a result of this protection (Fritts and Mech [1981] in the northwest), but they declined in a portion of the northeast, likely because deer numbers declined (Mech 1986). In 1973, wolf numbers in Minnesota were tentatively estimated to be 500–1,000 (Mech and Rausch 1975). The Eastern Timber Wolf Recovery Plan included a 1976 population estimate by L. D. Mech (Bailey 1978:50–52). He extrapolated telemetry-obtained wolf densities in 3 areas with ongoing wolf studies (Mech 1973, Fritts and Mech 1981, Berg and Kuehn 1982) to a range-wide estimate of 1,000–1,200 wolves.

In winter 1978–1979, information on wolf presence and density was obtained from MDNR wildlife biologists and managers, conservation officers, foresters, and parks personnel across the Minnesota wolf range, and from U.S. Forest Service forestry and wildlife personnel on the SNF (Berg and Kuehn 1982). All persons with field experience in their respective work areas were requested to map the areas occupied by wolves and to estimate the number of wolves in each area based on their best knowledge. There were 480 reports of wolves or their sign (64% of which were provided by MDNR wildlife managers and biologists), including wolf tracks (39%), direct observation of wolves (15%), radiotelemetry studies (6%), kill sites (4%), captured or dead specimens (2%), and howling (<1%); the specific source of information was not reported for 32% of observations. Excluding reports for which no group size was recorded ($n$ = 88), packs ($n$ = 303) were reported more frequently than single wolves ($n$ = 89). These 480 reports of pack size and location were mapped along with telemetry data from existing or recently completed studies (Mech 1973, Fritts and Mech 1981, Berg and Kuehn 1982) and extrapolated to areas without data, then summed to derive a statewide population estimate of 1,235 wolves, major ("primary") range of 36,500 km$^2$, and "peripheral" range (more developed and higher road access) of 55,600 km$^2$ (Fig. 1; Berg and Kuehn 1982).

In 1978, wolves in Minnesota were reclassified as "threatened" (U.S. Fish and Wildl. Serv. 1978), allowing federal and state authorities to kill them when livestock depredation was verified (Fritts 1982). In winter 1982–1983, Mech et al. (1988) queried northern Minnesota canid trappers regarding wolf distribution. These data, combined with the authors' knowledge of wolf distribution derived from conducting research and control programs, resulted in delineation of an estimated 59,900 km$^2$ of wolf range occupied by pairs or breeding packs of wolves. Subtracting the area of several large lakes that clearly were not wolf range, the resulting 57,050 km$^2$ of "occupied" range is still almost double that estimated by Stenlund (1955:14). Within this

region, the authors identified some areas without wolves; they also delineated an additional 40,500 km$^2$ of peripheral range that had habitat similar to contiguous occupied range and where no wolves or only lone wolves existed. In addition, results of Mech et al. (1988) supported findings of Thiel (1985) and Jensen et al. (1986) that suggested wolf survival was lower and wolf distribution was limited where road densities exceeded about 0.6 km/km$^2$, presumably because of enhanced levels of human access and thus human-caused mortality.

## CURRENT DISTRIBUTION AND NUMBERS

### *Methods*

In October 1988, under the auspices of the MDNR Commissioner, we requested that all field personnel in the MDNR Divisions of Fish and Wildlife, Forestry, Enforcement, Parks and Recreation, Waters, Minerals, and Trails and Waterways in the northern 66% of Minnesota record and submit the locations and numbers of wolves and wolf sign (e.g., scats and tracks) seen from November 1988 to March 1989. Knowledge of areas where wolves definitely were not present (wolves or their sign never seen or reported) also was solicited. The same request was made of federal government field stations (U.S. Department of Agriculture [USDA], Forest Service; U.S. Department of Interior, Fish and Wildlife Service [USFWS]; and National Park Service), forest products industry personnel, and northern county land departments. In addition to these winter observations, we recorded locations of wolf tracks noted on a statewide scent station survey during September 1988 (W. Berg, unpubl. data) and tallied wolf sign verified in summer and autumn 1988 by personnel of the USDA, Animal and Plant Health Inspection Service–Animal Damage Control (APHIS–ADC) wolf depredation program (W. Paul, unpubl. data, Grand Rapids, Minn.).

We recognize that the reliability of these observations is dependent on correct identification of wolves and wolf sign in the field. Coyotes (*C. latrans*), the only species whose physical appearance could reasonably be confused with that of wolves, occur throughout much of northcentral Minnesota (Berg and Chesness 1978). Although coyote tracks are significantly smaller than those of wolves, tracks of some large domestic dogs may be confused with those of wolves (Harris and Ream 1983). However, we believe that government natural resource personnel we queried most often were able to distinguish observations or sign of wolves and coyotes because of the disparity in size of body, tracks, and scats (designated criterion for wolf scat >2.5 cm diameter; Thompson 1952, Weaver and Fritts 1979) of the 2 species, as well as their difference in winter group/pack size (Berg and Chesness 1978, Fritts and Mech 1981, Fuller 1989). Tracks of large domestic dogs may have been more difficult to distin-

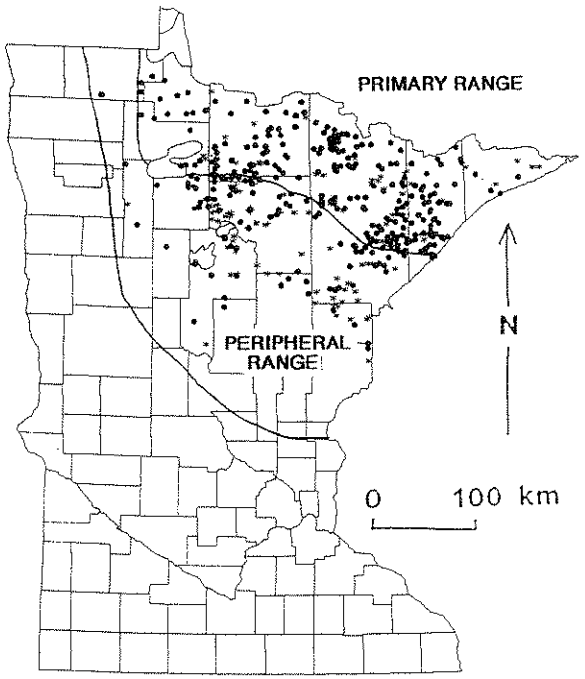


Fig. 1. Boundaries of major ("primary") and "peripheral" wolf range in Minnesota (Berg and Kuehn 1982:5) estimated from distribution of wolves or wolf sign (● = packs, * = single wolves) reported in 1979 (W. Berg and D. Kuehn, Minnesota Dep. Nat. Resour., Grand Rapids, unpubl. survey).

guish from those of wolves, but government natural resource personnel often are attuned to the presence of dogs in the forest because of their potential impact on deer in winter (Kreeger 1977). Most dogs are found near, and can be tracked to, residences, and groups of dogs often are composed of individuals whose size and tracks vary considerably. Still, some sign or observations of dogs or coyotes may have been ascribed to wolves, but we do not believe that these mistakes compromised the conclusions we have reached concerning wolf distribution in the state.

We also asked all participants to complete questionnaires for their work areas, indicating (1) if wolf numbers were nonexistent, low, medium, or high (a subjective, relative appraisal); (2) if in the last 5 years, the wolf population had decreased, increased, remained stable (a subjective, relative appraisal), or if no information was available; and (3) the number of persons contributing observations. A reminder was sent in March 1989 requesting responses be returned by 15 April 1989.

Wolf observation/location data from all sources were geographically coded to Universal Transverse Mercator Grid coordinates. Responses to the questionnaire were geographically coded to the approximate center of the work area of each observer or group of observers.

Observations were tallied by type and affiliation of observer and separated into those of packs or single wolves. For each observation of a pack or single wolf, the density of roads and human population in the corresponding township ($\sim$93 km$^2$) was recorded, based on data included in the Minnesota Land Management Inventory System (MLMIS), a statewide geographic information system (GIS). For these analyses, we included only permanent roads requiring routine maintenance that were accessible year-round by 2-wheel-drive vehicles. Human population densities were extrapolated from the 1980 U.S. Department of Commerce Census of Population and Housing data (U.S. Dep. Commerce 1982).

Wolf range occupied by breeding packs was delineated by first identifying all townships where packs or sign of packs was observed during 1988–1989. These data suggested that there was a southern and western limit of the contiguous range of wolf packs. In addition, townships north and east of this line that were similar in road and human population density to those where wolf packs were documented also were designated as occupied range. These usually were remote areas where no observers searched for wolf sign in 1988–1989 but where wolves generally were acknowledged to be present or had been present during previous surveys. Contiguous areas $\geq$200 km$^2$ (about 2 townships or 1 pack territory) south and west of the major occupied range that had road and human densities similar to areas with pack wolves were classified as potential wolf range (i.e., areas that could support wolf packs in the future).

Current statewide wolf numbers were estimated using 2 independent methods. First, we estimated the total number of packs in the state by (1) summarizing Minnesota telemetry data on winter wolf pack territory size, (2) estimating mean territory size and mean area of interstices among pack territories, (3) dividing total occupied wolf range by the mean area occupied per pack, and (4) multiplying the number of packs by the mean mid-winter pack size to estimate the total number of pack wolves present. This number was then increased to include the approximate percent (15%) of wolves not affiliated with packs (Fuller 1989).

We also estimated wolf numbers using the relationship found across North America between wolf density and ungulate biomass availability ($R^2 = 0.72$, 23 df, $P < 0.0001$; Fuller 1989:21). We calculated the number of deer and moose present in occupied wolf range and extrapolated to an estimate of total wolf numbers using the equation:

Table 1. Observations of wolves and wolf tracks, scats, and other sign in Minnesota reported by state, federal, county, and private natural resource personnel during 1988–1989.

| Affiliation | Observers | | Number of observations | | | | | Total observations | |
|---|---|---|---|---|---|---|---|---|---|
| | *n* | % | Tracks | Wolves | Ungulate kill site | Scats | Other[a] | *n* | % |
| Minnesota Dep. Nat. Resour. | | | | | | | | | |
| Wildlife | 74 | 20 | 150 | 54 | 15 | 17 | 6 | 242 | 19 |
| Forestry | 71 | 20 | 228 | 41 | 11 | 9 | | 289 | 23 |
| Parks | 42 | 12 | 74 | 16 | 5 | 9 | 1 | 105 | 8 |
| Enforcement | 30 | 8 | 29 | 9 | 2 | 1 | 4 | 45 | 4 |
| Trails and waterways | 21 | 6 | 38 | 5 | | 2 | | 45 | 4 |
| Other | 6 | 2 | 12 | 3 | | 2 | | 17 | 1 |
| Subtotal | 244 | 67 | 531 | 128 | 33 | 40 | 11 | 743 | 60 |
| U.S. For. Serv. | 38 | 10 | 82 | 17 | 6 | 6 | | 111 | 9 |
| U.S. Fish and Wildl. Serv. | 17 | 5 | 47 | 13 | | | 11 | 71 | 6 |
| U.S. Park Serv. | 9 | 2 | 11 | 9 | | | 6 | 26 | 2 |
| U.S. Dep. Agric.–APHIS | 3 | 1 | 63 | 1 | | | 6 | 70 | 6 |
| Subtotal | 67 | 18 | 203 | 40 | 6 | 6 | 23 | 278 | 22 |
| County land departments | 32 | 9 | 142 | 23 | 8 | 3 | 5 | 181 | 15 |
| Private paper companies | 6 | 2 | 14 | 5 | 2 | | | 21 | 2 |
| Other[b] | 13 | 4 | 5 | 12 | 2 | 1 | 1 | 21 | 2 |
| Grand total | 362 | 100 | 895 | 208 | 51 | 50 | 40 | 1,244 | 100 |

[a] Includes wolves captured or found dead ($n = 15$), packs studied by radiotelemetry ($n = 18$), howling ($n = 5$), and den sites ($n = 2$).
[b] Includes trappers and other private individuals ($n = 12$) and Minnesota Department of Transportation ($n = 1$).

$$Y = 3.4 + 3.7X, \quad (1)$$

where $X$ = deer-equivalent units/km$^2$ (deer = 1 unit, moose = 6 units) and $Y$ = the number of wolves/1,000 km$^2$ (Fuller 1989:21). Early winter deer densities in 5 deer management units were estimated using a deterministic model similar to that described by Lenarz (1987, 1991) that integrates age- and sex-specific mortality rates (Fuller 1990), age-specific reproductive rates (M. Lenarz, unpubl. data), and registered harvest (M. Lenarz, unpubl. data). The model is sensitive to starting density, and the fact that the model estimates the harvest of adult males (1984–1989) within 0–22% ($\bar{x} = 8\%$; M. Lenarz, unpubl. data) implies that the density estimates are fairly accurate. Moose density in 3 survey areas was estimated from aerial surveys following standardized methodology (Gasaway et al. 1986); in peripheral moose range, density was assumed to be 1 moose/50 km$^2$ (Fuller 1986).

## *Results*

*Distribution.*—Because our request for information was sent to field station addresses and >1 field person often worked at each station, we have no record of the number of potential respondents to our survey. However, observations of wolves or wolf sign were submitted by 362 individuals, of whom 67% were MDNR employees (Table 1), and we have no reason to believe there was a nonresponse bias that would affect our conclusions. Most (72%) of the 1,244 observations were of wolf tracks, but wolves were seen 218 times (18%). Overall, observations of wolf packs (56% of "groups" of ≥1 wolf) and wolves in packs (82% of all wolves) were more common than those of single wolves.

Both observation data and questionnaire results indicated a limit of contiguous range occupied by wolf packs (Fig. 2A), although some packs were found south of this line. Single

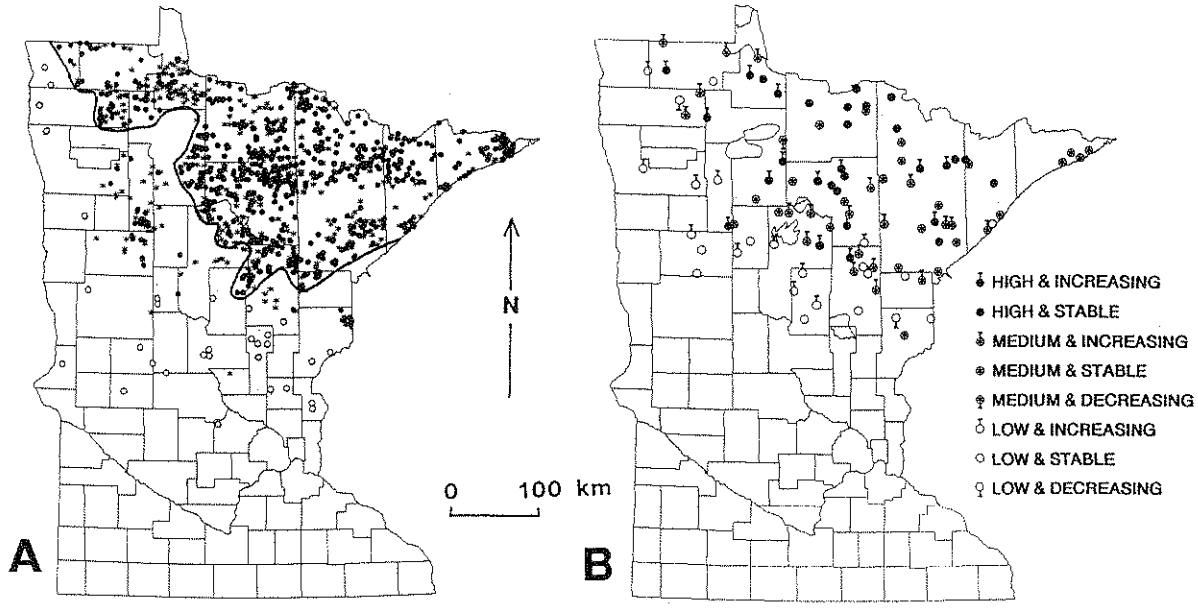


Fig. 2. (A) Distribution of wolves and wolf sign observed in Minnesota during 1988–1989 (● = packs, * = single wolves) and areas where no wolves occurred (o), and estimated southern and western limit of contiguous range occupied by wolf packs (solid line); and (B) subjective estimates of wolf population density and change (plotted at centers of work areas) by state, federal, and county natural resource personnel during 1988–1989.

wolves were observed throughout this range, but proportionately more were observed at the southern edge; also, the wolf population there was perceived as lower but increasing compared with other parts of wolf range (Fig. 2B).

In general, wolves occurred where both road density and human density were low; 88% of packs and 81% of single wolves were in townships with <0.70 km roads/km² and <4 humans/km² or with <0.50 km roads/km² and <8 humans/km² (Pearson's $\chi^2 = 5.29$, 1 df, $P < 0.0215$; Table 2). It should be noted that because of the nature of observers' activities, many records (a few of which may have been of large dogs) were obtained on or adjacent to roads and thus biased towards areas with relatively higher densities of roads and humans.

In addition to the townships known to be occupied by wolf packs (29,400 km²), many adjacent townships to the north of the limit of contiguous range occupied by wolf packs (23,700 km²) had road densities <0.70 km/km² and human population density <4/km², or road densities <0.50 km/km² and human

Table 2. Number of observations of packs and single wolves in townships of varying mean road and human population densities reported in Minnesota during winter 1988–1989 (Fig. 2A). Numbers in italics indicate 88 and 81% of pack and single wolf observations, respectively.

| Road density (km/km²) | Humans/km² | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Packs ($n$ = 643) | | | | | Single wolves ($n$ = 506) | | | | |
| | <1 | 1–<2 | 2–<4 | 4–<8 | ≥8 | <1 | 1–<2 | 2–<4 | 4–<8 | ≥8 |
| <0.50 | *301* | *84* | *23* | *20* | 2 | *187* | *66* | *21* | *18* | 6 |
| 0.51–0.60 | *35* | *28* | *11* | 6 | 0 | *35* | *25* | *16* | 4 | 1 |
| 0.61–0.70 | *29* | *25* | *14* | 3 | 0 | *29* | *18* | *10* | 4 | 0 |
| 0.71–0.80 | 2 | 5 | 5 | 5 | 3 | 6 | 11 | 6 | 4 | 0 |
| 0.81–0.90 | 4 | 9 | 3 | 5 | 4 | 1 | 6 | 5 | 8 | 2 |
| >0.90 | 3 | 2 | 4 | 3 | 5 | 2 | 3 | 5 | 5 | 2 |

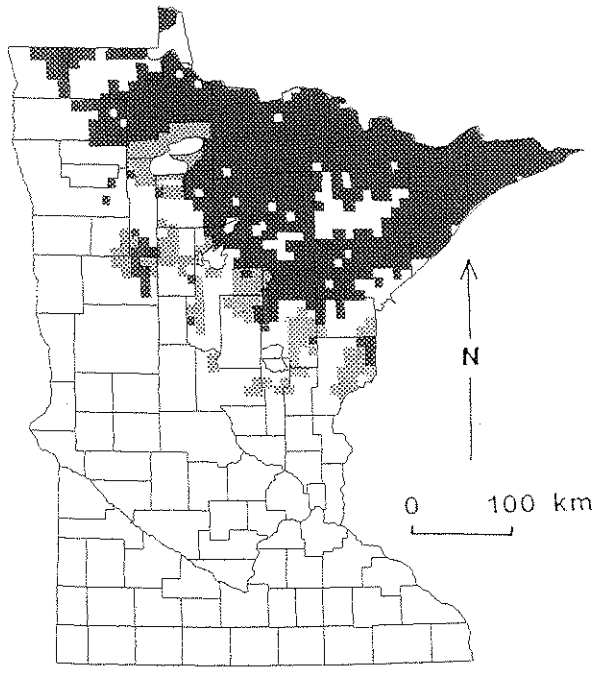


Fig. 3. Minimum estimated wolf range occupied by packs in Minnesota (dark shading) during 1988–1989, range that has potential to be occupied by packs in the near future (road density <0.70 km/km², and human density <4 humans/km²; light shading), and areas without wolves that do not have the potential to be occupied by packs (no shading).

population density <8/km². Thus, we estimated that ≥53,100 km² were occupied by wolf packs in 1988–1989 (Fig. 3). High road or human densities likely precluded the presence of wolf packs in several localities (~8,000 km²) within contiguous, occupied wolf range. Furthermore, some groups of townships south of the major occupied wolf range had road densities (<0.70 km/km²) and human densities (<4/km²) low enough that they may be occupied by packs in the future; this amounted to about 11,500 km². Much of this potential range is inhabited by single wolves, and wolf packs likely live in some areas where observations were not recorded. Thus, our estimate of the distribution of packs, and consequently wolf numbers (below), is conservative.

*Numbers.*—Since the late 1960's, wolves have been studied using radiotelemetry in almost all of Minnesota's wolf range (Table 3). Individual winter pack territories ranged in size from 40–664 km² but generally averaged 100–250 km² within study areas (Table 3); unweighted mean territory size for all studies was

Table 3. Territory size (km²) and mean mid-winter pack size determined from radiotelemetry studies of wolves in Minnesota, 1970–1989.

| Area | Years | Territory size | | | Pack size | | Reference |
|---|---|---|---|---|---|---|---|
| | | $\bar{x}$ | Range | $n$ | $\bar{x}$ | Range | |
| Northeast | 1971 | 110 | 52–145 | 5 | 8.0 | 5–10 | Van Ballenberghe et al. (1975) |
| | 1970–1973 | 186[a] | | 11 | 7.5 | 3–15 | Mech (1973) |
| | 1984–1985 | 183[b] | 59–323 | 9 | 5.3 | 4–7 | Mech (1986) |
| | 1988–1989 | 142 | 66–274 | 10 | 7.9 | 4–13 | L. D. Mech, U.S. Fish and Wildl. Serv., St. Paul, Minn., unpubl. data |
| Northcentral | 1974–1979 | 215[b] | 161–272 | 5 | 6.6 | 5–8 | Berg and Kuehn (1980, 1982) |
| | 1981–1986 | 116 | 51–223 | 33[c] | 5.7 | 2–12 | Fuller (1989) |
| | 1983–1986 | 87[d] | 40–135 | 3 | 2.7[d] | 2–4 | Fuller (1989) |
| Northwest | 1972–1977 | 260[b,e] | 77–664 | 22[c] | 4.6[e] | 2–9 | Fritts and Mech (1981) |
| North | 1988–1989 | | | 5 | 4.6 | 2–8 | P. Gogan and W. Route, Natl. Park Serv., International Falls, Minn., pers. commun. |
| East | 1979–1988 | 196 | 67–310 | 5 | 2.6 | 2–4 | R. Thiel, Wis. Dep. Nat. Resour., Tomah, Wis., pers. commun. |

[a] Mean territory size = size of survey area (2,806 ha) ÷ number of packs (11) × correction factor to account for average area between territories (0.73).
[b] Territory size recalculated from figures.
[c] Some packs represented more than once (i.e., in different winters).
[d] Newly formed territories outside main study area.
[e] Newly established population.

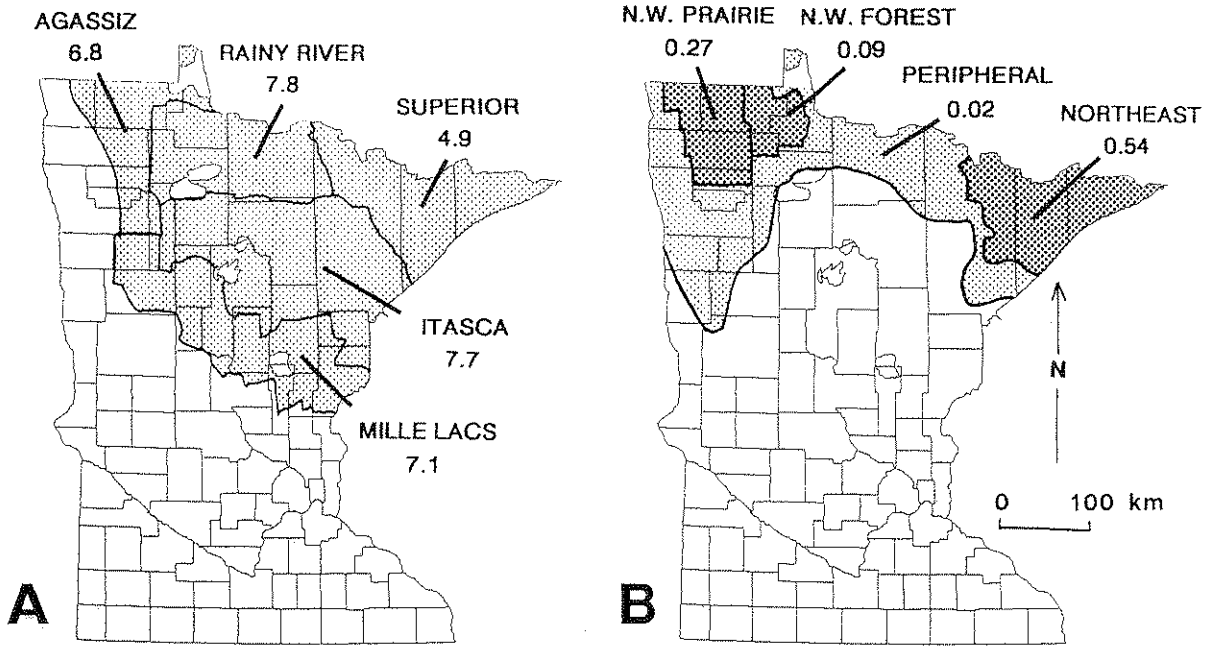


Fig. 4. Location of (A) deer management units and (B) moose survey areas and peripheral moose range used to calculate total ungulate biomass within occupied wolf range in northern Minnesota. Numbers indicate mean ungulate density (no./km$^2$) within each unit.

166 km$^2$ (90% CI = 133–200). Because packs are territorial, some areas between territories contain no pack wolves. These areas amounted to an additional mean of 37% (90% CI = 11.5) of areas encompassed by territories in north-central (31 and 45%; Fuller 1989: Fig. 1), northeastern (28–61%; Mech 1986: Fig. 1; L. D. Mech, U.S. Fish and Wildl. Serv., St. Paul, Minn, unpubl. data, 1988–1989), and northwestern Minnesota (17–40%; Fritts and Mech 1981: Figs. 12 and 13). On average, therefore, wolf packs in Minnesota occur at a density of about 1/228 km$^2$ of occupied range (166 × 1.37; 90% CI = 195–261). Given the conservative estimate of 53,100 km$^2$ of wolf range in Minnesota occupied by packs, the minimum number of packs is 233 (53,100/228; 90% CI = 203–272). Again, this estimate does not include packs that might occur in potential wolf range.

Sizes of individual packs in winter ranged from 2–15 but generally averaged 3–8 within study areas (Table 3). Unweighted mean pack size for all studies was 5.55 (90% CI = 4.5–6.6), and the calculated total of pack wolves is 1,293 (233 × 5.55; 90% CI = 1,137–1,498). If an estimated 15% of the population is composed of lone wolves, the minimum mid-winter number of wolves is 1,521 (1,293 ÷ 0.85; 90% CI = 1,338–1,762).

Wolf numbers also were estimated using ungulate abundance data. Modeling indicated that the weighted mean early-winter deer density in 1988–1989 was 6.83/km$^2$ for the portions of the 5 major northern deer management units (Fig. 4A) within occupied wolf range, and thus about 362,673 deer (6.83 × 53,100) lived there. Similarly, about 8,500 moose (weighted $\bar{x}$ = 0.24/km$^2$) lived in survey areas and peripheral range (Fig. 4B) encompassed by occupied wolf range (35,400 km$^2$). Thus, the total number of deer-equivalent units in occupied wolf range was 413,673 (362,673 + (8,500 × 6)), or 7.79/km$^2$. Using equation (1), wolf density would average 32.2/1,000 km$^2$, thus a wolf population of 1,710 (32.2 × 53.1). Assuming the un-

Table 4. Historical estimates of the wolf population and area of wolf range occupied by reproducing packs in Minnesota, 1950–1989.

| Years | Population | Major range (km²) | Reference |
|---|---|---|---|
| 1950–1952 | 450–700[a] | 31,080 | Stenlund (1955), this study |
| 1963 | 350–700 | | Cahalane (1964) |
| 1970 | 750 | 38,400[b] | Leirfallom (1970), Nelson (1971) |
| 1971–1972 | 736–950[a] | | This study |
| 1973 | 500–1,000 | 31,000 | Mech and Rausch (1975) |
| 1976 | 1,000–1,200 | | Bailey (1978) |
| 1979 | 1,235 | 36,500[c] | Berg and Kuehn (1982) |
| 1983 | | 57,050[d] | Mech et al. (1988) |
| 1989 | 1,500–1,750[a] | 53,100 | This study |

[a] See text for calculation of estimates.
[b] Area calculated by planimeter from figure in Leirfallom (1970), Nelson (1971) (excludes major lakes).
[c] Area calculated by planimeter from figure in Berg and Kuehn (1982) (excludes major lakes).
[d] Modified by excluding major lakes.

gulate biomass estimate to be accurate and applying the SE calculated for equation (1), the 90% CI of this estimate is 1,020–2,400.

The 2 estimates of wolf numbers are similar and imply that the statewide wolf population in winter 1988–1989 probably had increased to 1,500–1,750 (Table 4). The annual finite rate of population change ($\lambda$) since 1979 (1,235 wolves), assuming a 1989 population of 1,625, averaged 1.03. This is half of the estimated rate of increase during the first 9 years of legal protection (750 wolves in 1970; $\lambda = 1.06$).

## DISCUSSION

### *Estimated Change in Wolf Numbers*

Since the elimination of the bounty and the initiation of complete legal protection, wolves in Minnesota have increased in range and numbers. Our estimate of wolf range in 1989 parallels that derived by Mech et al. (1988), is double that from estimates of 20 years earlier, and indicates that wolf packs are common in areas where they were rare in the early 1970's. In addition, wolf numbers likely have doubled since then. The calculated annual increase in numbers since 1970 ($\lambda = 1.04$) is plausible. In other areas, annual rates of wolf population change have exceeded 1.15 (Keith 1983, Bergerud and Ballard 1988, Peterson and Page 1988). During 1974–1976, wolf numbers increased at a rate as high as 1.31 in rapid response to legal protection in northwestern Minnesota (Fritts and Mech 1981). And during 1980–1986, the annual rate of change averaged 1.02 in north-central Minnesota, where wolf densities were as high as almost anywhere in North America, wolf : deer ratios were low, and emigration likely exceeded immigration (Fuller 1989).

Moreover, we believe the assumptions in both population estimates are conservative. First, moose and deer harvests have increased during the past 15 years, and limited data suggest that ungulate abundance has increased (Table 5). A review of studies where wolves prey primarily on white-tailed deer indicates that wolf territories are larger where deer are less numerous (Fuller 1989:14). Because our estimate of mean territory size included data from packs studied 10–20 years ago when deer numbers likely were lower, our estimate of average territory size may be high; if so, the estimated number of packs in the state is minimal.

Also, the relationship between wolf and ungulate abundance varies with exploitation rates of wolves (Fuller 1989:21). Where exploitation is high (Ballard et al. 1987) or wolf populations are newly protected (Fritts and Mech 1981), the wolf : ungulate ratio is low. Conversely,

Table 5. Mean annual moose and white-tailed deer density and harvest (no./km²) in northern Minnesota (Minnesota Dep. Nat. Resour. files), 1972–1988.

| Years | Moose | | White-tailed deer | |
|---|---|---|---|---|
| | Density | Harvest[a] | Density[b] | Harvest[c] |
| 1972–1976 | 0.19[d] | 0.025 | | 0.38 |
| 1977–1981 | 0.24[d] | 0.032 | | 0.40 |
| 1982–1986 | 0.41[e] | 0.047 | 5.4 | 0.74 |
| 1987–1988 | 0.42[e,f] | 0.051 | 6.6 | 0.75 |

[a] Season open in odd-numbered years only. Harvest limited by single permits issued to parties of 4 hunters; mean party success rate was 90%.
[b] Weighted mean for 5 northern Deer Management Units in wolf range, combined (92,800 km²; Fig. 4A); survey data from 1972–1981 incomplete.
[c] Harvest limited since 1976 by issuing permits for harvest of antlerless deer.
[d] Weighted mean for northeast and northwest survey areas combined (27,040–29,640 km²; Karns 1982); sampling and survey techniques different from those used during 1982–1988 and estimate not corrected for observability bias.
[e] Weighted mean for northeast and northwest survey areas combined (22,700 km²; Fig. 4B).
[f] Incomplete survey in 1987 not included.

wolf : ungulate ratios are higher where wolves are protected (e.g., Oosenbrug and Carbyn 1982, Mech 1986), as they have been in Minnesota. We assumed an average exploitation rate, but wolf protection has been effective and the estimate of total wolf numbers derived from these data also may be conservative.

### *Potential Change in Wolf Numbers*

Although we did not document their presence, packs likely do or could survive on an additional 11,500 km² of range. It is unclear what role this area, and the wolves that may occupy it, might play in an assessment of the recovery status of the Minnesota wolf population. In any event, this range is substantially less than the 40,600 km² Mech et al. (1988) outlined as unoccupied range. However, Mech et al. (1988) also documented relatively high average road densities in the area (i.e., not suitable wolf habitat), and they did not infer that this area could be occupied in the future. If 11,500 km² of range were colonized, potential wolf numbers there can be estimated. Given conservative estimates of pack density (1/300 km²) and mean pack size (5), this range could support perhaps 190 pack wolves ((11,500 ÷ 300) × 5) at current ungulate, road, and human densities.

## MANAGEMENT CONSIDERATIONS

It is prudent to consider that drastic changes may occur in timber-harvesting practices (and thus ungulate abundance), human population density and distribution, legal status of wolves, impact of wolves on livestock, and public attitudes towards wolves. A comprehensive review of wolf population dynamics in North America (Fuller 1989) indicated that these changes can be viewed in 2 contexts. First, potential wolf density ultimately is limited only by ungulate availability, and second, rates of wolf population change often vary directly in response to human-caused mortality. It is unlikely that average ungulate abundance in northern Minnesota will decline significantly in the near future, given the policies of the MDNR and other agencies to manage ungulates, although a series of severe winters might profoundly affect winter ungulate survival and thus numbers. Human population growth and nonurban development are more likely to limit wolf population growth, or even reduce wolf range by increasing wolf mortality.

Human-caused mortality, as indexed by road density and thus human access, seems to limit wolf distribution and numbers in the Great Lakes area (Thiel 1985, Jensen et al. 1986, Mech et al. 1988, Fuller 1989, Mech 1989, this study). Data from Wisconsin, Michigan, and Minnesota suggest that under recent and current circumstances, wolf survival is usually assured at road densities no greater than about 0.70 km/km². The MDNR and the U.S. Forest Service restrict road densities to less than this threshold on public land they control, but almost 50% of current wolf range is under private, industrial, or county ownership where there are no such limits. We recommend that regular monitoring of statewide wolf distri-

bution and numbers, as well as monitoring road density and distribution, become essential priorities for state and federal agencies responsible for wolf management.

## SUMMARY

Wolves once ranged throughout Minnesota, but by the early 1900's, they were restricted to the forested northeastern half of the state. Wolf range continued to decrease and by the early 1950's, 500–700 wolves lived in about 31,000 km$^2$ of major range (occupied by reproducing packs), mostly within 100 km of Canada. By 1965, when Minnesota terminated bounties, perhaps 350–700 wolves remained. About 750 wolves were present in 1970 when their harvest was prohibited on the SNF. Wolves were protected throughout Minnesota in 1974. By 1979, an estimated 1,235 wolves inhabited 36,500 km$^2$ of major range, an annual finite rate of increase ($\lambda$) of 1.06 since 1970. By winter 1982–1983, range occupied by reproducing packs had expanded farther west and south and covered an estimated 57,050 km$^2$.

During winter 1988–1989, 362 state, county, federal, and private natural resource personnel provided 1,244 records of wolf observations and sign throughout northern Minnesota. Survey results, combined with GIS data on road and human population density, indicated wolf packs occupied a minimum of 53,100 km$^2$. Extrapolations of winter wolf territory and pack size, as well as ratios of wolf : ungulate biomass, indicate that Minnesota's wolf population had increased to about 1,500–1,750 since 1979 ($\lambda$ = 1.03). Future increase depends on the extent to which wolf packs colonize an additional 11,500 km$^2$ of potential range with road densities <0.70 km/km$^2$ or human densities <4 people/km$^2$, the abundance of ungulate prey, and the level of human-caused mortality.

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