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Chapter 2
Long-Term Research on Wolves in the Superior National Forest

L. David Mech

2.1 Background

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. This line of wolves had withstood not only the various natural environmental factors that had shaped them through their evolution but also the logging, fires, market hunting of prey animals, and even the bounties, aerial hunting, and poisoning that had exterminated their ancestors and their dispersed offspring only a few wolf pack territories away in more accessible areas. The dense and extensive stretch of wild land that is now labeled the Boundary Waters Canoe Area Wilderness had proven too formidable a barrier even for the foes of the wolf who had strived to eliminate the animal and had succeeded everywhere else in the contiguous 48 states of the 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 km off Minnesota's coast (Vucetich and Peterson, this volume). Those wolves had crossed Lake Superior's rare ice bridge to the 540-km^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.

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 an interesting 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 evolved in North America (*Canis lycaon*), such as inhabit southeastern Ontario (Wilson et al. 2000). Wolves with both types of genetic markers sometimes live in the same pack, and apparently

A.P. Wydeven et al. (eds.), *Recovery of Gray Wolves in the Great Lakes Region of the United States*,
DOI: 10.1007/978-0-387-85952-1_2, © Springer Science+Business Media, LLC 2009

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many wolves in Minnesota are hybrids between the two types (Mech and Federoff 2002; Wilson et al. unpublished data).

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 ground-breaking studies had provided some insights into the biology of wolves (e.g., Olson 1938; Murie 1944; Cowan 1947; Stenlund 1955; Mech 1966; Pimlott et al. 1969). However, because wolves were so scarce in the contiguous United States, and lived in such 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 radio-tracking (Cochran and Lord 1963). G.B. Kolenosky and Johnston (1967) had proved in Ontario that radio-tracking 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 radio-tracking to determine whether wolf packs were territorial (Mech and Frenzel 1971). My preliminary aerial observations during 1966–1967 and 1967–1968 had shown that there were several packs of different sizes and color combinations. However, without reliable identifiers for each pack, and without being able to find packs systematically, I had only a subjective notion that they were territorial. Thus, radio-tracking wolves from aircraft, which allowed both identifying individuals and systematically locating them, was the ideal method to answer this question.

2.2 Study Area

My study area encompassed some 2,060 km^2 immediately east of Ely in the east-central SNF (48°N, 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 (Fig. 2.1). 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 elevations ranging from 325 to 700 m above sea level. Winter temperatures below −35°C are not unusual, and snow depths (usually from mid-November through mid-April) generally range from 50 to 75 cm on the level. Summer temperatures rarely exceed +35°C. Conifers predominate in the forest overstory, 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*). However, as a result of extensive cutting and fires, much of the coniferous cover is interspersed with large stands of white birch (*Betula papyrifera*) and aspen

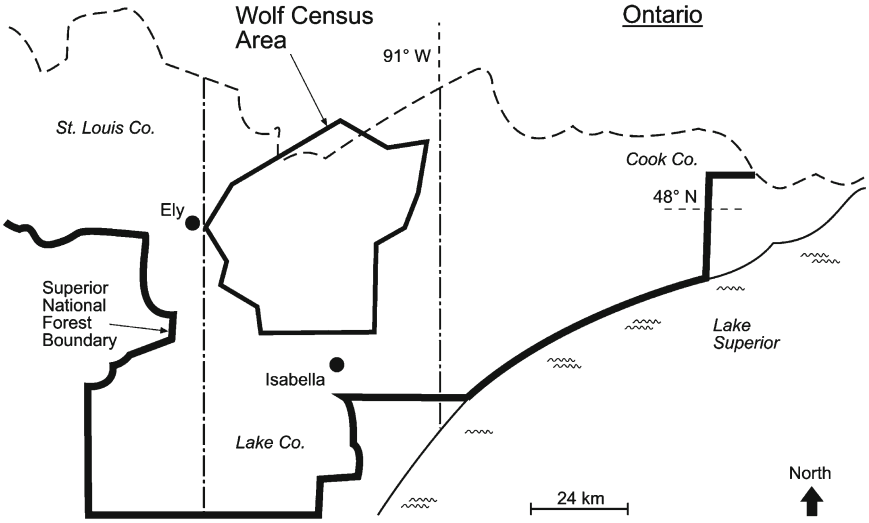

Fig. 2.1 The central Superior National Forest study area

(*Populus tremuloides*). Heinselman (1993) presented 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 high numbers of wolves (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 32% 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). 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 et al. 1975), since about 1975 the primary prey of wolves inhabiting the northeastern part has been moose, whereas wolves in the southwestern part have consumed primarily deer.

Year-around hunting and trapping of wolves was legal until October 1970 when they were fully protected on federal land within the SNF by the US Forest Service. In August 1974, wolves were protected under the Endangered Species Act of 1973. In 1978, wolves in Minnesota were reclassified to threatened but remained legally protected except for depredation control outside the SNF (Fritts et al. 1992). However, illegal taking of wolves continued, primarily in fall and winter (Mech 1977a, unpublished data). In March 2007, wolves in the upper Midwest, including Minnesota, were removed from the Endangered Species List though this ruling was recently overturned.

2.3 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 other 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, then by radio-tagging enough packs in the study area, I could 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 basic objective. The longer this study continued, the more valuable the data on changes in population size. The only other data available on wolf population trends were those from Isle Royale, which began in 1959 (Mech 1966) and continues today (Vucetich and Peterson, this volume). Those data are of great interest. However, they do pertain to an island with no emigration or immigration, and cannot fully represent most populations of wolves. The opportunity to gather long-term data on a population of mainland wolves and determine what drove the changes in that population was highly attractive.

The primary technique used has been live-trapping wolves in modified steel foot-traps, anaesthetizing each of them (except most pups), weighing them, blood sampling them, and outfitting them with a radio-collar (Mech 1974). Since 2000 my assistants, students, associates, and I also estimated the age of each wolf based on tooth wear (Gipson et al. 2000). We aerially radio-tracked 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 most wolves we saw during winter in each pack was considered the pack size. If a radioed pack territory fell partly outside the census area, the number of wolves I assigned to the census area was proportioned to the proportion of the territory in the area.

2.3.1 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 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 radioed pack in the study area each year. However, some packs died out, new ones formed, and not all packs were radioed each year. The existence of nonradioed packs in the study area in any year was inferred from voids in the maps of the territorial mosaic. Incidental observations of nonradioed packs and/or their tracks in these voids

indicated sizes of these packs. (Some data pertaining to individual packs in some years in this chapter may differ from data presented previously [Mech 1973, 1977a, 1986] because of reinterpretation of the data based on additional experience with these packs.) If data on individual packs were unavailable in any year, pack size estimates were made based on the previous and subsequent year's 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 in 1966–1967 and 1967–1968 were based solely on observations of nonradioed packs during intensive aerial observations. In the estimates of population trajectory for wolves presented in this chapter, I considered the number of lone wolves inconsequential because their proportion of the population was low 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 at 7–14% of the population (Mech 1973).

With monitoring the population density of wolves in the study area requiring the maintenance of radio-collars on several adjacent packs, the project became a data-gathering system that allowed several parallel studies. By knowing where wolf packs lived regularly and how many members each contained, Fred Harrington and I could 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 radioed each year varied, and over the 38 years of radio-tracking, some packs disappeared and many new ones were formed. Weights of both males and females peaked at 5 or 6 years of age, with mean peak weights of 40.8 ± 1.5 (SE) kg and 31.2 ± 2.4 (SE) kg, respectively (Mech 2006a). The age structure of the population between 2000 and 2004 was relatively young, with only 12% of animals >1-year-old being >5 years of age (Mech 2006b). Some wolves, however, lived to be 13-years old (Mech 1988). Most females 4–9 years of age had bred based on assessment of nipple sizes; those that had not bred had lower average weights than those that had.

Each radioed pack inhabited a separate territory, the first time that this fact was clearly established (Mech 1973). Pimlott et al. (1969, p. 78) had concluded that "the results are far from conclusive on the question of whether or not pack territoriality is involved." Mech (1970, p. 105) had speculated that wolf packs might even have "spatio-temporal" territories. Radio-tracking wolves in the SNF showed that wolves were territorial and that their territories were 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 is not in the scope of this chapter. Based on the MCPs of radioed wolf packs, territory sizes through winter 1973 varied from 125 to 310 km^2 (Mech 1974). However, during 1997–1999, the Farm Lake pack inhabited only 23–33 km^2, a density of 182–308 wolves per 1,000 km^2, 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 is still apparent (Fig. 2.2).

Maximum winter pack sizes during 233 radioed-pack-years (one pack radio-tracked 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 2–8 to 2–15 per year with means of 3.7 ± 0.5 (SE) to 7.9 ± 1.1 (SE); the SEs around these means show that individual packs in the study area tended to retain their basic sizes (Appendix). Approximately 67% of the packs included a maximum of two to six members during winter, and 90% included two to nine (Fig. 2.3).

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 1–2 km around the edge of a wolf-pack territory where neighboring packs travel but spend less time (Mech and Harper 2002), and wolves fight there if an encounter between packs occurs, often to the death (Mech 1994). Thus, prey seems to survive longer in these zones. When deer declined early in the study, most of those remaining inhabited these zones (Hoskinson and Mech 1976; Mech 1977b, c; Nelson and Mech 1981). Even after the deer population increased, we continued to find evidence of this relationship (Kunkel and Mech 1994).

Buffer zones between territories of wolf packs are quite important to territorial maintenance. Besides fighting there, adjacent packs also scent-mark disproportionately there (Peters and Mech 1975). No doubt howling in and near the buffer zone is also important. Harrington and Mech (1979, p. 243) estimated that each pack on

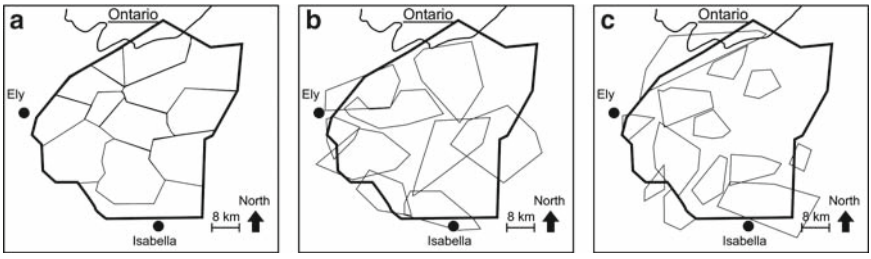

Fig. 2.2 The territorial structure of wolf packs in the central Superior National Forest study area. "A" represents the territorial structure from 1971 to 1973 but arbitrarily extends each pack's minimum convex polygon (*MCP*) to the boundaries of its neighbors (Mech 1973). "B" represents the actual MCPs for radioed packs during winter 1984–1985 (Mech 1986). "C" represents the same for 2006–2007. In 1984–1985, a nonradioed wolf pack with an estimated six wolves occupied an unknown part of the northeastern area, and in 2006–2007, a nonradioed pack of eight wolves occupied the northeastern area. Several aerial surveys over the east-central area indicated no wolves there during winter 2006–2007

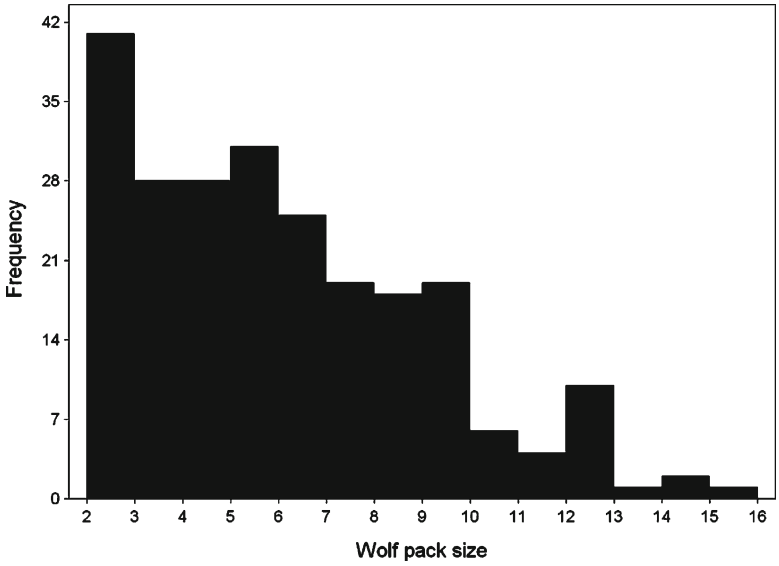

Fig. 2.3 Distribution of maximum winter pack sizes in the central Superior National Forest study area

average is within howling range of at least one neighboring pack about 78% 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."

2.3.2 Population Trends

In our 2,060-km^2 study area, numbers of wolves ranged from 35 to 87, with a mean of 59 and a median of 55 (Appendix), a density of 17–42 wolves per 1,000 km^2 with a mean of 28 per 1,000 km^2 and a median of 27 per 1,000 km^2. The population dropped between the winters of 1968–1969 to 1973–1974 and then increased ($r^2 = 0.33$; $P < 0.001$; Fig. 2.4). Mean pack size also increased after winter 1973–1974 ($r^2 = 0.21$; $P < 0.01$). In winter 2006–2007, the population was estimated to be 81 wolves, or 39 wolves per 1,000 km^2. Both the population and average-pack-size trend increased after 1973–1974 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 radioed packs ($r^2 = 0.35$; $P < 0.001$). Estimates of pack size and population change were accurate because radioed 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 dropped, and more wolves had to rely on moose. The decline in wolves through 1982 coincided with the decline in deer (Fig. 2.5), which in turn coincided with maximum cumulative 3-year snow depth

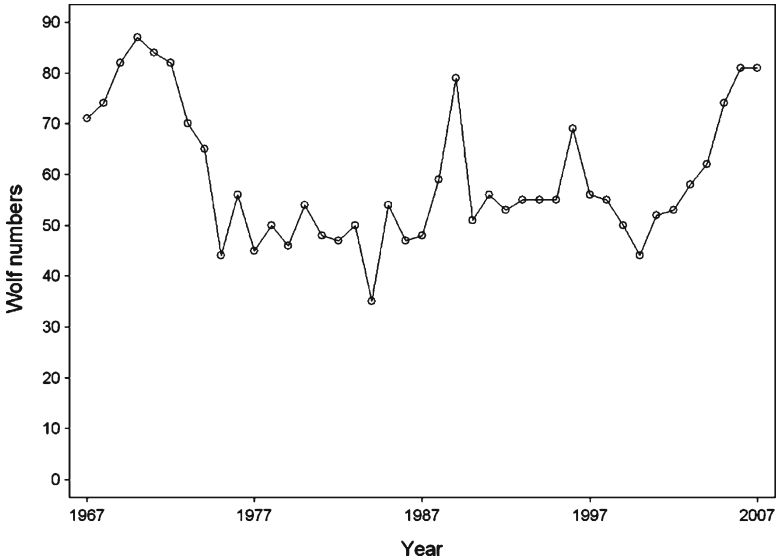

Fig. 2.4 Trend in size of the wolf population in the central Superior National Forest

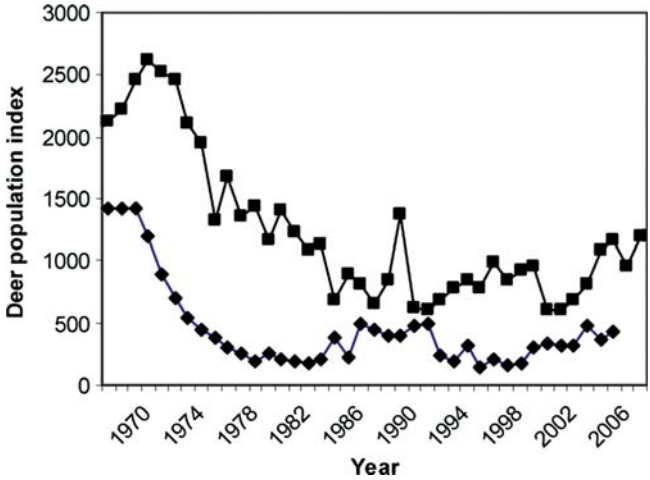

Fig. 2.5 Trend in sizes of the deer (*lower curve*) and wolf (*upper curve*) populations in southwestern portions of the central Superior National Forest study area. Wolf trend is actual wolf population times 30. (Updated from Fuller, Mech, and Fitts-Cochrane 2003, Fig. 6.6)

(Mech et al. 1987a). When the snowfall moderated in 1982–1983, deer began increasing again (Fuller et al. 2003). The trend for the wolf population that depended on deer declined curvilinearly, bottoming out 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 increasing trend (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 (M. Lennarz, MN DNR, personal communication).

Canine parvovirus (CPV) began affecting the wolf population in the early 1980s and continues to do so (Mech et al. 2008), greatly complicating the relationships among snow depth, wolves, and prey that had been so apparent. From 1984 to 2004, the annual change in the wolf population was negatively related to seroprevalence of CPV (r^2 = 0.51; P = < 0.01), and the change in the wolf population was related to an index of survival of wolf pups (r^2 = 0.22; P = 0.03) (Mech et al. 2008).

2.3.3 Dispersal

Our 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 1–3-year olds (Mech 1987; Gese and Mech 1991). Some dispersers floated around their natal population, covering as much as 4,100 km^2 (Mech and Frenzel 1971; Mech 1987). However, others dispersed farther and helped recolonize other parts of Minnesota, as well as Wisconsin and Michigan (Mech et al. 1995; Merrill and Mech 2000).

2.4 Studies of the Ecology of Deer

As I radio-tracked wolves, it became clear that to conduct a thorough study of wolf ecology, I also had to examine the natural history and ecology of its main prey, white-tailed deer. In 1973, I began radio-tagging deer in the same area and traced their movements, survival, and mortality along with those of the radioed wolves. Reed Hoskinson (Hoskinson and Mech 1976), and then Mike Nelson (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 et al., this volume). Ted Floyd used our radio-tagged deer to pioneer the technique of evaluating observability biases in aerial ungulate censuses and applied an adjustment for observability to our data (Floyd et al. 1979). We used this technique to count deer in winter through 1992 (Nelson and Mech 1986a, unpublished data), until funding constraints forced us to discontinue it. Since 1992, we have used buck harvest in the Isabella part of our area to index deer population trends (Mark Lenarz, MN DNR, personal communication). Deer numbers decreased in our area from the late 1960s

and 1970s, bottomed out about 1981, and have slowly and intermittently increased since (Fig. 2.5).

Between 1973 and 2007, we radio-collared 347 deer, mostly females. Besides learning much basic natural history about these deer (e.g., Hoskinson and Mech 1976; Nelson and Mech 1981, 1987, 1990; Nelson 1993; Mech and McRoberts 1990), we also found that during summer wolves only rarely killed adult females (Nelson and Mech 1986c), that wolf predation was greatest during deepest snow (Nelson and Mech 1986b), that daily predation rates during fall migration were 16–107 times that 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 nutrition of their grandmothers (Mech et al. 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 et al. 1970; Mech et al. 1971; Mech and Karns 1977), deer with low blood fat (Seal et al. 1978) and 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).

Condition of deer in winter depends on snow depth because the deeper the snow, the harder it is to find food (Verme 1968). Thus, we were not surprised to find that deer numbers and population trend were related to snow conditions (Mech et al. 1971, 1987, 1991; Mech and Karns 1977; McRoberts et al. 1995; c.f. Messier 1995).

2.5 Spin-Offs from, and Adjuncts to, the SNF Wolf Research

2.5.1 Development of a Capture Collar

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 weights, blood values, and conditions. Furthermore, the early collars we used often lasted for <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 if we could use radio signals to remotely dart and recapture a radio-collared wolf, I consulted my former coworker, Bill Cochran, who had pioneered radio-tracking (Cochran and Lord 1963). Cochran suggested using a squib, which was an electrically detonated match-head, like a tiny flashbulb. When a signal sent current through the squib, it flashed. Gunpowder in front of the squib would detonate, drive a dart, and inject a drug. That, however, would require 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 had to be wolf and water proof, 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, Kansas, came to the rescue. Ulysses (Ulie) Seal, an expert on drugs suitable to use in such a collar (Seal et al. 1970), completed the development team.

The time between conception and 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, and that company was interested enough in the concept of the collar to invest considerable time and funding to perfect it (Mech et al. 1984). We also tested the capture collar on several deer (Mech et al. 1990) and used it to conduct studies of year-around nutritional condition in deer (DelGiudice et al. 1992) and of capture stress (DelGiudice et al. 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 of the same wolf over long periods, as well as of 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 et al. 1998). Unfortunately, commercial companies found it much more lucrative to produce GPS collars than capture collars, so the latter soon became unavailable.

2.5.2 Blood Sampling

During the 1970s, Ulysses Seal began studying blood. 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 et al. 1975, 1978), the samples gained more significance in determining seroprevalence of CPV in our wolves (Mech et al. 2008).

2.5.3 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. Thus, Jane Packard, 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 et al. 1987; Seal and Mech 1983; Packard et al. 1983, 1985). As that project grew, Cheri Asa (Asa et al. 1985, 1990), James Raymer (Raymer et al. 1985, 1986), and Terry Kreeger (Kreeger et al. 1990, 1997) became additional collaborators. Glenn DelGiudice made use of both the captive wolf colony (Mech et al. 1987b) and the field studies in the SNF (DelGiudice et al. 1988, 1989) to begin investigations on the nutritional condition of various animals using analyses of urine in the snow.

2.5.4 Beyond the SNF

Several other spin-offs of research in the SNF contributed to increased knowledge of wolves and wolf recovery in the Midwest and elsewhere. Because radio-tracking 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 to study a wolf population just getting a toehold 290 km 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, radio-tag, and radio-track wolves. Many of them continued research on wolves in other areas (Berg and Kuehn 1982; Ream et al. 1991; Boyd et al. 1995; Meier et al. 1995; Fuller et al. 2003; Burch et al. 2005). Furthermore, we conducted an experimental reintroduction of four wolves into northern Michigan that demonstrated that translocated wolves held for only a week before release tended to return homeward (Weise et al. 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 radio-tracking studies of wolves (Boitani and Zimen 1979; Carbyn 1980; Peterson et al. 1984). Some of my technicians helped start projects in Portugal and Romania. Furthermore, the SNF project hosted biologists from Sweden, Israel, Portugal, Poland, Spain, Croatia, India, Italy, Mexico, Norway, Turkey, and Austria to receive training in wolf research techniques.

2.5.5 Wolf Depredation Control Program

Responses to complaints about livestock depredation had been conducted by the Animal Damage Control Branch of the US Fish and Wildlife Service, 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 keep within the directives of a court order while still attempting to reduce wolf depredations on livestock, taking minimal wolves, yet satisfying farmers and ranchers. I was appointed to direct the program, and I put Steve Fritts, with his new Ph.D. degree, in charge of it. Bill Paul, a recent technician on the SNF project, was hired as his main assistant. These two workers conducted a well-respected program that continues under the auspices of the USDA Wildlife Services (Fritts et al. 1992).

We tried many alternative nonlethal methods to reduce losses of livestock, such as translocating depredating wolves (Fritts et al. 1985), using “fladry” (flagging),

blinking lights, guard dogs, and taste aversion (Fritts et al. 1992), and conceived several others such as radio-controlled shock collars, radio-activated alarm systems, human-applied scent marking, and recorded howling. None was very effective or practical because the law allowed lethal control and the population was not so low (1,250 in 1978) that every last wolf needed to be preserved at all costs. Some of these concepts have since proven useful where lethal control is not allowed or where wolf numbers are so low that extraordinary means are justified (Musiani et al. 2003; Schultz et al. 2005; Shivik 2006).

2.6 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 wolf population on Isle Royale over 50 years is immeasurable (Vucetich and Peterson, this volume). However, the fact that population is restricted to an island with no regular immigration or emigration is problematic. The central SNF study is the longest-running, nonisland study of a wolf population. As such, it is extremely important to continue this investigation as long as possible. My hope is that this summary will help serve that end.

Acknowledgments This study was supported by the US Department of the Interior during its entirety through the US Fish and Wildlife Service, the National Biological Survey, and the US Geological Survey and Patuxent Wildlife Research Center, Midcontinent Wildlife Research Center, and Northern Prairie Wildlife Research Center, as well as by the US Forest Service through North Central Forest Experiment Station (now North Central Research Station) and the SNF. 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, and Valerie Gates. I especially thank M. E. Nelson, J. Renneberg, and T. Wallace as well as numerous volunteers and graduate students who assisted with the fieldwork. S. Barber-Meyer and D. J. Demma critiqued an early draft of the manuscript and offered helpful suggestions for improvement.

Appendix

Numbers of wolves in each pack in the east-central Superior National Forest study area. See Mech (1986) for 1966–1967 to 1984–1985. Underlines indicate pack was radioed; zeros, that the pack did not exist or was outside the census area; parentheses, that estimate was subjective; hyphens, that information unknown. Nonunderlined numbers not in parentheses are based on observation of nonradioed pack or its tracks. Entries with two numbers (e.g., 3 + 1) indicate different proportions of a pack in and outside the census area.

Winter	Birch Lake	Clear Lake	Ensign Lake	Farm Lake	Little Gabbro	Jack-pine	Mani-waki	Malberg Lake	Nip Creek	Pagami Lake	Perent	Quadga Lake	Saw-bill	Star-light	Wood Lake	Total[a]	Economy	
																	Deer[b]	Moose
1985–1986	6	0	0	0	3	7	8	7	0	1	0	5	2	0	8	47	27	20
1986–1987	8	0	(7)	0	3	3	4	(7)	0	(3)	0	8	2	0	3	48	22	26
1987–1988	5	0	(7)	0	4	2	(8)	(9)	0	5	0	(7)	8	0	4	59	28	31
1988–1989	9	0	4	0	8	6	12	11	0	(5)	0	6	12	0	6	79	46	33
1989–1990	4	0	5	0	5	5	5	3	0	5	0	3	14	0	2	51	21	30
1990–1991	4	0	0	0	5	6	4	2	0	3	0	5	5	0	2	56	20	36
1991–1992	4	0	7	0	6	11	0	7	0	9	0	3	4	0	2	53	23	30
1992–1993	3	0	-	0	5	14	0	6	0	11	0	-	2	0	4	55	26	29
1993–1994	4	0	0	0	4	11	0	(8)	0	15	0	(0)	4	0	9	55	28	27
1994–1995	6	0	5	0	3	12	2	6	0	12	0	0	4	0	5	55	26	29
1995–1996	10	0	4	0	5	12	3	9	0	14	0	0	6	0	4	69	33	36
1996–1997	6	0	6	0	3	10	3	12	0	2	0	0	5	0	7	56	28	28
1997–1998	3	0	6	2	6	9	3	8	1	2	0	0	5	0	5	55	31	24
1998–1999	3	0	6	4	4	9	0	4	2	5	0	0	3	0	6	50	32	18

Winter	Birch Lake	Clear Lake	Ensign Lake	Farm Lake	Little Gabbro	Jack-pine	Mani-waki	Malberg Lake	Nip Creek	Pagami Lake	Perent	Quadga Lake	Saw-bill	Star-light	Wood Lake	Total[a]	Economy	
																	Deer[b]	Moose
1999–2000	2	0	6	3 + 1	1 + 1	9 + 1	0	12	0	3	0	0	4 + 1	0	4	44	20	24
2000–2001	3	0	10	4	2	9	0	11	0	6	0	0	5	0	2	52	20	32
2001–2002	2	0	2	6 + 1	2	6	0	12	1	4	0	0	7	0	3	53	23	30
2002–2003	2	5	7	2	2	7	0	6 + 6	1	2	3	0	7	0	5	58	27	31
2003–2004	3	7	6	5 + 1	1	7	0	4 + 4	3	2	4	0	5 + 1	0	7	62	36	26
2004–2005	1	12	6	6	0	7 + 1	0	2 + 2	4 + 4	0	8	2	9	5	9	74	39	35
2005–2006	0	7	8	10	0	7	0	8	0	0	9	8	8 + 3	8	8	81	32	49
2006–2007	2	8	7	12	0	6	0	8	3	0	7	6	4 + 3	3	9	81	40	41
N[c]	28	14[d]	15		25	28	11	12		13		15	28		30			
Range	2–10	2–9	2–10		2–8	2–14	3–13	2–12		2–15		2–8	2–14		2–9			
Mean	4.1	3.7	6.3		3.9	7.3	7.5	7.9		6.6		4.9	6.0		5.4			
SE	0.4	0.5	0.8		0.4	0.6	0.9	1.1		1.1		0.5	0.6		0.5			

[a]The difference between the total and the sum of the pack numbers represent additional wolves in unknown packs straddling the census area border

[b]From 1977–1978 to 1983–1984, excludes the Malberg Pack; from 1984–1985 through 1988–1989 excludes the Malberg, Quadga, Maniwaki, and Ensign Packs; in 1989–1990, excludes packs excluded previously and Sawbill Pack; from 1990–1991 through 1999–2000 excludes packs excluded previously and Pagami Pack; after 2000–2001, excludes packs excluded previously and Perent and Starlight Packs

[c]These summary data are only for packs with at least 11 years of data, from 1966–1967 to 2006–2007. See Mech (1986) for the pack size data from 1966–1967 through 1984–1985

[d]Data in this summary column are for the Harris L. Pack (Mech 1986) which had disappeared by 1985–1986; *SE* standard error

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