2016

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Published in Perry, M. C. , ed., The History of Patuxent –America's Wildlife Research Story (2016)
U. S. Geological Survey Circular 1422, 255 p. https://doi.org/10.3133/cir1422

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L. David Mech

The gray wolf (*Canis lupus*) was one of the first species placed on the Endangered Species List in 1967. The Endangered Species Act of 1973 legally protected the wolf along with other listed species.

Patuxent Wildlife Research Center (Patuxent) in Laurel, MD, began its Endangered Wildlife Program in 1966, and U.S. Fish and Wildlife Service (USFWS) biologist Ray Erickson was assigned to lead it. In 1973, I was transferred to the program from Region 3 of the USFWS, having been employed there since 1969 to study wolves in Minnesota.

Endangered Species Act protection of the wolf fostered its quick population response, and wolf numbers began to increase in their reservoir in northeastern Minnesota and adjacent Canada and expand throughout northern Minnesota and eventually into Wisconsin and Michigan. In 2009, the number of wolves in Minnesota was approximately 3,000, and there were at least 1,500 in Wisconsin and Michigan.

This chapter describes Patuxent's wolf research, which continued into 1993 when Congress incorporated the USFWS's Endangered Wildlife Research Program into the National Biological Survey (NBS). Eventually the NBS merged with the U.S. Geological Survey, and the long-term wolf research program was transferred to the Northern Prairie Wildlife Research Center. Through all the administrative changes, Patuxent's wolf research project continued through the various agencies into the present (2016).

The text that follows is modified from Mech (2009).

The seeds for the blossoming of the wolf (*Canis lupus*) population throughout the upper Midwest were embodied in a long line of wolves that had persisted in the central part of the Superior National Forest (SNF) of northeastern Minnesota, probably since the retreat of the last glaciers more than 10,000 years ago. This line of wolves had withstood not only the various natural environmental factors that had shaped them through their evolution, but also logging, fires, market hunting of prey animals, bounties, aerial hunting, and poisoning. These factors had exterminated their ancestors and dispersed their offspring to only a few wolf pack territories in the more accessible areas. The dense and extensive stretch of wild land that is now known as the Boundary Waters Canoe Area Wilderness had proven too formidable a barrier even for the foes of the wolf, which had striven to eliminate the animal and had succeeded everywhere else in the contiguous United States. The wolves of the SNF became the reservoir for the recolonization of wolves throughout Minnesota and into neighboring Wisconsin and the Upper Peninsula of Michigan.

The only other part of the 48 contiguous United States where wolves still survived in the late 1960s was Isle Royale in Lake Superior, just 32 kilometers (km) (20 miles [mi]) from Minnesota's coast (Vucetich and Peterson, 2009). Those wolves had crossed Lake Superior's rare ice bridge to the 540-square-kilometer (km^2) (208-square-mile [mi^2]) island from Ontario (or possibly Minnesota) in 1949. At that time, Isle Royale was a national park, and the wolves that reached the island were fully protected there from bounties, poisons, and aerial hunting.

Dave Mech, U.S. Fish and Wildlife Service, drugging wild wolf in Minnesota to radiocollar it, early 1970s. Photo by Don Elsing, U.S. Forest Service.

U.S. Fish and Wildlife Service wildlife technicians radiocollaring a wolf in Minnesota, mid-1980s. Photo by U.S. Fish and Wildlife Service.

The wolves of the central SNF also were those that wildlife biologist, wilderness enthusiast, and writer Sigurd Olson (1938) had trailed in the snow in the late 1930s and that Milt Stenlund (1955) had studied later. Although neither worker realized it, molecular geneticists would eventually debate whether the wolves they studied were a blend of animals descended from the most recent colonization of North America across the Bering land bridge (*Canis lupus*), such as those in northwestern Canada and Alaska, and wolves that putatively evolved in North America (*Canis lycaon*), such as those that inhabit southeastern Ontario (Wilson and others, 2000). Wolves with both types of genetic markers sometimes live in the same pack, and apparently many wolves in Minnesota are hybrids between the two types (Mech and Federoff, 2002; Wilson and others, 2009).

When the last remaining 700 or so wolves inhabiting Minnesota, most of them in the SNF, were placed on the Federal Endangered Species List in 1967, it was only logical to begin studying them. A few groundbreaking studies had provided some insights into the biology of wolves (for example, Olson, 1938; Murie, 1944; Cowan, 1947; Stenlund, 1955; Mech, 1966; Pimlott and others, 1969); however, because wolves were so scarce in the contiguous United States and lived in low densities and inaccessible areas where they did survive, much basic information about wolves was unknown. Fortunately, when wolves were declared endangered, wildlife researchers were beginning to apply the revolutionary technology of radiotracking (Cochran and Lord, 1963). Kolenosky and Johnston (1967) had proved in Ontario that radiotracking wolves was practical. This technique promised to greatly enhance the ability of researchers to discover many new things about the behavior and ecology of wolves.

In 1968, I began a pilot project in the central SNF using radiotracking to determine whether wolf packs were territorial (Mech and Frenzel, 1971). My preliminary aerial observations during 1966–67 and 1967–68 had shown that several packs of different sizes and color combinations were present in the area. Without reliable identifiers for each pack, however, and without being able to find packs systematically, I had only a subjective notion that they were territorial. Therefore, radiotracking wolves from aircraft, which allowed both identifying individuals and systematically locating them, was the ideal method to answer this question.

Study Area

My study area encompassed about 2,060 km^2 (795 mi^2) immediately east of Ely in the east-central SNF (48° N.

Aerial radiotracking of wolves in Minnesota by U.S. Fish and Wildlife staff, mid-1980s. Photo by U.S. Fish and Wildlife Service.

Aerial observation of radiocollared wolves in Minnesota as part of the ongoing U.S. Fish and Wildlife Service wolf census, mid-1980s. Photo by U.S. Fish and Wildlife Service.

92° W.). Although somewhat smaller than the areas I have reported on earlier, this area encompassed the core of that region in which I have been able to monitor the wolf population during the entire 40-year study (1966–2006) (fig. 1). The area represents only a small percentage of the total range of wolves in Minnesota.

Topography in the study area varies from large stretches of swamps and uneven upland to rocky ridges, with altitudes ranging from about 325 to 700 meters (m) (1,066–2,297 feet [ft]) above the National Geodetic Vertical Datum of 1988. Winter temperatures below -35 degrees Celsius (°C) (-31 degrees Fahrenheit [°F]) are not unusual, and snow depths (from about mid-November through about mid-April) generally range from 50 to 75 centimeters (cm) (20–30 inches [in.]). Summer temperatures rarely exceed 35 °C (95 °F). Conifers, including jack pine (*Pinus banksiana*), white pine (*P. strobus*), red pine (*P. resinosa*), black spruce (*Picea mariana*), white spruce (*P. glauca*), balsam fir (*Abies balsamea*), white cedar (*Thuja occidentalis*), and tamarack (*Larix laricina*), predominate in the forest overstory. As a result of extensive cutting and fires, however, much of the coniferous cover is interspersed with large stands of white birch (*Betula papyrifera*) and aspen (*Populus tremuloides*). Heinselman (1993) presents a detailed description of the forest vegetation.

In the northeastern half of this area, as well as immediately north and east of it, the overwintering population of white-tailed deer (*Odocoileus virginianus*) was extirpated by about 1975 by a combination of severe winters, maturing vegetation, and a large wolf population (Mech and Karns, 1977), and the area has remained devoid of wintering deer ever since (Nelson and Mech, 2006). Moose (*Alces alces*) inhabit the entire area but occur at a higher density in the northeastern half. In spring, about a third of the deer inhabiting the southwestern half of the study area migrate into the northeastern half or beyond and return in fall (Hoskinson and Mech, 1976; Nelson and Mech, 1981). American beavers (*Castor canadensis*) occur throughout the study area, but generally are available as prey only from about April through November. Although all three prey species are consumed by wolves in the region (van Ballenberghe and others, 1975), the primary prey of wolves inhabiting the northeastern part has been moose since about 1975, whereas wolves in the southwestern part have consumed primarily deer.

Year-round hunting and trapping of wolves were legal until October 1970, when wolves were fully protected on Federal land within the SNF by the U.S. Forest Service. In August 1974, wolves were protected under the Endangered Species Act of 1973. In 1978, wolves in Minnesota were reclassified as threatened, but remained legally protected except for depredation control outside the SNF (Fritts and others, 1992). Illegal taking of wolves continued, however—primarily in fall and winter (Mech, 1977b; Mech and Hertel, 1983). Wolves in the upper Midwest, including Minnesota, were removed from the Endangered Species List in March 2007.

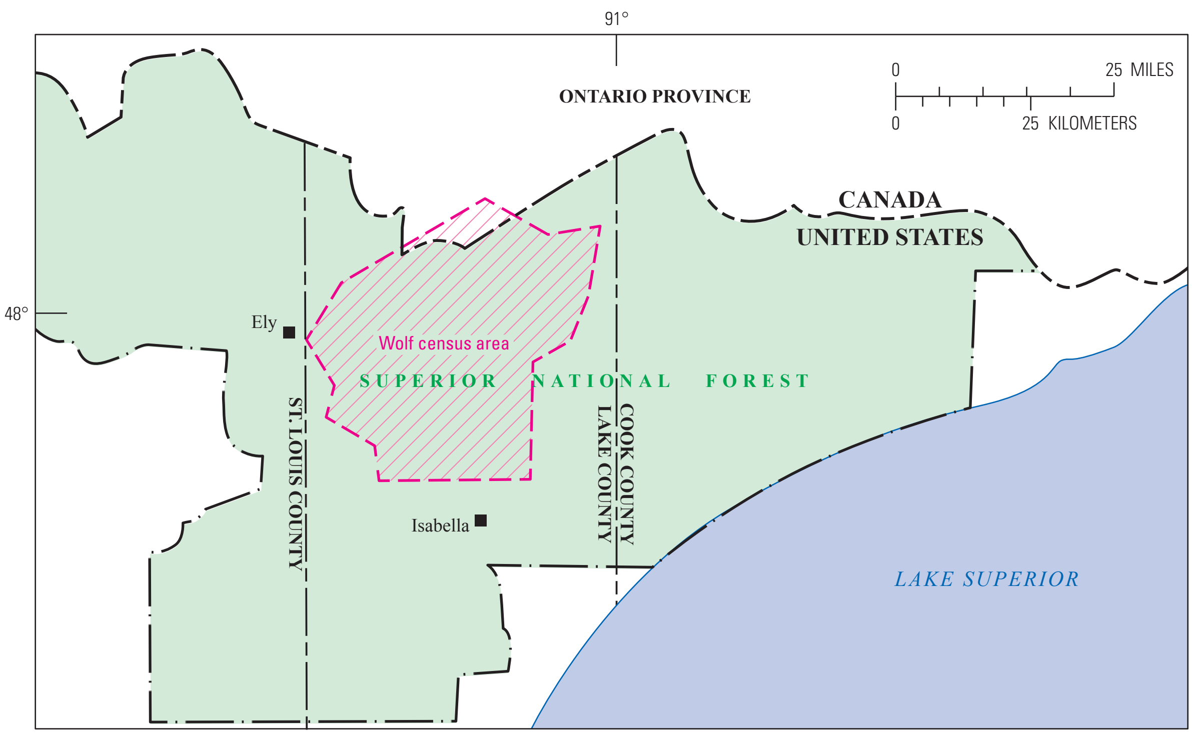

Figure 1. Location of the central Superior National Forest study area, Minnesota. (Modified from Mech, 2009)

Long-Term Research on Wolves, Wolf Packs, and Population Trends

My main objective at the beginning of the study was to determine spacing in the wolf population, but I also realized that by being able to find and identify each marked pack, I could obtain much additional information. For example, during winter I could count pack members, determine how consistently each pack maintained its size, track its movements, find and examine its kills, and locate marked wolves after death. In addition, if the packs were territorial, radiotagging a sufficient number of packs in the study area would allow me to determine the total number of wolves there by locating each pack and counting the pack members.

Over the long term, monitoring the population trajectory of wolves in the SNF became my primary objective. The longer this study continued, the more valuable the data on changes in population size became. The only other data available on wolf population trends were those from the Isle Royale study, which began in 1959 (Mech, 1966) and was continued by other researchers (Vucetich and Peterson, 2009). Although those data are of great interest, they characterize an island with no emigration or immigration and therefore cannot fully represent most populations of wolves. The opportunity to gather long-term data on a population of mainland wolves and determine the factors that drove the changes in that population was highly attractive.

The primary technique used has been live-trapping wolves in modified steel foot-traps, anesthetizing each animal (except most pups), weighing them, sampling their blood, and outfitting them with a radiocollar (Mech, 1974). Since 2000, my assistants, students, associates, and I also have estimated the age of each wolf on the basis of tooth wear (Gipson and others, 2000). We aerially radiotracked the wolves at least weekly during most years, and observed and counted them as often as possible, primarily from December through March (Mech, 1973, 1986). The largest number of wolves we saw during winter in each pack was considered to be the pack size. If the territory of a radiocollared pack fell partly outside the census area, the number of wolves assigned to the census area was multiplied by the percentage of the territory that fell in the area.

Territoriality of Wolf Packs

Each time we located a wolf, we recorded its location. We plotted these locations from October 1 through March 30 and from April 1 through September 30 each year, and used minimum convex polygons (MCPs) (Mohr, 1947) to represent territories (Mech, 1973, 1977b, 1986).

Pack territories based on radio locations were delineated for each radiocollared pack in the study area each year; however, some packs died out, new ones formed, and not all packs were radiocollared each year. The existence of nonradiocollared packs in the study area in any year was inferred from voids in the maps of the territorial mosaic. Incidental observations of nonradiocollared packs and (or) their tracks in these voids indicated the sizes of these packs. (Some data pertaining to individual packs in some years in this chapter may differ from data presented previously [Mech, 1973, 1977c, 1986] as a result of a reinterpretation of the data on the basis of additional experience with these packs.) If data on individual packs were unavailable for any year, pack-size estimates were made on the basis of the previous and subsequent years' data for packs occupying those territories. Because an unknown portion of the territories of some of these packs may have fallen outside the census area, these data are not precise. Data collected in 1966–67 and 1967–68 were based solely on observations of nonradiocollared packs during intensive aerial observations. In the estimates of population trajectory for wolves presented here, I considered the number of lone wolves to be inconsequential because they represented only a small proportion of the population, and most of these individuals were dispersers accounted for by using the maximum numbers in each pack. During the earlier part of the study, lone wolves were estimated to constitute 7 to 14 percent of the population (Mech, 1973).

U.S. Fish and Wildlife Service staff examining wolf-killed deer, Minnesota, mid-1980s. Photo by U.S. Fish and Wildlife Service.

Because monitoring the population density of wolves in the study area required the maintenance of radiocollars on several adjacent packs, the project became a data-gathering system that allowed several parallel studies. Knowing where wolf packs lived regularly and how many members each contained allowed Fred Harrington and me to approach on foot and howl to them under various conditions to determine their responses (Harrington and Mech, 1979). By tracking known packs in the snow and examining their scent marks, Roger Peters and I could describe and quantify scent-marking behaviors (Peters and Mech, 1975). Russell Rothman and I conducted a similar study on newly formed pairs of wolves (Rothman and Mech, 1979).

From 1968 through 2006, we live-trapped 712 wolves (119 female pups, 141 male pups, 239 females ≥1 year old, and 213 males ≥1 year old) in the study area, for a total of 1,044 captures of wolves from 15 or more packs. The number of packs radiocollared each year varied, and over the 38 years of radiotracking, some packs disappeared and many new ones formed. Weights of both males and females peaked at 5 or 6 years of age, with mean peak weights of 40.8 kg (89.9 pounds [lbs]) ± a standard error (SE) of 1.5 kg (3.3 lbs) and 31.2 kg (68.8 lbs) ± a SE of 2.4 kg (5.3 lbs), respectively (Mech, 2006a). From 2000 to 2004, the age structure of the population was relatively young, with only 12 percent of animals more than 1 year old being more than 5 years old (Mech, 2006b). Some wolves, however, lived to be 13 years old (Mech, 1988). Most females 4 to 9 years of age had bred, as determined by assessing nipple sizes; those that had not bred had lower average weights than those that had.

The study clearly established for the first time that each radiocollared pack inhabited a separate territory (Mech, 1973). Pimlott and others (1969, p. 78) had concluded that "the results are far from conclusive on the question of whether or not pack territoriality is involved," and Mech (1970, p. 105) had speculated that wolf packs might even have "spatio-temporal" territories. Radiotracking wolves in the SNF showed that they are territorial and that their territories are spatial (Mech, 1973). The wolves advertised and defended their territories by howling (Harrington and Mech, 1979), scent-marking (Peters and Mech, 1975), and direct aggression (Mech, 1994).

Analysis of wolf-pack territory size was not in the scope of this study. On the basis of MCPs of radiocollared wolf packs, territory sizes varied from 125 to 310 km² (48–120 mi²) through winter 1973 (Mech, 1974). During 1997–99, however, the Farm Lake pack inhabited only 23 to 33 km² (9–13 mi²), a density of 182 to 308 wolves per 1,000 km² (472–798 per 1,000 mi²), the highest density ever reported (Mech and Tracy, 2004). The overall territorial structure gradually shifted over the years, although some semblance of the early structure was still apparent in 2006–07 (fig. 2).

Maximum winter pack sizes during 233 radiocollared pack-years (1 pack radiotracked for 1 year = 1 pack-year) varied from 2 to 15 and averaged 5.6 ± 0.20 (SE). Maximum winter pack sizes for 11 packs with at least 11 years of data varied from 2 to 8 to 2 to 15 per year, with means of 3.7 ± 0.5 (SE) to 7.9 ± 1.1 (SE); the small standard errors around these means show that individual packs in the study area tended to retain their basic sizes. Approximately 67 percent of the packs included a maximum of two to six members during winter, and 90 percent included two to nine (fig. 3).

One of the more novel findings of our long-term study was the concept of the buffer zone between wolf-pack territories (Mech, 1977c). There appears to be an area of 1 to 2 km (0.6–1.3 mi) around the edge of a wolf-pack territory where neighboring packs travel but spend little time (Mech and Harper, 2002), and wolves fight there, commonly to the death, if an encounter between packs occurs (Mech, 1994). Therefore, prey seem to survive longer in these zones. When the deer population declined early in the study, most of those

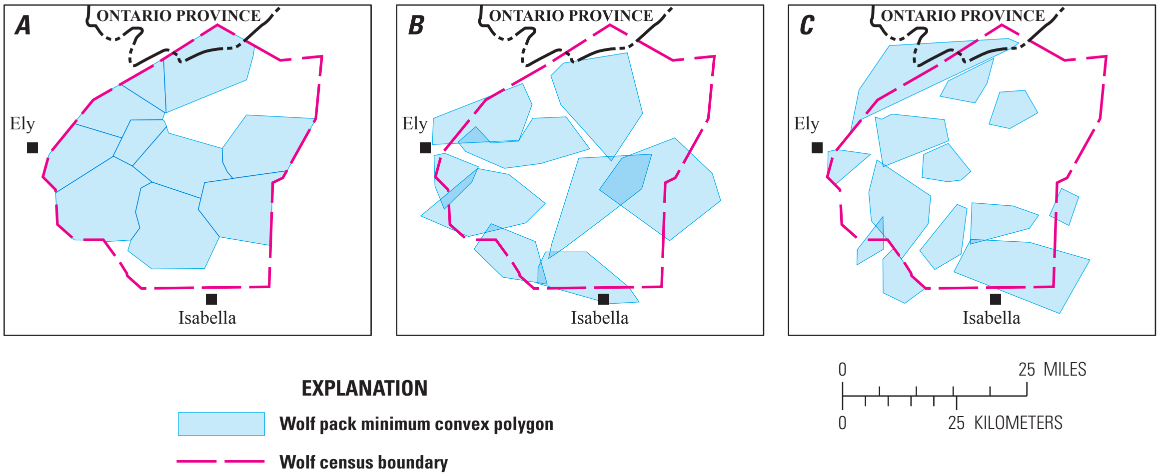

Figure 2. Territorial structure of wolf packs in the central Superior National Forest study area, Minnesota. *A*, represents the territorial structure from 1971 to 1973, but arbitrarily extends each pack's minimum convex polygon (MCP) to the boundaries of its neighbors (Mech, 1973). *B*, represents the actual MCPs for radiocollared packs during winter 1984–85 (Mech, 1986). *C*, represents the same for 2006–07. In 1984–85, a nonradiocollared wolf pack consisting of an estimated six wolves occupied an unknown part of the northeastern area, and in 2006–07, a nonradiocollared pack of eight wolves occupied the northeastern area. Several aerial surveys over the east-central area indicated that no wolves were present during winter 2006–07. (Modified from Mech, 2009)

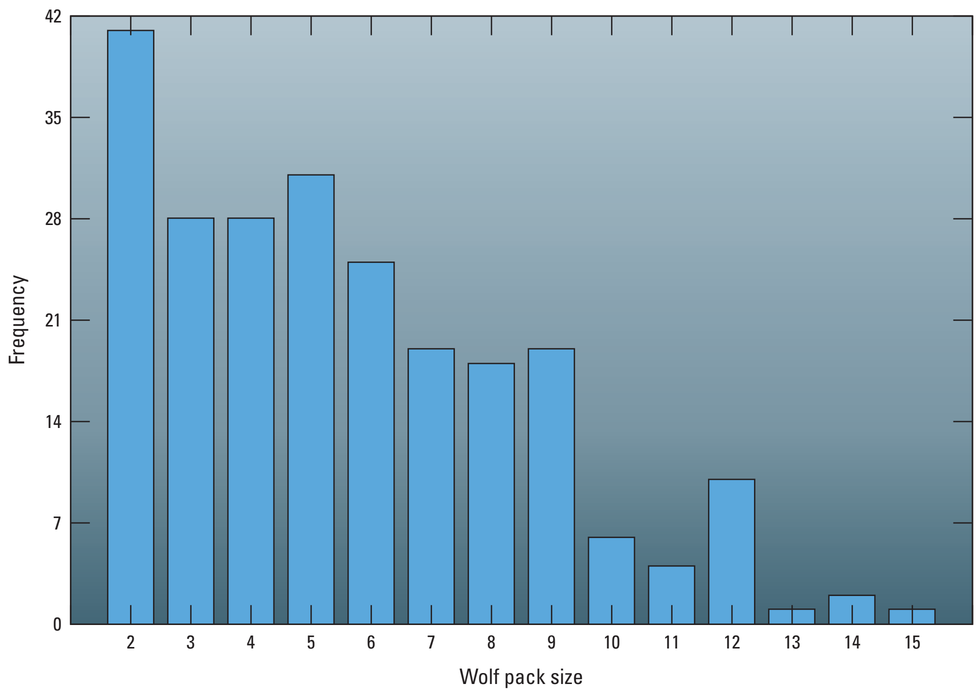

Figure 3. Distribution of maximum winter pack sizes in the central Superior National Forest study area, Minnesota, winter 1966–67 through winter 2006–07. (Modified from Mech, 2009)

remaining inhabited these zones (Hoskinson and Mech, 1976; Mech, 1977a, c; Nelson and Mech, 1981). Even after the deer population increased, we continued to find evidence of this relation (Kunkel and Mech, 1994).

Buffer zones between territories of wolf packs are important to territorial maintenance. In addition to fighting, adjacent packs scent-mark disproportionately there (Peters and Mech, 1975). Howling in and near the buffer zone undoubtedly also is important. Harrington and Mech (1979, p. 243) estimated that each pack on average is within howling range of at least one neighboring pack about 78 percent of the time, and "the probability of one pack hearing another, and the probability of encounters both increase when packs approach one another at a common border."

Population Trends

In our 2,060-km^2 (795-mi^2) study area, numbers of wolves ranged from 35 to 87 with a mean of 59 and a median of 55, and a density of 17 to 42 wolves per 1,000 km^2 (44–109 per 1,000 mi^2) with a mean of 28 per 1,000 km^2 (73 per 1,000 mi^2) and median of 27 per 1,000 km^2 (70 per 1,000 mi^2). The population decreased between the winters of 1968–69 and 1973–74 and subsequently increased ($r^2 = 0.33$; $P < 0.001$) (fig. 4). Mean pack size also increased after winter 1973–74 ($r^2 = 0.21$; $P < 0.01$). In winter 2006–07, the population was estimated to be 81 wolves, or 39 wolves per 1,000 km^2 (101 per 1,000 mi^2). Both the population and average-pack-size trends increased after 1973–74 at a mean annual rate of 0.01. Annual changes in the estimated size of the wolf population were related to annual changes in mean sizes of radiocollared packs ($r^2 = 0.35$; $P < 0.001$). Estimates of pack-size and population change were accurate because radiocollared packs were easily located and counted several times each winter.

From the beginning of the study through about the late 1980s, the proportion of wolves on a deer economy in our area decreased, and more wolves had to rely on moose. The decline in wolves through 1982 coincided with the decline in deer (fig. 5), which in turn coincided with maximum cumulative 3-year snow depth (Mech and others, 1987a). When the snowfall moderated in 1982–83, the number of deer began increasing again (Fuller and others, 2003). The trend for the wolf population that depended on deer declined curvilinearly, reaching a minimum about 1991 and gradually increasing through 2007 ($r^2 = 0.86$; $P < 0.00001$). The wolf population in the northern, northeastern, and eastern parts of the area that preyed increasingly on moose showed a reverse-sigmoid increase ($r^2 = 0.80$) from about 1978 through 2007, related ($r^2 = 0.12$; $P = 0.06$) to an increase in abundance of moose from 3,900 individuals in 1978 to 6,460 in 2007 (Mark Lennarz, Minnesota Department of Natural Resources, written commun., 2006).

Canine parvovirus (CPV) began affecting the SNF wolf population in the early 1980s and had its greatest effect

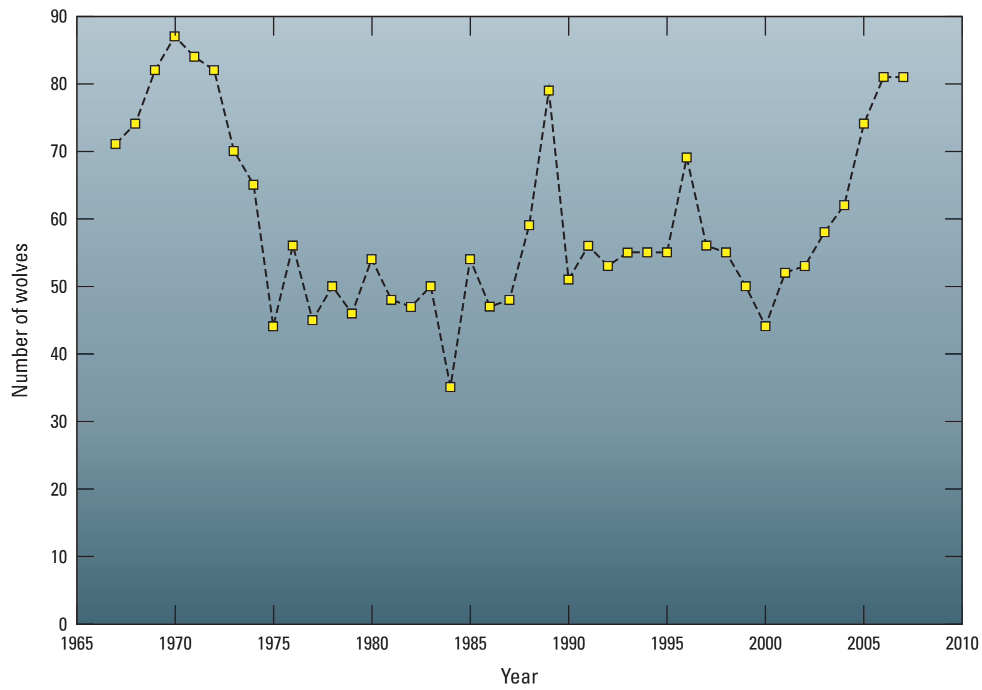

Figure 4. Size of the wolf population in the central Superior National Forest, MN, 1967–2007. (Modified from Mech, 2009)

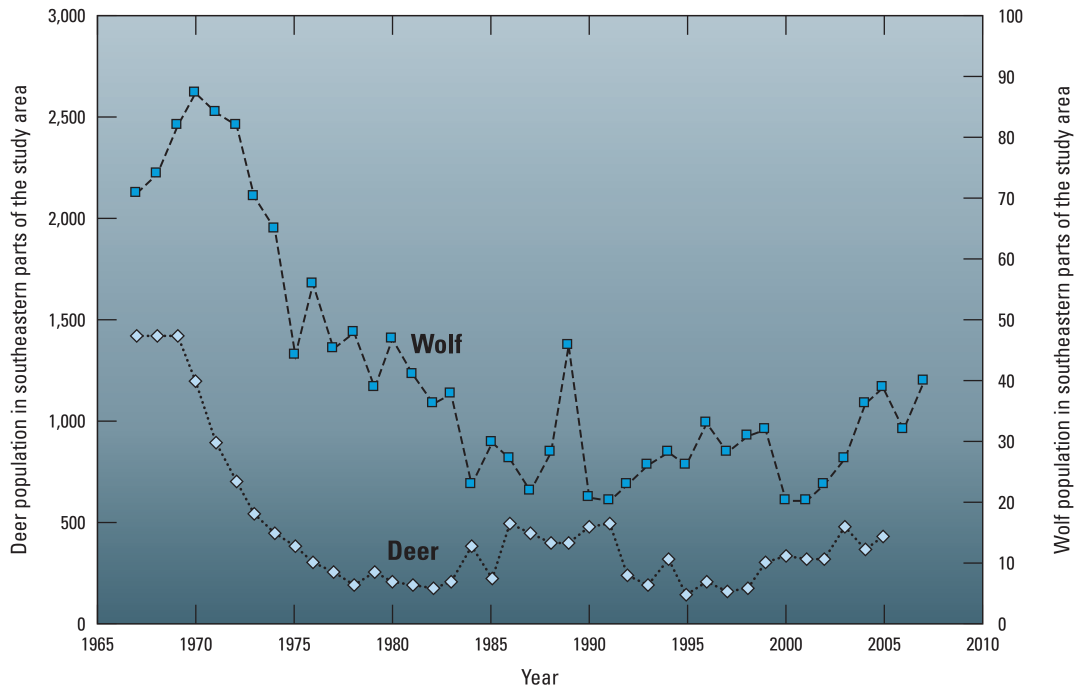

Figure 5. Size of the deer (1967–2005) and wolf (1967–2007) populations in southeastern parts of the central Superior National Forest study area, Minnesota. (Modified from Fuller and others, 2003, fig. 6.6)

from 1987 to 1993, after which the wolf population gained resistance (Mech and Goyal, 2011). From 1987 to 1993, the annual change in the wolf population was negatively related to seroprevalence of CPV (r = -0.92; P = < 0.01). The relation between CPV seroprevalence and an index of survival of wolf pups was r =- 0.73 (P = 0.06) (Mech and Goyal, 2011).

Dispersal

The wolf population occurred at a high density, and packs occupied most of the available space. Any excess production of pups therefore resulted in their dispersal as 1- to 3-year-olds (Mech, 1987; Gese and Mech, 1991). Some dispersers became nomadic in the general vicinity of their natal population, covering as much as 4,100 km^2 (1,577 mi^2) (Mech and Frenzel, 1971; Mech, 1987). Others, however, dispersed farther and helped recolonize other parts of Minnesota, as well as Wisconsin and Michigan (Mech and others, 1995; Merrill and Mech, 2000).

Studies of Deer Ecology

As I radiotracked wolves, it became clear that a thorough study of wolf ecology would require examination of the natural history and ecology of their main prey, white-tailed deer. In 1973, I began radiotagging deer in the same area and traced their movements, survival, and mortality along with those of the radiocollared wolves. Reed Hoskinson, University of Minnesota (Hoskinson and Mech, 1976), and then Mike Nelson, U.S. Fish and Wildlife Service (Nelson and Mech, 1981; Nelson, 1993), conducted the initial studies of deer. Mike remained with the project as a collaborator in charge of deer research (DelGiudice and others, 2009). Ted Floyd joined us as a graduate student and used our radiotagged deer to pioneer the technique of evaluating observability biases in aerial ungulate censuses, applying an adjustment for observability to our data (Floyd and others, 1979). We used this technique to count deer in winter through 1992 (Nelson and Mech, 1986a), until funding constraints forced us to discontinue it. Since 1992, we have used buck harvest in part of our area to index deer population trend. The number of deer in our area decreased from the late 1960s and 1970s, reached a minimum about 1981, and has slowly and intermittently increased since then (fig. 5).

From 1973 to 2007, we radiocollared 347 deer, mostly females. In addition to learning much basic natural history about these deer (for example, Hoskinson and Mech, 1976; Nelson and Mech, 1981, 1987, 1990; Nelson, 1993; Mech and McRoberts, 1990), we found that wolves rarely killed adult females during summer (Nelson and Mech, 1986c), that wolf predation was greatest when snow was deepest (Nelson and Mech, 1986b), that daily predation rates during fall migration were 16 to 107 times those of deer in wintering areas or yards (Nelson and Mech, 1991), that survival of adult females was related to the nutritional condition of their mothers, and that survival of yearlings to 2-year-olds was related to the nutritional condition of their grandmothers (Mech and others, 1991).

We learned that condition was an important factor predisposing deer to predation by wolves, and various measures of condition provided evidence. Wolves tended to kill old deer (Mech and Frenzel, 1971; Mech and Karns, 1977; Nelson and Mech, 1986a); deer with abnormalities (Mech and others, 1970; Mech and others, 1971; Mech and Karns, 1977); deer with low blood fat (Seal and others, 1978); deer with low marrow fat (Mech and Frenzel, 1971; Mech, 2007); and newborn fawns of below-average weight and (or) with low serum urea nitrogen (Kunkel and Mech, 1994).

Deer condition in winter depends on snow depth because the deeper the snow, the more difficult it is to find food (Verme, 1968). Therefore, we were not surprised to find that the size of, and trend in, deer populations were related to snow conditions (Mech and others, 1971; Mech and Karns, 1977; Mech and others, 1991; Mech and others, 1987a; McRoberts and others, 1995; but see Messier, 1995).

Follow-Up Studies from, and Adjuncts to, the Superior National Forest Wolf Research

While trapping wolves in the SNF, I quickly realized that if we could capture them more easily, we could examine them more often and better monitor their weight, blood values, and condition. Furthermore, the early collars we used commonly did not last even 1 year, so replacing them was important. The longer data were collected, the more complete a picture we could gain of the natural history of packs and the spatial organization of the population.

To determine whether radio signals could be used to remotely dart and recapture a radiocollared wolf, I consulted my former coworker, Bill Cochran (University of Minnesota), who had pioneered radiotracking (Cochran and Lord, 1963). Cochran suggested using a squib—an electrically detonated matchhead, like a tiny flashbulb. When a signal sends current through the squib, it flashes. Gunpowder in front of the squib detonates, drives a dart, and injects a drug. This technique, however, requires a radio receiver attached to the dart to pick up the signal, and an electrically detonated dart small enough to be attached to a wolf collar. The dart also has to be wolf- and waterproof, and in a position to inject a drug into a wolf. We designed the mechanism, but needed a talented machinist to produce the experimental prototypes. Lee Simmons, Director of the Henry Doorly Zoo in Topeka, KS, came to the rescue. Ulysses (Ulie) Seal of the U.S. Veterans Administration Hospital, Minneapolis, MN, and an expert on drugs suitable for use in such a collar (Seal and others, 1970), completed the development team.

The time between conception and availability of a working dart collar was about 10 years. Sometime during the final development, Rick Chapman, a graduate student on the project, was hired by 3M Company, which had sufficient interest in the concept of the collar to invest considerable time and funding to perfect it (Mech and others, 1984).

We also tested the capture collar on several deer (Mech and others, 1990) and used it to conduct studies of year-round nutritional condition in deer (DelGiudice and others, 1992) and of capture stress (DelGiudice and others, 1990). We then tested the collar successfully on wild wolves (Mech and Gese, 1992) and used it to obtain such elusive types of data as serial weights and blood values on the same wolf over long periods, as well as field metabolic rates (Nagy, 1994). The most important contribution of the capture collars, however, was unexpected. To facilitate recovery of the collar in case it failed, Chapman invented a remote-release mechanism. When that mechanism was applied to global positioning system (GPS) collars, then being developed, biologists could retrieve the GPS collars to download the data (Merrill and others, 1998). Unfortunately, because commercial companies found it much more lucrative to produce GPS collars than capture collars, the latter soon became unavailable.

Blood Sampling

During the 1970s, Ulie Seal began studying aspects of blood that had direct application to our studies. I then began a productive collaboration with him, collecting blood from both wolves and deer. Although my main objective was to determine the nutritional condition of my study animals (Seal and others, 1975; Seal and others, 1978), the samples gained more significance for their usefulness in determining seroprevalence of CPV in our wolves (Mech and Goyal, 2011).

Studies of Captive Wolves

As these projects produced new information, they also spawned many questions. Some could be answered with additional field studies, but others required a different approach. Therefore, Jane Packard (Texas A&M University), Ulie Seal, and I set up a colony of captive wolves that could be observed closely and examined frequently, blood-sampled, and otherwise studied intensively (Seal and others, 1987; Seal and Mech, 1983; Packard and others, 1983, 1985). As that project grew, Cheri Asa, St. Louis Zoo (Asa and others, 1985; 1990), James Raymer, University of Indiana (Raymer and others, 1985, 1986); and Terry Kreeger, University of Minnesota (Kreeger and others, 1990, 1997) became additional collaborators. Glenn DelGiudice (University of Minnesota Ph.D. student) made use of both the captive wolf colony (Mech and others, 1987b) and the field studies in the SNF (DelGiudice and others, 1988, 1989) to begin investigations of the nutritional condition of various animals by using analyses of urine in the snow.

Beyond the Superior National Forest

Several other spin-offs of research in the SNF increased our knowledge of wolves and wolf recovery in the Midwest and elsewhere. Because radiotracking was so productive in the SNF where the wolf population had been long established and occurred at high density, I wanted to use the same techniques to examine a recently colonized wolf population. For this I recruited Steve Fritts (USFWS) to study a recently established wolf population 290 km (181 mi) away in northwestern Minnesota (Fritts and Mech, 1981).

We also assisted the Minnesota Department of Natural Resources in starting a research project on wolves in north-central Minnesota similar to the SNF study. We taught colleagues, students, and technicians how to live-trap, anesthetize, radiotag, and radiotrack wolves. Many of them continued research on wolves in other areas (Berg and Kuehn, 1982; Fuller and others, 2003; Boyd and others, 1995; Meier and others, 1995; Burch and others, 2005; Ream and others, 1991). Furthermore, we conducted an experimental reintroduction of four wolves into northern Michigan that demonstrated that translocated wolves held for a week tended to return homeward (Weise and others, 1979).

Biologists in other areas became interested in doing similar studies, so I was invited to Italy; to Riding Mountain National Park, Canada; and to Alaska to help organize their first radiotracking studies of wolves (Boitani and Zimen, 1979; Carbyn, 1980; Peterson and others, 1984). Some of my technicians helped start projects in Portugal and Romania. Furthermore, the Patuxent wolf project hosted biologists from Sweden, Israel, Portugal, Poland, Spain, Croatia, India, Italy, Mexico, Norway, Turkey, and Austria to receive training in wolf research techniques in the SNF study area.

Wolf Depredation Control Program

Responses to complaints about livestock depredation had been managed by the Animal Damage Control Branch of the USFWS, but in 1978, when wolves in Minnesota were reclassified from endangered to threatened, I was asked to design a control program for wolves. This program had to stay within the directives of a court order while still attempting to reduce wolf depredations on livestock—that is, taking a minimal number of wolves, yet satisfying farmers and ranchers. I was appointed to direct the program, and I assigned Steve Fritts, with his newly minted Ph.D. degree, to run it. Bill Paul, a newly hired technician on the SNF project, was his main assistant. These two workers conducted a well-respected program

that continues under the auspices of the U.S. Department of Agriculture Wildlife Services (Fritts and others, 1992).

We tried many alternative nonlethal methods to reduce losses of livestock, such as translocating depredating wolves (Fritts and others, 1985), and using "fladry" (flagging), blinking lights, guard dogs, and taste aversion (Fritts and others, 1992), and conceived several other methods such as radiocontrolled shock collars, radioactivated alarm systems, human-applied scent marking, and recorded howling. None proved to be very effective or practical because the law allowed lethal control and the population was not so low (1,250 in 1978) that every last member needed to be preserved at all costs. Some of these concepts have since proved useful where lethal control is allowed or where wolf numbers are so low that extraordinary means are justified (Shivik, 2006; Musiani and others, 2003; Schultz and others, 2005). Fritts eventually was promoted to assistant leader of the Endangered Species Wildlife Research Program at Patuxent under leader Randy Perry, who had assumed Erickson's position when he retired. Fritts later went on to head the USFWS's wolf reintroduction into Yellowstone National Park with Ed Bangs.

Future Directions

To understand the functioning of natural wolf populations, it is important to follow the long-term trend of at least one long-extant population. The value of the information that science has obtained from the Isle Royale wolf population over 50 years is immeasurable (Vucetich and Peterson, 2009); however, the fact that the population is restricted to an island with no regular immigration or emigration is problematic. Because the central SNF study is the longest running, non-island study of a wolf population, continuing this investigation as long as possible is critical. Patuxent deserves credit for supporting this important work during its first two and a half decades.

Acknowledgments

This study was supported during its entirety by the U.S. Department of the Interior through the U.S. Fish and Wildlife Service (USFWS), the National Biological Survey, and the U.S. Geological Survey (USGS) (Patuxent, Midcontinent, and Northern Prairie Wildlife Research Centers), as well as by the U.S. Forest Service through the North Central Forest Experiment Station (now the North Central Research Station) and the Superior National Forest. Private funding sources included the New York Zoological Society, the World Wildlife Fund, the Mardag Foundation, the Special Projects Foundation of the Big Game Club, Wallace Dayton (Big Game Club), and Valerie Gates (Gates Family Foundation). I especially thank M.E. Nelson, J.J. Renneberg, and Tim Wallace (USFWS) as well as the many volunteers and graduate students who assisted with the field work. Shannon Barber-Meyer (USGS) and D.J. Demma (Alaska Department of Fish and Game) critiqued an early version of the manuscript and offered helpful suggestions for improvement.

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Muskrat (*Ondatra zibethicus*) on water, Patuxent Research Refuge, Laurel, MD, 1980. Photo by Matthew C. Perry, U.S. Fish and Wildlife Service.