# Chapter 4
# An Overview of the Legal History and Population Status of Wolves in Minnesota

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## 4.1 Introduction

The modern history of wolf populations in Minnesota, like other areas, is as much a story about humans as it is about wolves. While competition among wolves is in large part driven by the availability of resources such as food and space (Fuller et al. 2003; Packard 2003), wolf–human interactions are a function of real "competition" as well as perceived conflict or fear. Cultural attitudes have clearly played a major role in the dynamics between wolves and humans (Boitani 1995; Fritts et al. 2003). Such human–wolf dynamics are not constant. Cultural attitudes change, the number of people (and livestock) living in close proximity to wolves changes, and the availability and degree of dependence on shared resources changes. Our goal is to examine the legal and population history of wolves in Minnesota, but in so doing we provide a manifestation of human–wolf dynamics, and provide context for understanding the changes in these dynamics through time. We summarize changes in the legal status of wolves and changes in wolf distribution and abundance. We also highlight ecological factors associated with a changing wolf population, and provide an overview of the methods used by the Minnesota Department of Natural Resources (DNR) to monitor the statewide wolf population.

## 4.2 The Legal History of Minnesota's Wolves

The legal history of wolves in Minnesota is a tale of public policy extremes. From statehood (1858) until about 1970, wolves were completely unprotected in all of Minnesota, and for an extensive portion of this time, wolves were actively persecuted by the federal and state government, as well as by private citizens. Following passage of the Endangered Species Preservation Act of 1966, a precursor to the Endangered Species Act of 1973, the Department of Interior classified the eastern timber wolf as endangered in 1967. This law allowed for legal protections

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to be instituted on federal lands, and in 1970, the majority of the Superior National Forest (SNF) was closed to the taking of wolves. While the SNF is a small portion of Minnesota, this closure probably protected a significant proportion of wolves present in Minnesota at that time. After passage of the Endangered Species Act of 1973, wolves in all of Minnesota were afforded complete federal protection in 1974. In effect, with the signing of a pen, Minnesota's wolves went from no legal protections to complete legal protection. From 1974 to 1978, wolves could only be killed in defense of human life.

### *4.2.1 Bounty Era (1849–1965)*

Soon after the Minnesota territory was organized in 1849, the Minnesota legislature authorized counties to pay a $3 bounty for wolves. Authorization for bounty payments was made biennially by the state legislature, and the bounty system remained in place until 1965. During this period, numerous changes were made to the bounty system, including the payment amounts, funding source (county and/or state), and requirements for payment approval. Bounty payments ranged from $3 per animal in the beginning of the program, to $35 per animal in the latter years. Initially, bounty payments were the responsibility of counties, followed by various cost-sharing arrangements between counties and the state, with the state assuming full responsibility in the latter years (Minnesota DNR, unpublished data).

From 1946 to 1964, it was legal under the bounty program for private citizens to obtain permits to shoot wolves from airplanes. However, aerial shooting over the Boundary Waters Canoe Area (BWCA), a "stronghold" for wolves at the time, was eliminated in 1950 when all flights under 1,200 m were prohibited. During the first year that aerial shooting by private citizens was allowed, Stenlund (1955) noted that one operator took 38 wolves by this method. He also noted that wolves quickly learned to avoid open lakes when they heard airplanes approaching.

Early records of the total bounty take are sparse and complicated by the lack of record-keeping distinction between coyotes and wolves. The most reliable records for wolves are for the period 1952–1964, when an average of 188 wolves were submitted for bounty payment each year, at an average annual cost of $6,144. Stenlund (1955) also reported 290 and 295 wolves submitted for bounty in 1950 and 1951, respectively.

In addition to the bounty program, state personnel were involved in wolf removal from the late 1940s through the mid-1950s, including via aerial shooting. Outside the BWCA, aerial shooting by state personnel continued until 1954, and other forms of wolf control (shooting and trapping) by state employees ended in 1956. From 1949 to 1953, ~140–150 wolves were taken annually by state employees (Minnesota 1980). The take by state employees dropped to ~80 animals per year during the final years of the program (1954–1956).

### 4.2.2 Postbounty, Pre-ESA Era (1965–1973)

In 1969, the Minnesota legislature authorized a directed predator control program. The program was a stark contrast to the bounty system, which encouraged unrestricted and widespread take to reduce the wolf population. Under the new program, private trappers certified by the state were authorized to remove wolves only from designated areas where losses of livestock had been verified. Hence, the program was focused on ameliorating localized conflicts, not population reduction. As compensation for control work, certified trappers were paid $50 per wolf. From 1969 until wolves were federally protected in 1974, an average of 65 wolves were removed annually as part of this program (Minnesota DNR 1980), substantially fewer than were removed during the era of bounties and government control. After wolves became federally protected in 1974, management of human–wolf conflicts in Minnesota shifted to federal agencies.

### 4.2.3 Federal Protection Era (1974–2007)

Wolves were neither federally nor state protected (except on the SNF) in Minnesota until 1974 when they were listed under the US Endangered Species Act of 1973. From 1974 to 1978, wolves were federally classified as an endangered species (Refsnider, this volume) with no provisions for lethal control in response to depredations on livestock. In 1978, the federal status of Minnesota's wolves changed from endangered to threatened, thereby allowing lethal control of depredating wolves under federal guidelines. From 1978 to 2007, an average of 91 (range 6–216) wolves were taken annually by federal employees as part of depredation control activities (Ruid et al., this volume).

After passage of a state endangered species act in 1974, wolves were state-classified as an endangered species, down-listed to state threatened in 1984, and removed from the state's list of threatened and endangered species in 1996. However, the federally threatened status of Minnesota's wolves did not change until 2007, when federal protection of wolves in the Great Lakes region was finally removed. Management authority for wolves in Minnesota now resides with the state and Indian tribes, and wolves are classified as a protected mammal.

### 4.2.4 Current State Management

The state's wolf management plan (Minnesota DNR 2001) went into effect with federal delisting in 2007. Under the plan, control of depredating wolves continues in Minnesota using guidelines specified in state statutes, and in a majority of wolf range is similar to federal guidelines for wolf depredation take from 1978 to 2007.

Two state wolf management zones were established in the plan, differing only in depredation policies. In Zone A (Fig. 4.1), which constitutes ~85% of current wolf range, wolves may be taken by private citizens, under certain conditions, if they pose an immediate threat (as defined in state statutes) to livestock or domestic pets under owner supervision. Furthermore, when losses of livestock or pets have been verified as wolf depredations, the state will provide a governmental or state-certified private trapper to remove wolves in a defined area. These same rules apply in Zone B, but landowners, under certain conditions, are given added flexibility (immediate threat does not apply) to take wolves to protect livestock, and they may individually hire a state-certified trapper to protect livestock in a defined area. A Minnesota state statute prohibits the public harvest of wolves for the first 5 years after federal delisting. After that period, the Minnesota DNR is authorized to prescribe and regulate public harvest of wolves, but must provide an opportunity for public comment.

It is difficult to quantify the specific effects various historic control programs had on Minnesota's wolf population. In northeastern Minnesota, the area in which wolves had largely been restricted by the 1950s, Stenlund (1955) estimated that the combination of take by private citizens (bounty) and state employees in the early 1950s may have removed 41% of the wolf population, annually. He further pointed to evidence that the wolf population during this time was relatively stable, concluding that control efforts neither reduced wolf populations nor allowed the population to potentially increase. Even if Stenlund (1955) was correct, it is likely that statewide

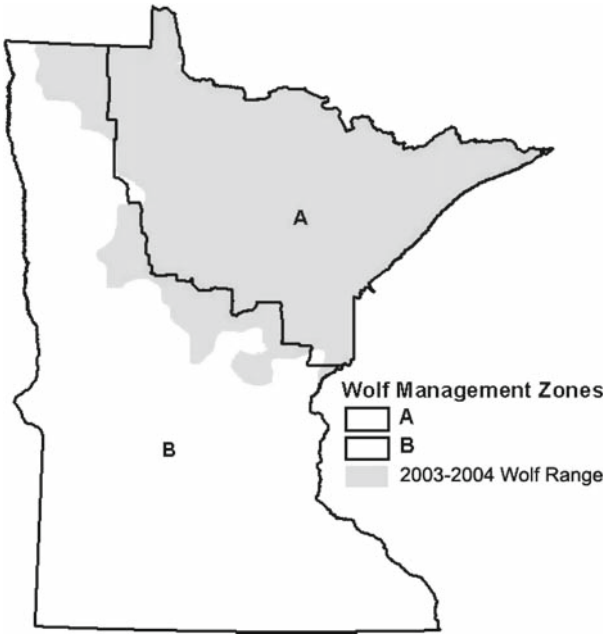


**Fig. 4.1** State wolf management zones in Minnesota in relation to the contiguous wolf range delineated in 2003–2004

control efforts had spatially and temporally varying effects on Minnesota's wolf population. Persecution undoubtedly played an important role in once eliminating wolves from all but the remote forests of Minnesota adjacent to Canada. However, population changes are complicated by other factors also affecting wolf ecology, in particular major changes in Minnesota's landscape that affected the distribution and abundance of prey species of wolves (DelGiudice et al., this volume). Hence, the population history of wolves in Minnesota is not only a manifestation of human attitudes and the legal history of wolves, but also the history of their prey.

## 4.3 The Population History of Minnesota's Wolves

### *4.3.1 Pre-European Settlement Era*

When the Endangered Species Act of 1973 was passed, the only remaining population of wolves in the lower 48, excluding those on Isle Royale, was in northern Minnesota. As early as 1938, Olson (1938), with reasonable accuracy, offered such a prediction of future wolf distribution. As one progresses backward in time, the distributional "picture" of wolves in Minnesota, while still quite coarse, is much clearer than their abundance. At the time Minnesota was settled by Euro-Americans, the distribution of wolves likely encompassed the entire state (Herrick 1892; Surber 1932). Based on reported density estimates for wolves exposed to prey populations similar to those that historically existed in Minnesota, Mech (2000) speculated that the original wolf population may have numbered between 4,000 and 8,000 wolves.

### *4.3.2 Bounty Era (1849–1965)*

By 1900, and perhaps sooner, wolves were rare in the southern and western portions of Minnesota (Herrick 1892; Surber 1932), no doubt a combined result of wolf persecution and extirpation (or near so) of the bison and elk herds that once roamed this region (DelGiudice et al., this volume). By 1930, the range of wolves in Minnesota had further contracted to the north, with the remaining wolves surviving primarily in portions of the forested counties bordering Canada (~31,000 $km^2$; Stenlund 1955). Stenlund (1955) noted that early Forest Service records indicate that 300–600 wolves may have occupied the SNF from 1914 to 1931. However, interpretation is complicated by the changing acreage of the SNF during this time, and different personnel responsible for making the reports. Based on his work in the 1920s and 1930s, Olson (1938) provided an estimate of 250 wolves occupying a 6,500-$km^2$ area of the SNF immediately adjacent to Canada, or 1 wolf per 26 $km^2$. In the late 1940s to mid-1950s, Stenlund (1955) estimated that between 205 and 273 wolves occupied a 10,600-$km^2$ area in northeastern Minnesota. Stenlund's

(1955) larger study area overlapped that of Olson's (1938), suggesting a population decline in this area from 1 wolf per 26 km$^2$ in around 1930 to 1 wolf per 44 km$^2$ in around 1950. Stenlund (1955) attributed this wolf decline to a reduction in deer populations. The decline in the deer herd was attributed primarily to maturation of the forest following turn-of-the-century logging (which initially led to deer population increases), and overbrowsing by the abundant deer population in the mid- to late 1930s.

While these studies provided some indication of the density of the wolf population on portions of the SNF, we do not know whether such density estimates applied to the remainder of the wolf range, nor do we know the precise extent of statewide wolf distribution at that time. Stenlund (1955) extrapolated his results to an 18,000-km$^2$ area of northeastern Minnesota and estimated 300–400 wolves. However, this 18,000-km$^2$ area represented only 60% of what he delineated as primary wolf range at the time. If the density estimates were applicable to all primary wolf range, we estimate as many as 700 wolves in Minnesota between 1920 and 1960. If we use Olson's (1938) estimate of 1 wolf per 26 km$^2$ when prey was more abundant, and assume a similar primary wolf range, we estimate ~1,200 wolves in Minnesota at that time. This may be an overestimate because control efforts outside of these study areas (i.e., outside SNF) were likely successful at reducing wolf density. But it is also possible that Stenlund (1955) underestimated *primary* wolf range in the early 1950s, as evidenced by the consistent bounty take of wolves in areas outside, but adjacent to, the primary range. Clearly, any estimate of wolf numbers in Minnesota from 1920 to 1960 remains somewhat speculative. We conclude that the wolf population in Minnesota following European settlement did not likely drop below 300–400 animals, and that the population from 1920 to 1960 may have ranged from 400 to 800 animals, perhaps highest during the late 1930s and early 1940s when deer were abundant and persecution of wolves may have temporarily diminished as a result of World War II.

While wolf control efforts may have increased following World War II, several "protective" changes subsequently occurred from the mid-1950s to the late 1960s. Aerial shooting of wolves was eliminated in the BWCA in the early 1950s, aerial shooting by state personnel outside this area ended in 1954, and all forms of wolf control by state personnel ended in 1956. In addition, the bounty system was terminated in 1965. Mech et al. (1971) and Mech (1973) believed that the wolf population during this period increased due to less wolf control, but there was no indication of major increases in the population. Cahalane (1964) reported between 350 and 700 wolves in Minnesota in the early 1960s, based on a questionnaire survey to game departments and other independent professionals.

### *4.3.3 Postbounty, Pre-ESA Era (1965–1973)*

The Minnesota DNR estimated 750 wolves were present in Minnesota in 1970 based on a survey of field personnel (Leirfallom 1970), but Nelson (1971) believed

this represented a minimal estimate. This is near the upper end of the population estimates for the period 1920–1960. While much uncertainty remains in these numbers, the apparent lack of a significant increase in wolf numbers might suggest wolf control was not a major limiting factor at the time. Alternatively, the potential for wolves to increase in the 1960s may have been hampered by declining habitat quality for deer, overharvest of deer by humans, and the severe winters of the late 1960s that negatively affected deer populations (Mooty 1971). In spite of the potentially significant legal changes that occurred from the late 1950s through the 1960s, we believe the best information available suggests the wolf population was relatively stable to slightly increasing.

### *4.3.4 Federal Protection Era (1974–2007)*

The mid-1970s represents the beginning of notable wolf population recovery in Minnesota. As noted above, the Minnesota DNR estimated there were ~750 wolves in the state in 1970 (Leirfallom 1970; Nelson 1971), with primary wolf range (~39,000 $km^2$) ~25% larger than reported by Stenlund (1955) in the early 1950s. Fuller et al. (1992) later reviewed all available data, and independently concluded that the wolf population numbered at least 736–950 wolves in 1970, supporting the opinion that 750 was a minimal population estimate.

While wolf density appears to have declined in parts of northeastern Minnesota in the early 1970s (Mech 1973, 1986), a radio-telemetry study from 1972 to 1976 in the expanding northwestern portion of the wolf range documented that a rapid increase in the wolf population was occurring there, apparently a result of greater protections provided by the Endangered Species Act (Fritts and Mech 1981). By the mid-1970s, Mech (in Bailey 1978), using the best available information, estimated the statewide population at 1,000–1,200 wolves, an increase from what Mech and Rausch (1975) had tentatively estimated in 1973 (500–1,000). Shortly thereafter, the Minnesota DNR conducted another statewide survey in winter 1979–1980 and derived a population estimate of 1,235 wolves (Berg and Kuehn 1982). While Berg and Kuehn (1982) concluded primary wolf range had changed little since 1970, peripheral wolf range had expanded south and west. In the year that survey report was published (1982), the first wolf pack was confirmed to have recolonized Agassiz National Wildlife Refuge, an area that remains along the northwestern border of Minnesota's wolf range 25 years later.

#### 4.3.4.1 Recent Efforts to Monitor Wolf Populations

The 1970 population estimate represented the first official effort by the state to estimate the statewide wolf population, and for the next 30 years, population estimates were derived at ~10-year intervals (every 5-year starting in 1998). The 1970 estimate was based on a questionnaire to wildlife and enforcement personnel in the DNR in which they were

asked to provide their best estimates of wolf numbers and distribution in their work areas. Ten years later, the winter 1979–1980 survey also relied on field knowledge to document areas occupied by wolves, but used density information derived from five study areas where wolves were radio-marked to supplement field observations of wolf density (Berg and Kuehn 1982). While all subsequent surveys followed a similar conceptual approach, numerous changes were made in 1988–1989.

Details of the methodology used since 1988 were first provided by Fuller et al. (1992). While the advent of radio-telemetry, geographic information systems (GIS), and global positioning systems (GPS) has allowed more detailed monitoring and mapping of wolf populations, Minnesota's survey is an ad hoc method that relies on multiple pieces of information. Counting elusive carnivore populations over large areas, particularly in forested habitats, remains a difficult task. Minnesota's 400+ wolf packs occupy nearly 80,000 km$^2$. Radio-marking all (or most) packs in a given year or using mark-recapture (without harvest as an option for "recapture") would be impractical, if not impossible. Distance sampling methods (e.g., Buckland et al. 2004) are not logistically feasible for secretive carnivores in densely forested landscapes. Other approaches have been employed for predicting or estimating abundance of large carnivores. Approaches based solely on prey or habitat assessments (Fuller 1989; Boyce and Waller 2003) may be useful for estimating potential abundance of large carnivores, but may not always match realized abundance due to other time-varying factors (e.g., disease, weather). Newer aerial sampling methods (Becker et al. 1998; Patterson et al. 2004) show promise. However, they may be difficult to apply during the course of a single winter in broad expanses of dense forest, particularly where abundant deer populations make aerial confirmation of wolf tracks challenging. Recent attempts to use such aerial surveys in Minnesota have not succeeded due to poor snow conditions (2006) and other logistical limitations. Nevertheless, we feel the current survey has served its intended purpose, and adequately documented changes in the distribution and abundance of wolves.

#### 4.3.4.2 Steps in Conducting Recent Surveys

The steps in conducting Minnesota's recent wolf population surveys are listed below (see also Table 4.1):

1. A majority of natural resource field personnel in the state (county, state, tribal, and federal) were provided maps and asked to record all detections of wolf sign during the course of their normal winter (~October through April) work duties. Primary data included the sign location and the estimated number of wolves. This information was supplemented with data obtained from two annual carnivore track surveys (scent station and winter track surveys), USDA-verified depredations, and known territories from radio-marked packs.
2. Using this information, in conjunction with data on forest cover, deer density, human and road density, and professional opinion of field staff, a contiguous *total* wolf range was delineated.

3. To estimate the amount of area within total wolf range that was *occupied,* observations of wolf sign from the current winter survey were entered into a GIS System. Any township (9.7 km × 9.7 km survey block) within total wolf range that included an observation of a pack (>1 wolf traveling together) was deemed occupied.
4. To account for lack of sampling in some areas, townships within total wolf range were also deemed occupied by a pack if the density of humans and roads was below the thresholds reported in Fuller et al. (1992), specifically road density <0.7 km/km$^2$ and human density <4 per km$^2$, or road density <0.5 km/km$^2$ and human density <8 per km$^2$.
5. Summing (3) and (4) yielded an estimate of the amount of occupied wolf range.
6. The average territory size (minimum convex polygon) obtained from all current radio-marked packs in the state was multiplied by 1.37 (Fuller et al. 1992) to account for vacant spaces between adjacent packs, which may be real or a byproduct of imperfect delineation of territories. This number was divided by the amount of occupied range to estimate the number of packs across the state.
7. The estimated number of packs was multiplied by mean winter pack size obtained from repeat aerial observations of marked packs, yielding an estimate of population size (for pack wolves).
8. This estimate of pack wolves was divided by 0.85, under the assumption that ~15% of the total population is composed of lone wolves (Fuller 1989; Fuller et al. 2003).
9. Confidence intervals (CI) were generated using bootstrap resampling of the data on pack and territory size, and did not incorporate uncertainty in estimates of occupied range, percent lone wolves, or size of interstitial spaces.

#### 4.3.4.3 Recent Population Growth and Range Expansion

We compared key results from surveys among the three most recent surveys (Table 4.1). Population estimates generated from this survey were for mid-winter, near the low point of the annual cycle. Based on these surveys, Minnesota's wolf population appears to have quadrupled in size between 1970 (~750 wolves) and 2004 (~3,000 wolves), while total contiguous wolf range more than doubled to >88,000 km$^2$. Population increases in Minnesota up until 1998 appear to have largely been through range expansion, though some density increases in previously occupied areas appear to have occurred as well. Results from the winter 2003–2004 survey suggest that range expansion ceased, at least temporarily, around the mid- to late 1990s. The increase in the wolf population estimate for winter 2003–2004 compared to that for winter 1997–1998 was primarily through increased wolf density (Erb and Benson 2004), attributed to a reduction in average size of pack territories. Assuming linear rates of change between the periodic population surveys, growth rate of Minnesota's wolf population ranged from 3% to 6% annually from 1970 to 2004. From 1978 to the present, an additional 2–8% of the population was removed in response to verified depredations (Ruid et al., this volume).

**Table 4.1** Summary of methods and key results from Minnesota's wolf surveys, 1988–2004

| | Winter 1988–1989 (Fuller et al. 1992) | Winter 1997–1998 (Berg and Benson 1998) | Winter 2003–2004 (Erb and Benson 2004) |
|---|---|---|---|
| 1. | Field personnel from natural resource agencies ($n$ = 154 work stations) submitted maps with wolf sign observations, including the estimated number of wolves at each location | Field personnel from natural resource agencies ($n$ = 179 work stations) submitted maps with wolf sign observations, including the estimated number of wolves at each location | Field personnel from natural resource agencies ($n$ = 102 work stations) submitted maps with wolf sign observations, including the estimated number of wolves at each location |
| 2. | Opportunistic field observations, supplemented by carnivore scent station surveys, USDA-verified depredations, and territories delineated for marked packs ($n$ = 1 "point" per pack), yielded 1,244 observations… | Opportunistic field observations, supplemented by carnivore scent station and winter track surveys, USDA-verified depredations, and territories delineated for marked packs ($n$ = 1 "point" per pack), yielded 3,659 observations | Opportunistic field observations, supplemented by carnivore scent station and winter track surveys, USDA-verified depredations, and territories delineated for marked packs ($n$ = 1 "point" per pack), yielded 1,719 observations |
| 3. | Contiguous wolf range was delineated including 93% of townships with pack observations, and covered 60,229 km$^2$ of northern Minnesota. To compensate for a lack of systematic sampling, townships with <0.7 km/km$^2$ roads and <4 humans/km$^2$ or <0.5 km/km$^2$/roads and <8 humans/km$^2$ were included even if wolf packs were not detected in this survey | Contiguous total wolf range was delineated including 99% of townships with pack observations, and covered 88,325 km$^2$ of northern Minnesota. To compensate for a lack of systematic sampling, townships with <0.7 km/km$^2$ roads and <4 humans/km$^2$ or <0.5 km/km$^2$/roads and <8 humans/km$^2$ were included even if no wolf packs were detected in this survey | Contiguous total wolf range was delineated including 99% of townships with packs as determined from all databases, and was the same as 1998 (88,325 km$^2$). To compensate for a lack of systematic sampling, "modeled" townships with <0.7 km/km$^2$ roads and <4 humans/km$^2$ or <0.5 km/km$^2$/roads and <8 humans/km$^2$ were included even if no wolf packs were detected in this survey |
| 4. | Within total wolf range, unoccupied townships (~8,000 km$^2$) with no pack (>1 wolf) detections and not fitting the human/road model, were subtracted from total area to estimate **total occupied wolf range (~53,000 km2)** | Within total wolf range, unoccupied townships (14,405 km$^2$) with no pack (>1 wolf) detections and not fitting the human/road model, were subtracted from total area to estimate **total occupied wolf range (73,920 km2)** | Within total wolf range, unoccupied townships (20,473 km$^2$) with no pack (>1 wolf) detections and not the fitting human/road model, were subtracted from total area to estimate **total occupied wolf range (67,852 km2)** |

| | | | |
|---|---|---|---|
| 5. | **Mean MCP territory size (166 km2)** derived from telemetry studies conducted from 1970 to 1989 ($n$ = 108 packs) was divided into occupied range (after multiplying by 1.37 for interstitial pack area) to estimate number of packs (~233). | **Mean MCP territory size (140 km2)** derived from current telemetry studies ($n$ = 36 packs) was divided into occupied range (after multiplying by 1.37 for interstitial pack area) to estimate number of packs (~385) | **Mean MCP territory size (~102 km2)** derived from current telemetry studies ($n$ = 24 packs) was divided into occupied range (after multiplying by 37% for interstitial pack area) to estimate number of packs (~485) |
| 6. | **The mean winter pack size (5.55)** derived from telemetry studies conducted from 1970 to 1989 ($n$ = 108 packs) was multiplied by the number of packs to estimate total pack wolves (1,293) | **The mean winter pack size (5.4)** derived from current telemetry studies ($n$ = 36 packs) was multiplied by the number of packs to estimate total pack wolves (2,079) | **The mean winter pack size (~5.3)** derived from current telemetry studies ($n$ = 24 packs) was multiplied by the number of packs to estimate total pack wolves (2,567) |
| 7. | Lone wolves were assumed to account for ~15% of the population and were incorporated (1,293/0.85) to yield a **total estimate of 1,521 wolves** (CI 90% = 1,338–1,762). A **separate population estimate (1,750 wolves, CI 90% = 1,020–2,400**) was based on wolf/ungulate biomass ratios | Lone wolves are assumed to account for ~15% of the population and were incorporated (2,079/0.85), to yield a **total estimate of 2,445 wolves (90% CI 1995–2905)** | Lone wolves are assumed to account for ~15% of the total population and were incorporated (2,567/0.85), to yield a **total estimate of 3,020 wolves (90% CI 2301–3708)** |

*USDA* United States Department of Agriculture

While there is little question that elimination of coordinated wolf persecution in the 1950s and 1960s, and subsequent legal protections in the early 1970s, played an important role in wolf recovery, we believe that growth of the deer herd (DelGiudice et al., this volume) played an equally important role. Average size of wolf territories, as summarized during the periodic wolf surveys, has steadily declined (Table 4.1), and the estimate of average territory size (102 km$^2$) during the winter 2003–2004 survey appears to be the smallest published for any multipack study in Minnesota (Fuller et al. 2003; Gogan et al. 2004), as well as smaller than published estimates from most other areas of North America. Continuing range "saturation" also may have played a role in declining territory size, because colonizing wolf populations exhibit declines in average size of pack territories as the populations become established (Fritts and Mech 1981; Hayes and Harestad 2000; Wydeven et al., this volume). Nevertheless, available prey abundance is arguably the most important ecological factor influencing wolf social and population dynamics. Assuming other factors remain constant, prey abundance is negatively correlated with territory size and positively correlated with population size (Mech and Boitani 2003a; Fuller et al. 2003). The deer population in Minnesota's wolf range is at historic highs in the twenty-first century (DelGiudice et al., this volume), allowing individual wolf packs to survive in smaller areas. Given the low correlation between average pack size and prey biomass (Fuller et al 2003), the lack of major change in average pack size (Table 4.1) is not unexpected.

## 4.4 The Future of Wolves in Minnesota

Range recolonization by wolves in Minnesota appeared to have ceased in the mid- to late 1990s. Total contiguous wolf range in Minnesota was estimated at ~88,000 km$^2$ in 1998 and 2004, of which ~70,000 km$^2$ was deemed occupied in 2004. Mladenoff et al. (1995), based on habitat modeling, predicted there was ~50,000 km$^2$ of "favorable" wolf habitat in what has been considered primary wolf range in Minnesota (Zone A; Fig. 4.1). Minnesota's currently occupied wolf range, which includes areas (Zone B; Fig. 4.1) not considered by Mladenoff et al. (1995), is ~70,000 km$^2$. As in Wisconsin (Mladenoff et al. 1999), it is clear that wolves have expanded into areas previously thought to be less favorable. Nevertheless, at a coarse spatial scale, the current distribution of wolves in Minnesota is reasonably similar to the projections of Mladenoff et al. (1995).

Whether wolf range in Minnesota will expand in the future is difficult to predict. Minnesota's wolf management plan imposes no geographic or numeric limit on the wolf population, instead focusing on alleviation of wolf-human conflicts where they occur (Minnesota DNR 2001). The extensive distribution of wolves at the time of Euro-American settlement indicates that wolves are not habitat specialists. Although numerous factors can influence wolf distribution and abundance, two factors – prey abundance and human-caused mortality – are likely the best predictors of possible range expansion in the future. Without large herds of bison and elk

roaming the former prairie, now primarily an agricultural landscape, we do not believe that current prey (i.e., deer) density in the majority of southern and western Minnesota is capable of sustaining a viable wolf population, even in the absence of human-caused mortality. Nevertheless, deer populations capable of sustaining wolf packs in this region do exist in some areas of fragmented forest along or adjacent to river valleys.

We believe the area with the greatest potential for future re-colonization, based on prey biomass, is in southeastern Minnesota. Although wolves can disperse substantial distances (Treves et al., this volume), this area is distant from the current population of wolves, and establishment of packs may be hindered by the developed landscape they must travel through to get there. However, prey is not limiting, and wolf packs may eventually establish in this region, perhaps similar to, or even connected with, the "isolated" wolf population now established in central Wisconsin (Thiel et al., this volume). There may be greater potential for wolf mortality in southeastern Minnesota associated with livestock depredation control, vehicle collisions, and increased rates of illegal killing (more people, accessible landscape, and wolves will be more visible). Nevertheless, wolf populations can sustain high annual mortality rates, perhaps in excess of 50% (Fuller et al. 2003), and we doubt that potential human-caused mortality will preclude the possibility of a small and relatively isolated wolf population establishing in southeastern Minnesota. However, if packs do establish in isolated patches of southern Minnesota, we doubt they would account for >5% of the total wolf population in the state. We foresee primary wolf range in Minnesota remaining largely contained within the 88,000-km$^2$ area delineated by Berg and Benson (1998).

Based on results from the winter 2003–2004 Minnesota wolf survey, wolf density was ~4.5 wolves per 100 km$^2$. Overall, winter density estimates from localized studies in Minnesota have ranged from ~1 wolf per 100 km$^2$ to 6 wolves per 100 km$^2$ (Olson 1938; Stenlund 1955; Mech 1973, 1986; Van Ballenberghe et al. 1975; Berg and Kuehn 1980; Fritts and Mech 1981; Fuller 1989; Gogan et al. 2004). Pimlott (1967) suggested that intrinsic factors likely limit density of wolves to ≤4 wolves per 100 km$^2$, but a few studies have since documented localized winter densities of ≥5 wolves per 100 km$^2$ (e.g., Van Ballenberghe et al. 1975; Peterson and Page 1988; Fuller 1989). Most researchers now agree that extrinsic factors (i.e., prey biomass) likely impose the upper limit to wolf density.

Mech (1998), using previous growth rates, projected that the Minnesota population would reach 3,500 wolves by 2005, but assumed the increase would likely be through additional range expansion. While his projection is within our confidence bounds for the population estimate in winter 2003–2004, wolves did not continue to expand their range after 1997–1998. A population of 3,500 wolves, but within the area deemed occupied in 2003–2004 (Table 4.1), would yield a range-wide density estimate of ~5.2 wolves per100 km$^2$. Whether future surveys will support this scenario is unknown, but it's clear that Minnesota's wolf population is near the highest densities previously reported in the literature, excluding Isle Royale (Fuller et al. 2003). We also believe that wolf density in northern Minnesota is likely higher today than before European settlement, a result of increases in prey biomass from

landscape alterations that transformed the ungulate community from a low-density, moose-caribou prey base into a high-density, white-tailed deer prey base (DelGiudice et al., this volume).

While we do not anticipate significant expansion of wolf range in Minnesota, wolf numbers will undoubtedly fluctuate. Prey availability, disease and parasites, and human-caused mortality will, to varying degrees, play a role in future wolf population dynamics. The future of deer seems secure, and it's possible that deer populations in some areas may further increase as a result of alterations of forest structure and lack of severe winters induced by climate change. While some level of illegal killing of wolves will continue to occur, human attitudes toward wolves are much improved and we do not foresee any dramatic changes that will single-handedly dictate the fate of the wolf population in Minnesota. Human development and population growth in northern Minnesota may pose greater challenges by increasing wolf-human conflicts and vehicle collisions, and creating greater opportunity for illegal killing as a result of more roads, people, and forest fragmentation. Coexistence in increasingly developed areas will not only be dependent on human tolerance of wolf activity, but also on the ability of wolves to tolerate increasingly fragmented forests with more human activity. Finally, while much is known about which diseases and parasites can affect wolves (Kreeger 2003), we know less about their role in limiting or regulating wolf populations and factors that may influence their prevalence and persistence in wolf populations (e.g., wolf density, proximity to domestic animals, and weather). Studying potential population effects of diseases or parasites can be extremely challenging, but monitoring prevalence will improve our understanding and ability to predict outbreaks.

Maintaining or improving human attitudes toward wolves will be a key component of future wolf management, with education and responsive conflict management front and center. While human-wolf conflicts need to be addressed, in so doing we must not forget to acknowledge the many values of wolves. Wolves can play an important role in restoring natural ecosystem dynamics (e.g., Mech and Boitani 2003b; Ripple and Beschta 2004; Rooney and Anderson, this volume), are aesthetically valued by many people, may contribute to tourism (Schaller 1996; Fritts et al. 2003) or recreational opportunity, and are culturally important to Native Americans (David, this volume). The return of wolf populations to the Great Lakes region is indeed a success story, for wolves and for many people.

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