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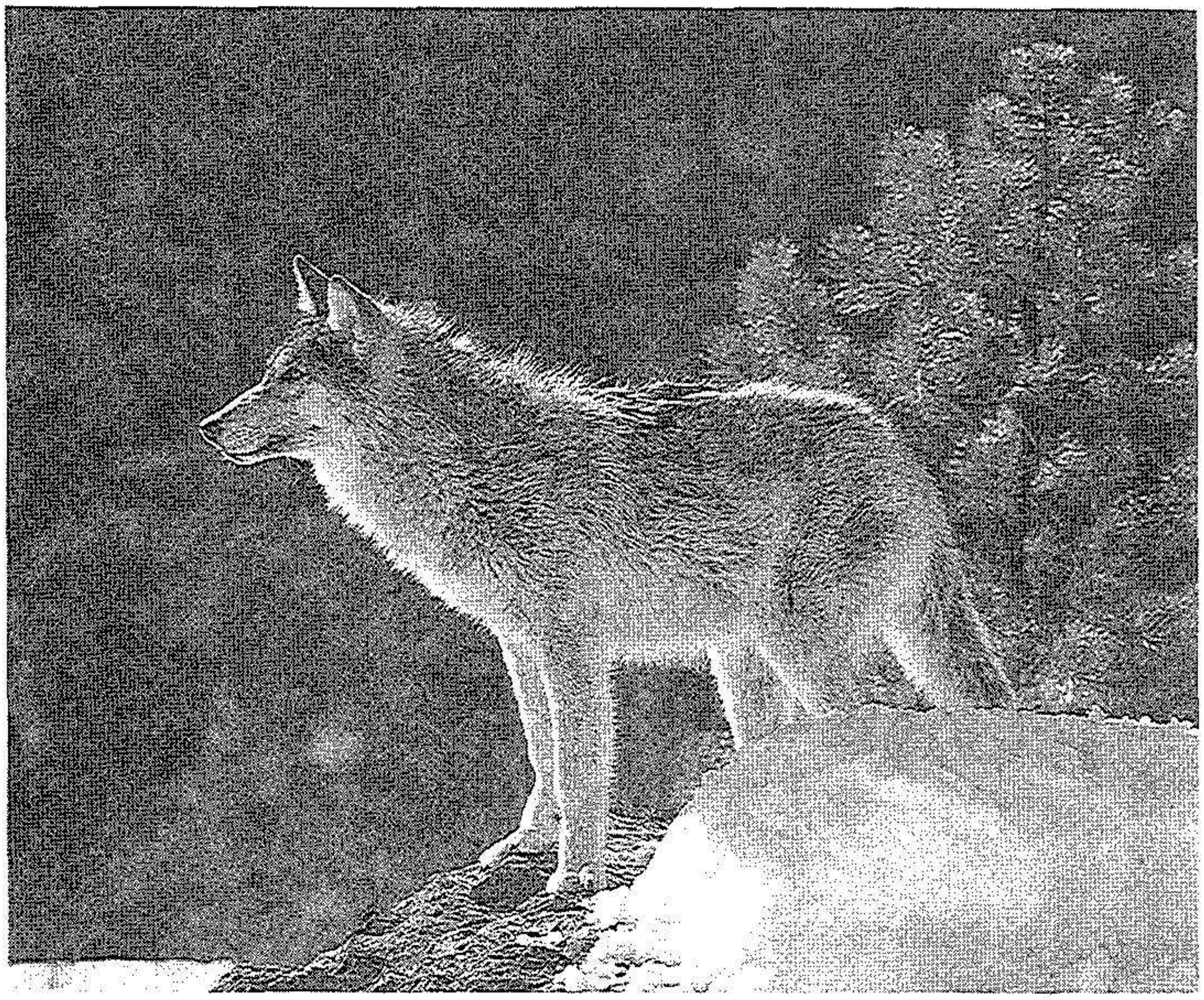

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Cover photo: Gray wolf (*Canis lupus*). Photo by Alan and Sandy Carey.

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Ecological Issues on Reintroducing Wolves Into Yellowstone National Park

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Frontispiece. A gray wolf (*Canis lupus*) gnaws on a moose (*Alces alces*) antler. Photo by Alan and Sandy Carey.

Preface

Yellowstone National Park was established in 1872, but harvest of its big game animals continued through the 1880's. Thousands of elk (*Cervus elaphus*), bighorn sheep (*Ovis canadensis*), deer (*Odocoileus* spp.), antelope (*Antilocapra americana*), moose (*Alces alces*), and bison (*Bison bison*) were killed for their meat, tongues, and hides. Their carcasses were strychnine-poisoned to kill coyotes (*Canis latrans*), wolves (*Canis lupus*), and wolverines (*Gulo gulo*). In 1886, the U.S. Army was assigned to guard and protect Yellowstone's features and wildlife, but there was still pressure to control predators.

In 1914, the U.S. Congress passed a law to eliminate predatory animals from all public lands, including national parks. By 1922, some people questioned the destruction of wolves in Yellowstone, but from 1914 to 1926, more than 100 wolves were killed in the park. Wolf pack activity was eliminated and has not been confirmed since the 1930's. About the same time, more than 100 mountain lions (*Felis concolor*) and more than 4,000 coyotes were killed in Yellowstone.

By 1933, National Park Service policy stated that "no native predator shall be destroyed on account of its normal utilization of any other park animal" and that "no management measure or other interference with biotic relationships shall be undertaken prior to a properly conducted investigation." Yet predator control continued in Yellowstone National Park through the 1934–35 winter. Predators still were controlled outside park boundaries with cyanide "coyote getters" and Compound 1080 baits until stopped by an executive order in the early 1970's.

The Endangered Species Act of 1973 recognized that economic growth and development may endanger some fish, wildlife, and plants. The act provides for conserving endangered and threatened species and the ecosystems on which they depend and states "[It is] the policy of Congress that all Federal departments and agencies shall seek to conserve endangered species and threatened species."

The gray wolf is listed as endangered in the contiguous 48 states except Minnesota, where it is listed as threatened. Under provisions of the Endangered Species Act, the U.S. Fish and Wildlife Service produced a *Northern Rocky Mountain Wolf Recovery Plan* in 1980. A revised plan was approved on 3 August 1987. The plan offered strategies for conserving gray wolves in the northern Rocky Mountains. Three areas were considered appropriate for wolf recovery: northwestern Montana, central Idaho, and the Greater Yellowstone area. The plan projected that wolves would naturally colonize the first two areas. In fact, a small wolf population did colonize an area of northwestern Montana during the 1980's, and wolf activity has been reported in central Idaho.

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The 1987 wolf recovery plan recommended reintroducing wolves to Yellowstone because natural recolonization seemed unlikely. In 1987, Congressman Wayne Owens (Utah) introduced H.R. 3378 "to require the National Park Service to reintroduce wolves into Yellowstone National Park." In 1989, Congressman Wayne Owens introduced H.R. 2786 "to provide for a timely analysis [Environmental Impact Statement] of all factors relating to the restoration of gray wolves to Yellowstone" and established a timetable for selecting and implementing the preferred alternative. Separate from provisions in the Endangered Species Act, Senator James McClure (Idaho) introduced S. 2674 in 1990 to reestablish wolves in Yellowstone National Park and the central Idaho wilderness areas. Other congressional members expressed strong opposition to wolf reintroduction. Because of the controversy over wolf restoration, in 1988 the Senate–House Interior Appropriations Conference Committee allotted $200,000 to the National Park Service and U.S. Fish and Wildlife Service to study five questions and issues involving wolf restoration in the Greater Yellowstone area:

1. The issue of whether wolves would or would not be controlled either in or outside the park;
2. How would a reintroduced population of wolves affect the prey base in Yellowstone National Park and big game hunting in areas surrounding the park;
3. Would a reintroduced population of wolves harm or benefit grizzly bears in the vicinity of the park;
4. The issue of clarification and delineation of wolf management zone boundaries for reintroduction; and
5. An experienced wolf coordinator with the U.S. Fish and Wildlife Service will oversee the program in full cooperation with the National Park Service (see H.R. Report 862, 100th Congress, 2nd Session, 1988, pages 14–15).

Steven H. Fritts was appointed Northern Rocky Mountain Wolf Recovery Coordinator, Montana–Wyoming Field Office, U.S. Fish and Wildlife Service. His appointment fulfilled the item 5 requirement.

The National Park Service and U.S. Fish and Wildlife Service used three approaches to answer items 1–4: extensive literature surveys; consultation and compilation of opinions from 15 North American experts on wolves, bears, and ungulates (Delphi technique), as well as consultation with Eurasian wolf or bear scientists; and development of predator–prey simulation models. Wildlife agencies from Idaho, Montana, and Wyoming provided data for many of the chapters in this monograph.

The findings from the collected data are presented in this monograph. The conclusions and opinions presented in these chapters are those of the authors and Delphi panelists. The authors were asked to evaluate the potential effects of wolf recovery in Yellowstone in relation to the four items. They were not asked to evaluate the desirability of wolf recovery in Yellowstone.

Some questions remained, and funding to study these questions was appropriated in 1990. Some questions may never be definitively answered unless wolves are experimentally restored and studied in Yellowstone.

Study Area

The Greater Yellowstone area is composed of Yellowstone and Grand Teton national parks (including the John D. Rockefeller Memorial Parkway), six national forests (Gallatin, Custer, Shoshone, Bridger–Teton, Targhee, and Beaverhead), and state and private lands. Federal agencies administer 69% of this land. Private individuals, Indian tribes, and state agencies control 24, 4, and 3% of the land, respectively. The Greater Yellowstone area is located in northwestern Wyoming, south-central Montana, and southeastern Idaho.

Yellowstone National Park and other federal, state, and private lands immediately adjacent to the park (about half of the Greater Yellowstone area) were the primary study areas. Glaciated, quaternary-volcanic deposits cover most of the 8,995-km^2 area in Yellowstone National Park. Elevations range from 1,500 m to above 3,300 m. Between 2,100 m and 2,600 m elevation, forested rhyolite plateaus are dominant in central portions of the park.

The park has long, cold winters and short, cool summers. Most precipitation falls as snow and ranges from 26 cm in Gardiner, Montana (north entrance), to 205 cm in the southwestern portion of the park. Average temperatures range from −12°C in January to 13°C in July, with extremes ranging from −54° to 37°C.

Approximately 80% of the park is forested. Lodgepole pine (*Pinus contorta*) dominates about 80% of the forested area and occurs between 2,300 and 2,600 m. Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) compose about 9% of the forested area and occur above 2,600 m. Whitebark pine (*Pinus albicaulis*) can be a major component of most of the spruce–fir zone. Nonforest plant communities occur throughout the park.

Yellowstone National Park's northern winter range sustains the largest concentration of ungulates in the Greater Yellowstone area. The 100,000-ha winter range extends northwestward from the Lamar and Gardiner river drainages (within the park) and along the Yellowstone River to Dome Mountain (outside the park). Eighty-three percent of the winter range lies within the park and 17% lies within the Gallatin National Forest and private lands.

Elevations of the northern winter range are lower (1,500 to 2,400 m) than those in the park interior. The northern range is warmer and drier than the rest of the park, having less than 75 cm total precipitation. Average precipitation increases with elevation, ranging from 26 cm near Gardiner, Montana, to 55 cm near the higher-elevation Lamar Ranger Station.

The region is steppe or shrub steppe, consisting of grassland or sagebrush (*Artemisia* spp.) grassland communities. Conifers, primarily Douglas-fir (*Pseudotsuga menziesii*), occur as scattered individuals or in small stands at higher elevations on north slopes. Conifers and aspen are dominant in about 41 and 2% of the northern range, respectively. Riparian shrub areas compose about 0.4% of the northern range.

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NORMAN BISHOP
YELLOWSTONE NATIONAL PARK

Reintroductions and Translocations of Wolves in North America

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Abstract. Reintroductions and translocations of gray wolves (*Canis lupus*) and red wolves (*Canis rufus*) were reviewed to evaluate the possibility of reintroducing gray wolves to the Greater Yellowstone area, central Idaho, and other areas of the United States mentioned in recovery plans; and to evaluate the feasibility of wolf translocation as a management action with problem wolves. Previous reintroductions involved either captive-produced or wild-captured wolves, but only one deliberate reintroduction of wild-captured gray wolves is known. Several wild wolves have been translocated in management actions. If possible, only wild wolves should be reintroduced because they already are practiced at obtaining food and do not associate humans with food. Reintroduced or translocated wolves may attempt to return home and, soon after release, may orient movements toward home and travel extensively. Groups of wolves released in unfamiliar surroundings usually separate immediately, whether related or not. Pups are more likely than adults to linger at the release site and temporarily settle in the vicinity. Translocated adult wild wolves have a good chance of surviving, but special care must be taken with pups. The tendency toward extensive independent movements by each wolf after release demonstrates that a "soft" release is preferable. Soft releases should involve a lengthy acclimation in a large enclosure at the release site to condition wolves to the new area. Techniques used by the red wolf project should be considered for possible use. The next few reintroductions and management action translocations are not likely to proceed predictably because of limited experience with this facet of wolf management and individual differences in wolf behavior. Multiple releases over a few years would greatly improve the chances of establishing a self-sustaining, viable population. Careful documentation of each experimental reintroduction and translocation is essential so succeeding attempts can build upon previous experiences.

Man has been relocating animals for much of human history. According to Nielsen (1988), the motivation has been sentimentalism, curiosity, or the desire to establish populations of wild animals that could be hunted, trapped, or in some way used. Franzmann (1988) commented that most Alaska wildlife translocations were performed to provide recent human immigrants with familiar animals for fur and meat. Most reintroductions, even in recent times, have also involved game species for hunting, trapping, or other uses (Boyer and Brown 1988; Griffith et al. 1989). At least

93 species were translocated (nearly 700 translocations each year) in Australia, Canada, New Zealand, and the United States since the Endangered Species Act of 1973 was passed (Griffith et al. 1989).

The reintroduction of rare native species is receiving increased attention and public support. Such efforts aim to bolster genetic heterogeneity of small populations, establish satellite populations that reduce the risk of species loss from unpredictable catastrophic events, and hasten the recovery of species after the habitat has been restored or specific limiting factors have been corrected. However, reintroductions of threatened, endangered, or sensitive species are still relatively uncommon and, when tried, are often unsuccessful (46% successful; Griffith et al. 1989). Reintroduction attempts involving birds have had a high failure rate (Long 1981; Cade 1986; Griffith et al. 1989). Reintroductions of mammals are relatively uncommon (Nielsen and Brown 1988; Kleiman 1989).

Translocation is a potential management tool in situations where wild animals are a threat to domestic animals or game species or a nuisance or threat to humans. Transport of wild animals to another area where the potential for conflicts is lower may be more socially acceptable than killing them, especially when endangered or threatened species are involved. A majority of states conducted translocation programs in 1985. Although the principal purpose was to restore animals to their native habitat, translocation of nuisance or depredating animals was another common objective (Boyer and Brown 1988). The carnivores most commonly translocated as nuisance or depredating animals were bears (Ursidae), raccoons (*Procyon lotor*), and river otters (*Lutra canadensis*).

Reintroduction of endangered species may become a more important means of maintaining or increasing biodiversity (Griffith et al. 1989). Griffith et al. (1989) pointed out that if current patterns of habitat loss continue, natural communities may become restricted to disjunct habitat fragments, and intervening development may disrupt dispersal and gene flow between areas of suitable habitat. Thus, artificial restoration may become an essential management strategy. Reintroduction is the only hope for realizing such important conservation goals as reestablishment of the red wolf (*Canis rufus*) to the wild (Phillips and Parker 1988; Parker and Phillips 1991).

One species potentially benefitting from reintroduction is the gray wolf (*Canis lupus*), which is extirpated from much of its range in the 48 contiguous states. The species is classified as endangered in all these states except Minnesota, where it is classified as threatened. Recovery plans for the eastern timber wolf (U.S. Fish and Wildlife Service 1978), the Mexican wolf (U.S. Fish and Wildlife Service 1982), and the northern Rocky Mountain wolf (U.S. Fish and Wildlife Service 1987) identify reintroduction as a technique to restore populations in certain unoccupied parts of former range. In the northern Rockies, the wolf is naturally recolonizing northwestern Montana (Ream and Mattson 1982; Ream et al. 1991), which is one of three recovery areas identified in the Northern Rocky Mountain Wolf Recovery Plan (plan; U.S. Fish and Wildlife Service 1987). According to the plan, the probability of wolves naturally recolonizing Yellowstone (another of the three recovery areas) was low, and reintroduction was recommended. Central Idaho is the other recovery area identified in the plan. The recovery team believed that wolves would recolonize Idaho without a reintroduction; however, after 15 years of encouraging wolf reports, no solid evidence exists that Idaho supports a breeding wolf population (T. Kaminski and J. Hansen, Montana Cooperative Wildlife Research Unit, Missoula, unpublished report; J. Johnston and J. Erickson, Boise National Forest, unpublished report).

The objectives of this paper are to examine existing data on reintroducing or translocating wolves and to assess translocating problem wolves as a management action. Interim wolf control plans for Montana, Wyoming, Idaho, and northeastern Washington (U.S. Fish and Wildlife Service 1988) call for translocation of problem wolves as a key component of problem-wolf management in the early stages of recovery. Wolves may need to be controlled in the event of depredations on domestic animals, nuisance behavior, and possibly when excessive predation on big game conflicts with state ungulate management objectives (Fritts 1990; Peek et al. 1991). Dealing with problem wolves is an acute management dilemma, since they are classified as endangered and each individual is important to the population. Public opinion is divided on killing wolves that prey on livestock. About one-third of Montana, Idaho, and Wyoming respondents in a survey disagreed that "if wolves in the Yellowstone area killed livestock the problem wolf should be killed" (Bath and Phillips 1990). Translocation of problem wolves—either within Yellowstone National Park or within the Greater Yellowstone area—has been suggested as one means of dealing with problem wolves there (Fritts 1990). After reintroduction, some Greater Yellowstone area wolves could exhibit nuisance behavior and would have to be controlled.

The terms *translocation*, *introduction*, and *reintroduction* have not received standard use in the literature. For this discussion of wolves, I define *translocation* as the artificial movement of wild wolves from one location and release in another location—within the current geographical range of the species—for resolving conflicts or for research. *Reintroduction*, as used here, refers to the release of captive-raised or wild wolves into an area that was part of their original geographical range—but from which they have declined or disappeared—for establishing a viable free-ranging population. *Introduction* refers to the release of wolves into an area outside their original geographical range for establishing a new free-living population. The term *relocation* (or *relocated*) is inclusive of any of the above.

Hard release refers to the immediate and direct release of wolves into a new environment. *Soft release* refers to the gradual release of wolves from a temporary enclosure (captivity) to a free-ranging situation. During captivity, they should have basic husbandry care and possibly live prey; be disturbed as little as possible; and generally be given time to be calmed, monitored, and conditioned. The holding period can be a few days or as much as several weeks or months. Obviously, soft release is a relative term depending largely on the duration of holding at the release site and the freedom of the wolves to conduct basic (minimum) biological activities.

Methods

I reviewed scientific literature on wolf relocations of any type and reviewed parameters of those reintroductions and translocations to draw conclusions for their applicability to the Yellowstone, central Idaho, and other northern Rocky Mountain recovery areas. Results of two recent translocations in Montana are also included (Bangs et al., in preparation), as are pertinent findings of the ongoing red wolf reintroduction program in the southeastern United States (Phillips and Parker 1988; Parker and Phillips 1991; Phillips et al., in preparation).

Previous Reintroductions and Translocations of Wolves

Only six relocation programs of gray wolves have occurred, all within the United States. About 131 individual gray wolves—some captive-raised and some caught in the wild—have been relocated. Three attempts have been made to reestablish wild populations of gray wolves; two of those involved captive-raised wolves, and one involved wild-captured wolves (Merriam 1964; Mech 1966; Weise et al. 1975; Allen 1979). Another experience involved a strictly experimental release of captive wolves in Alaska (Henshaw and Stephenson 1974). Wolf managers have attempted to resolve depredation problems by translocating wolves in Minnesota and Montana (Fritts et al. 1984, 1985; Bangs et al., in preparation). Further, the experiences gained in the red wolf program that attempted to reestablish that species in the southeastern United States are relevant. All these efforts provided valuable information on the survival and behavior of relocated wolves.

Case Histories

Isle Royale National Park

A plan was implemented to reintroduce wolves to Isle Royale National Park before wolves were known to have returned on their own (Mech 1966; Allen 1979). In 1952, two male and two female wolves from the Detroit

Zoo were released on this 544-km^2 island in northwestern Lake Superior. The plan called for maintaining them in pens and allowing them to come and go at will; the hope was that they would leave on their own and eventually revert to the wild. The wolves were transported to the park on 9 August. One wolf soon escaped from the hogwire pen, and the other three were promptly released to avoid risks of injury from the wire. The wolves soon began harassing the caretakers and quickly became a nuisance to the local populace by seeking food wherever people could be found. Although the wolves showed no reluctance to approach people, the humans certainly were scared of the wolves. Consequently, the National Park Service trapped the wolves and transported them 48 km away. The following day the wolves were back harassing tourists. Eventually, two of the wolves were shot, and one was trapped and removed from the park; the fourth escaped capture. The last (fourth) animal, a yearling male, did not return to the tourist lodge and was reported seen by the public a year later. Wild wolves immigrated to the island by about 1948, so the sighting may or may not have been of this wolf, and the fate of the yearling male is unknown.

Coronation Island

Captive-raised wolves were introduced on another island in 1960. The site was Coronation Island, a 73-km^2 island in southeastern Alaska (Merriam 1964, 1966). The island is at the outer edge of a group of islands that make up Alexander Archipelago, approximately 8 km from the nearest island (Kuiu). The climate is maritime; water between islands does not freeze. No record exists of wolves ever inhabiting the island. Black-tailed deer (*Odocoileus hemionus*) were abundant enough to overbrowse the habitat, and some were dying from malnutrition.

Two male and two female 19-month-old captive wolves were released on the island as part of a study to examine relations between Sitka black-tailed deer and wolves. The wolves survived and learned to prey on deer. Wolf numbers steadily increased over 5 years. By summer 1965, at least 7 adults and two pups were present for a density of one wolf per 7.8 km^2, the highest density ever reported. After 1965, the wolf population declined but persisted. Predation by the wolves was thought to reduce the deer numbers to the point that conditions of the habitat improved and evidence of deer malnutrition decreased. Analyses of 609 wolf scats showed the percentage of scats containing deer increased from 78% in 1961 to 96% in spring of 1965. After 1965, a marked reduction in the number of scats containing deer was seen. Harbor seal (*Phoca vitulina*) became the second most important food in wolf scats, but whether these animals were killed or scavenged was not known.

Few other details are known. No information was obtained on postrelease behavior and movements. The island was uninhabited, so no potential existed for the wolves to approach humans, as on Isle Royale. In all likelihood the wolves would have sought out humans for food, had people been present. Henshaw et al. (1979) commented that the originally released wolves likely survived and reproduced because they were able to exploit easily obtainable marine resources.

North Slope of Alaska

In 1972, a group of five 2-year-old wolves from the Naval Arctic Research Laboratory in Barrow, Alaska, was experimentally released (Henshaw and Stephenson 1974; Henshaw et al. 1979). The animals—two males and three females—were selected from the animal colony at the lab. They had been caged outdoors in steel mesh enclosures and fed fish and reindeer meat.

Before release, the social and individual behavior of these wolves contrasted with those of three other groups. This particular group was thought most likely to maintain cohesiveness after release and thus was selected. None of these animals were tame (i.e., all responded cautiously to humans). On 11 August, the wolves were captured, anesthetized, placed in holding cages, and transported by air (a 1.25-h flight) to a release site. They were then transported by truck and riverboat to a release site about 280 km southeast of Barrow and the lab where they were raised. Total transit time was about 6.5 h. The wolves remained in a holding pen until the drugs wore off. A caribou carcass was placed near the cage for food. Three wolves had been fitted with radio collars that failed after a few days. There was little human activity in the release area. A nearby mountain was used to observe the behavior of the animals in the release vicinity. No resident wolves were observed in the area, although wolves were known to be present at an estimated density of 1/180 km^2. Small mammals were common in the release area.

In the first few hours after release, the wolves played around the pen and caribou carcass. Soon, all wolves made excursions away from the pen. A subordinate female left the group by morning of the second day. During days 4 through 7, after consuming the caribou, the wolves began to explore and moved farther from the release site individually and in pairs. On the sixth day, another female separated from the group. On days 7 through 11, another female failed to return from a foray. After suspending observations at the release site, reports of wolves were received from near the town of Umiat (6.7 km west of the release point), an oil-drilling camp (feeding from a garbage box), and near a fishing camp. Ultimately, four of five animals reentered civilization; three were shot within 7 months, one returned to the animal compound in Barrow after 17 weeks, and one was not recovered.

Little is known about the behavior of the wolves between departure from the release site and their fatal encounters with humans. The wolves were not known to capture prey. Three individuals were associated with wild wolves when they were killed, so they may have shared in the kills made by the wild wolves. A significant finding was that all the released wolves were attracted to human activity. Interestingly, the dominant wolf in the group showed the least fear of people. The three deaths in the experiment resulted from the wolves approaching humans or human habitation, probably because they associated humans with food.

The data on final locations of the wolves strongly suggest they were trying to return home. One wolf succeeded in homing to Barrow and two others were killed after moving 140 and 160 km toward Barrow. The home pen had been near an airport, and the researchers suspected that noise from large aircraft was the cue used in homing. The sound of large aircraft can be heard for great distances in that area when weather is favorable. The distance moved—282 km—by the wolf that returned to Barrow is the longest homing distance known for a gray wolf (Henshaw and Stephenson 1974; Rogers 1988). Factors motivating these captive-raised wolves to return home were probably quite different from those of wild wolves.

Perhaps the most important finding of this study was that these captive-raised wolves released into the wild maintained an affinity for humans—or at least for manifestations of civilization. Once humans were located, the wolves tended to stay near them, suggesting they associated humans with food (Henshaw et al. 1979). Another important finding was their failure to stay together and exhibit any form of pack behavior.

Upper Peninsula of Michigan

A reintroduction of wolves into the Upper Peninsula of Michigan in the 1970's has been the only effort to reestablish a wild population using wild-captured gray wolves; therefore, the project is of special interest (Weise et al. 1975). It was a joint effort of the Michigan Department of Natural Resources, U.S. Fish and Wildlife Service, Northern Michigan University, The Huron Mountain Wildlife Foundation, and the National Audubon Society. Wild wolves were used in this project because they were assumed to be accustomed to avoiding people and finding food for themselves and because the earlier releases indicated that captive-raised wolves did not fare well in the wild.

Two male and two female wolves, thought to be from a single pack, were captured in northern Minnesota by a professional trapper in December 1973–January 1974. They were penned outdoors in Minnesota, first individually and then together. Interactions of the four were friendly. One female (#10) generally kept to herself, suggesting she was a low-ranking wolf or possibly not a member of the pack to which the other three belonged. On 5 March 1974 the four were anesthetized, vaccinated, blood-sampled, ear-tagged, radio-collared, and prepared for transport to their release site. They were then flown to Michigan and driven by van to a holding pen 56 km northwest of Marquette. Time from drugging in Minnesota to release into the Michigan pen was about 12 h. Size of the pen was 7.62 × 7.62 × 3.6 m (height). Four road-killed white-tailed deer (*Odocoileus virginianus*) had been placed inside the pen, and five road-killed deer and a black bear (*Ursus americanus*) carcass were positioned within 0.8 km of the pen for food after release.

While captive in Minnesota, these wild wolves lost from 11 to 20% of their body weight despite eating about 3.6 kg/day. They consumed 2.5 kg/day during their 1-week captivity in Michigan. They completely consumed two deer carcasses in the pen but did not feed from the other two.

Project personnel had planned the release for mid-March for a variety of reasons: (1) Deer in the release area are concentrated and vulnerable at that time; (2) whelping by the dominant female in April might increase her attachment to the new area (two of the wolves had been observed copulating in captivity in mid-February, but there was no indication either whelped, denned, or searched for a den after release); and (3) deep snow normally hinders travel by wolves at that time of year. Plans called for the released wolves to be radio-tracked from the air and ground to study movements and behavior.

The pen door was opened and the wolves left at dusk on 12 March after being held 1 week on site. All left within about 15 min. The wolves traveled as a group, except for #10, who immediately went in a different direction. The researchers identified four phases in the movements of the group of three (the pack). A postrelease phase (first 2 days) was characterized by confusion and indecision. During a directional movement phase lasting 10 days, the pack left the release vicinity and traveled 64 km (direct distance) to the southwest. During an exploratory phase lasting 7 weeks, the pack covered a 4,224-km^2 area. Movements were long, with much zigzagging and revisiting of certain general areas. One wolf separated from the breeding pair and was 82 km from them on one occasion yet managed to reunite with them within a few days.

Eight weeks after release, the wolves had begun to settle into a territory (settled phase) of 637 km^2. The group remained there from 7 May to 6 July. On 6 July, the alpha male was found dead near a highway where he had been struck by an automobile. Thereafter, the alpha female left the territory and drifted in the manner typical of a lone wolf. She was caught in a coyote trap and shot on 19 September. The third wolf from the pack, a 2- to 3-year-old male, split from the other two in mid-June and traveled as a loner. He was found shot in the head and chest on 20 July about 39 km southeast of where the pack had settled.

Movements of wolf #10 were noticeably different from those of the other three wolves. Rather than linger briefly in the release area (postrelease phase), #10 quickly left and, by the end of the day after release, she was 25 km to the southeast. By the fourth day, she was 58 km from the release site; however, by day 8, she was back within 6.4 km of the release site and within 0.4 km of it on day 12. Otherwise, her movements suggested no attempt to locate the other three wolves. From release until early September, #10 made nine trips (from the general vicinity of the release area) about 32 km to the southeast and then back to the release vicinity. She slowly broke out of this pattern in September, gradually moved westward, and finally made a substantial westward move in October. She was shot by a deer hunter on the second day of deer season (16 November).

Movements of the pack of three during the directional phase suggested an attempt to return home; the direction traveled was only 33° off the home direction. After 13 days, the wolves were 68 km closer to home than at the release site. If they were trying to return home, that tendency ended after about 2 weeks. Weise et al. (1975) speculated that if the wolves were initially trying to return home, they might have become discouraged by failure to encounter familiar terrain, encountering too many obstacles or confusion from encountering too much human activity. Wolf #10 traveled in a perpendicular direction from the others, and there was no evidence that she was trying to return home. However, her movements were highly directional for months. Evidence showed that movements of all the wolves were influenced by human disturbances to the habitat.

Weise et al. (1975) commented that during the pack's directional and exploratory phases of movement, they were observed by humans an unusually high number of times, increasing their vulnerability. This fact probably was related to being outside their own territory and to their persistence in traveling. Resident packs would have slept instead. The pack frequently traveled near human-populated areas and probably traveled more during daylight than it would have in its home territory. On the other hand, wolf #10 was seen fewer times than the pack, apparently because she spent considerable time in a more remote area and explored less extensively.

Feeding behavior of the wolves was similar to nontranslocated wolves. They killed at least three deer and were believed to have taken several others. The condition of the two wolves that could be examined postmortem indicated they were adequately nourished. The wolves scavenged at dumps frequently, especially soon after release. When wolves are preoccupied with moving, searching for food in garbage dumps is not surprising, and garbage dumps were more common in the release area than in their former territory.

As expected, none of the four wolves showed the affinity for humans or human-occupied areas that was obvious in the captive-raised wolves described for Isle Royale, Coronation Island, and Alaska's North Slope. Humans, nonetheless, were the sole cause of mortality that prevented the wolves from becoming established. Weise et al. (1975) attributed this to negative human attitudes toward wolves in that area and to accessibility of humans to wolf range. Other than those two important factors, there seemed to be no reason for this wolf reintroduction to have failed.

Minnesota

The majority of wolf translocations were conducted in northern Minnesota in 1975–78 by the U.S. Fish and Wildlife Service (Fritts et al. 1984, 1985). That program involved removing wolves from farms (where they were preying on or threatening livestock) to areas as far away from livestock as feasible. Between 1975 and 1978, the endangered classification of the wolf in Minnesota prevented federal and state officials from killing even problem wolves. A program of translocation into remote forested areas of the state within wolf range was undertaken as the next best option. Altogether, 107 wolves were translocated; 9 of that number were translocated twice, and 1 three times. Sixty-two adults or yearlings and 45 pups were involved. Pups weighed 7.7 to 21.3 kg. Fifteen adults and 4 pups were ear-tagged and fitted with radio collars. The remaining 88 wolves were only ear-tagged.

The wolves were captured at Minnesota farms and transported in wire cages 50–317 km direct distance northward to eastward, except for three that were taken westward. Most wolves were released in the northwestern part of Superior National Forest. Within 2 days of capture, 87% of the releases were made; five wolves were held indoors for 52–73 days before being released. Wolves were transported and released individually in 41 instances. Groups of wolves were released as follows: 14 groups of 2; 8 of 3; 2 of 4; 2 of 5; and 1 of 6. Within these groups, two members of the same pack were released together in eight instances and three from the same pack in six instances. No acclimation pen was used at the release sites and no food was provided.

Wolves were merely extracted from their transport cages—usually in daylight—whereupon they usually ran into the cover of the forest (hard release). Most releases were during July through September, the primary period of depredation by wolves on livestock in Minnesota (Fritts 1982). Resident wolves were thought to be in all release areas, and populations of white-tailed deer, the primary food of wolves in Minnesota, were believed to be moderate to high in the main release areas.

Information on behavior and survival of the translocated wolves came from radio-tracking, recaptures by U.S. Fish and Wildlife Service research and control personnel, state wolf research personnel, Ontario Department of Lands and Forests personnel, and private citizens. Because wolves were protected in the United States during the period, deaths of some wolves undoubtedly were unreported. Seventeen wolves were radio-tracked for 1–588 days. Returns were obtained from 16 of the 88 wolves that were only ear-tagged for identification.

Most radio-tagged wolves left release sites within a few days. Eight adults began directional movements within 10 days, while five did so within 24 days. Pups generally left release sites later and moved more erratically than adults. One radioed pup was killed and eaten by two adults from another pack that had been released with it and its two littermates. The other three radioed pups settled near their release sites for 40–146 days before traveling to new areas. One female pup left in April, after 146 days. She traveled 51 km northward, then returned to her release site in May and stayed until July before leaving again.

No apparent tendency existed for related or unrelated wolves to remain together after they left release sites. Two littermate pups were exceptions—they remained together for 19 days before separating, and one adult and one pup from the same pack were found together on one occasion 6 weeks after release. Each of three radio-tagged pups and at least four ear-tagged pups survived the winter after release, even though they were apparently alone. Seven wolves released as pups and recovered as yearlings or adults attained or maintained normal adult weights.

Annual survival rate of the radio-tagged pups was 0.70, compared to 0.59 for wolves released as yearlings or adults. The average minimum survival time of the radioed wolves and the 16 recovered ear-tagged wolves combined was 342 ± 54 days (1–1,369). The survival rates calculated for the radio-tagged sample were similar to those calculated for wolves (mostly pack members) from other areas of Minnesota. Of the 12 wolves that died from causes other than control activities, at least 8 died in October through March. Mortality of nonradioed wolves in Minnesota is also highest during this period (Van Ballenberghe et al. 1975; Mech 1977; Fritts and Mech 1981; Fuller 1989).

Initial travel direction of the radioed adult wolves away from the release sites was between south and west, averaging only 33° off home directions. The small sample of pups did not show the same tendency. Patterns of movement of radioed wolves ranged from highly directional to much back and forth wandering (Fritts et al. 1984). Some wolves seemed to use reference points in their travels; returns to familiar locations were followed by moves in a different direction. The same behavior was seen in one of the reintroduced Michigan wolves (Weise et al. 1975). Eleven of 16 radio-tracked wolves veered several degrees to the right (west) during their travels, apparently due to encounters with large open-pit mines and areas of human activity. Travel rates (average) during directional travel that could be determined were 1.8, 2.4, 3.5, and 8.4 km/day, much less than the maximum rate wolves are capable of traveling.

The greatest known movement away from a release site was 302 km (straight line). Final locations of the radio-tagged wolves averaged 110 km from release sites and 67 km for ear-tagged wolves. Several ear-tagged wolves were recaptured by the U.S. Fish and Wildlife Service near a farm only 51 km from their release site, biasing these averages for ear-tagged wolves.

Among the 32 wolves for which one or more endpoints were determined, 9 of 15 translocated 50 to 64 km returned home (one homed twice), whereas none of 20 wolves that were moved 65 to 317 km returned home.

Mean distance traveled by 8 adults that homed was 54 km. With these translocation distances, about 7.5% of the wolves were known to return home. Others (nonradioed) may have homed without being recaptured in the home area.

Of the translocations for which the outcomes were known, 26% resulted in homing, but this is a biased result because of the manner in which the data were collected (intensive, long-term trapping at a farm that was relatively near the release sites). No pups homed from either distance. One wolf that homed and was translocated again returned home within 11 days to a farm that was 55 km from the release site. Telemetry data revealed that homing tendency in some translocated wolves was strong for months, but probably eventually waned after failing to reach familiar surroundings.

Five of the eight adults that homed were thought to be older, high-ranking pack members (including one lactating female), suggesting higher motivation or better navigation and orientation ability in older animals. Among the 107 wolves translocated, 14 (13%) were recaptured by the U.S. Fish and Wildlife Service at or near farms, following reports of livestock depredations or harassment.

Eventually, behavior of the translocated wolves reverted to that of dispersing lone wolves. Having been removed from a territory or any familiar ground and stripped of social ties with other wolves (at least in most instances), translocated wolves seemed to be in search of a mate and a territory. At least 5 of 16 radio-tracked wolves eventually associated with other wolves; 3 found a mate and a territory, and 2 probably reproduced.

Overall, translocated wolves in these studies showed a tendency to return to or travel through areas with high potential for conflicts with humans. Some possible explanations include (1) homing behavior or other tendency to move southward (toward area of greater human use); (2) avoidance of resident wolves, forcing these wolves into marginal habitat; (3) attraction to livestock; and (4) possible attraction to the type of environment in which they had been living when captured.

There was no indication that these wolves showed affinity for humans except possibly a tendency to approach human settlements to use livestock carrion. A pup settled temporarily near a livestock carcass dump from mid-January to late February. Although humans were the main cause of death, avoidance of humans is typical behavior for wolves in Minnesota, despite their protected status (Mech 1977; Fritts and Mech 1981; Berg and Kuehn 1982; Fuller 1989).

Montana

Wolves were translocated in management actions in 1989 and 1991 in northwestern Montana, where wolves are listed as an endangered species and are recolonizing on their own (Bangs et al., in preparation). The 1989 translocation was by the U.S. Fish and Wildlife Service in response to depredations on cattle at a ranch about 40 km west of Kalispell. This effort involved two 4-month-old pups, weighing about 18.6 kg, captured on 26 August 1989; a 2-year-old adult male, captured on 7 September; and the mother of the pups, captured on 8 September 1989. One pup was not captured and remained in the area until May 1990, when it killed calves and was shot as a control action by an authorized federal agent. All wolves except the adult female were captured in foot traps; the female was darted from a helicopter. The wolves were housed temporarily (6 to 18 days) in a veterinary clinic and fed road-killed deer. None gained or lost weight in captivity. They were radio-collared, transported by helicopter, and released in Glacier National Park on 14 September. All wolves were under light anesthesia when released. Direct distance from the capture locations to the release site was 103 km. A temporary enclosure had been planned, as was the placement of deer carcasses at the release site; however, the plans were altered by a last-minute change in release sites.

The wolves were radio-located by aircraft daily during the first 2 weeks after release and less often thereafter. The adult female and adult male immediately left the pups behind. The pups moved only 1.9 and 7.4 km (direct distance) away from the release site before starving to death by 26 and 28 September (12 and 14 days postrelease). They remained together or within 0.4 km of one another during the 12 days from release until death of the first pup. The second pup died within 8.8 km of the first pup. Instead of following the drainage out of the park toward the southwest, as the adults did, the pups seemed confused and moved to higher areas where food was scarce. The stomach of the second pup contained a small amount of human garbage, probably obtained from a remote campsite.

About 16 days after release and 20 km from the release site, the adult male settled at a cattle ranch just outside Glacier National Park. During attempts to drive him from the area, he was observed to be emaciated because of a foot infection. He was euthanized by the U.S. Fish and Wildlife Service on 1 October. The foot condition was related to a capture injury that was not thought to be serious while in captivity. The animal lost 9.1 kg postrelease.

The adult female moved away from the release site first. Within 24 h after release she traveled 16 km and was 31 km away by the second day. By the third day after release, she had crossed a mountain range; she also swam a 1–3.5-km-wide reservoir that was in her southwestward path. Her direction to this point was only 35° off her homeward bearing. She moved extensively over the next 4 to 5 weeks, during which time she was radio-located about 24 times. Initial direction of her movement was southwest, which was generally homeward, but obstacles, such as Flathead Lake (13 km wide) and the city of Kalispell, repeatedly deflected her homeward movement. She crossed high mountain passes several times during her extensive moves. The wolf could not be found on several occasions, so the extent of her wanderings likely were greater than indicated by the radiotelemetry data. She seemed to settle temporarily (for about 2 months in winter) in an area with wintering white-tailed deer before resuming an extensive movement pattern.

The wolf paired with a male in February northwest of Missoula where a large gray wolf had been seen before her arrival. The pair established a territory that was 169 km southwest of her release site and 109 km south–southeast of her previously known territory. The pair produced six pups in spring 1990. The female's area was remarkably similar to her previous one; it was within a large river valley with abundant white-tailed deer, considerable livestock production, and several human residences. No evidence was obtained to indicate that this wolf depredated on livestock after translocation. She was illegally killed in late May.

In the case of this wolf and her pack mates, there was an alternate explanation for the initial travel being in the direction of home: they were released into a drainage that opened to the southwest. Point-to-point radio locations for the female indicated that before pairing she traveled a minimum of 483 km (actual distance was undoubtedly much greater) and averaged 4.2 km/day. There was no indication of what this wolf ate after being translocated.

The second management translocation of wolves in Montana occurred in April 1991. Four 11-month-old littermates, orphaned offspring of the adult female previously described, killed livestock at a ranch 48 km northwest of Missoula on 29 March and 2 April. Three of the four young wolves (two females and a male) were captured by darting from a helicopter on 6 April, held for 7 days in a vet clinic, and released in Glacier National Park on 13 April. The release site was 140 km northeast of the capture site. The wolves were placed in a culvert trap for helicopter transport to the release site and were released together in a fully alert state. All were radio-collared. Two skinned deer carcasses were left at the site.

One day after release the trio had moved 8 km to the south and crossed a highway. By the next day, they were still together and had returned to the vicinity of the release site. On 16 and 18 April, they were still together in the release area. On 20 April, the male and one female were found in the Bob Marshall Wilderness but were separated by about 13 km; their locations were about 30 km from the release site. The other female could not be found on this date. The three wolves were not known to travel together again after 20 April. One of the females killed two to four lambs on 23 May and was darted from a helicopter the next day and brought into captivity permanently. The male was found dead at the bottom of a shallow lake near Big Fork on 14 June. Investigation revealed he had been shot. The remaining female was shot by a rancher, reportedly as it was attacking cattle near Condon on 17 June. Thus, all three wolves were dead or otherwise out of the wild within 65 days of release. Distances from the release site of the three, respectively, were 42, 40, and 74 km. Final locations were 120, 42, and 13° off the homeward compass bearing. The initial southward travel away from the release sites by these wolves could have been the effect of topography—that is, following a drainage that led southward out of Glacier National Park. The fourth wolf, which was not translocated, apparently killed no additional livestock, at least through 1991.

Red Wolf Reintroduction Project In North Carolina

The U.S. Fish and Wildlife Service has gained considerable experience with reintroduction of the red wolf, a species closely related to the gray wolf. Red wolf releases involve captive-raised individuals or their first generation offspring. The primary reintroduction site is the Alligator River National Wildlife Refuge, North Carolina, and the effort there is the focus of this discussion. The refuge is located on a large peninsula. The immediate area is sparsely populated and contains few livestock. Total area of the refuge plus adjacent U.S. Department of Defense land is about 190 km^2. From 14 September 1987 to 14 December 1990, 29 wolves were released. About 44 will be released before the end of the 5-year experiment (Phillips et al., in preparation). Animals released to date (mid-December 1990) include eight adult males, eight adult females, two yearling males, one yearling female, four male pups, and six female pups. Eight of these wolves were released in 1987, four in 1988 (two were rereleases), 14 in 1989 (three were rereleases), and 10 in 1990 (two were rereleases). At present about 17 red wolves reintroduced in the wild may be there.

Red wolf projects on islands (Bull's, Horn, St. Vincents, and Durant) support the refuge project. Pups are produced in acclimation pens on these small islands. The family group is released, and after 6 to 7 months the adults and pups are recaptured. The adults are placed back in the pen for a repeat captive reproduction, while the pups are transported to a holding area for eventual release to the wild. This strategy increases the size of the overall population and provides a pool of wild-raised experienced animals for permanent release (M. K. Phillips, personal communication). Early in this work, two pairs were experimentally reintroduced to Bulls Island, North Carolina, in 1976 and 1978. One pair that was kept in a pen 6 weeks before release split up, and one wolf headed for the mainland about a week later. The other pair was kept on the island for about 6 months and remained there 8 months after release (Carley 1981).

Red wolves are transported from the island projects and captive facilities to the refuge. Before release, they are held in 225-m^2 acclimation pens. Because females ovulate in the last half of February, adult males and females are placed together no later than the end of January. Optimum acclimation varies on a case-by-case basis within 3 to 6 months (Phillips et al., in preparation). Human contact is kept to a minimum during acclimation; wolves are fed no more than three times a week, and pens are not entered unless necessary. Attempts are made to provide the wolves with naturalistic experiences. As release approaches, the wolves are weaned from their high-protein dog chow to an all-meat diet. Live prey placed in the pens provides an opportunity for wolves to develop predatory skills (Phillips and Parker 1988).

The release procedure is varied by age or relationship of wolves released. Results show that adults with pups are best released when the pups are young (12 to 14 weeks), so midsummer is the appropriate time (Phillips et al., in preparation). Adults without pups are best released during mid- to late fall. This provides the animals maximum time before they have to contend with potentially heavy parasite loads (Phillips and Parker 1988; M. K. Phillips, personal communication). Release is effected by merely leaving a pen door open and allowing the wolves to exit voluntarily.

Supplemental food is provided after the wolves leave the pens. White-tailed deer carcasses are used at first because carcasses seem to cause the wolves to restrict their movements for at least a few days, and scat analysis indicates that deer are an important food. After about 3 to 4 weeks, 2.3-kg logs of primarily horse meat (termed canine diet) are provided for the wolves to eat (Phillips et al., in preparation).

All released wolves have spent 12 to 24 h near the release sites before starting to explore the surrounding area. Once they start wandering, they periodically returned to the release area and started to show affinity for other specific areas in their developing home range. All but two wolves made the transition from subsidized food to self-sufficiency in a few weeks (Phillips and Parker 1988; Phillips et al., in preparation). Generally, the postrelease movement of younger wolves has been more restricted. Movements of two 9-month-old red wolves were very restricted after only 1 week in a holding pen. A yearling and a 2-year-old also stayed at the release area after an acclimation period of 80–82 days (Phillips 1988).

Thirteen pairs of red wolves have been released so far. Some individuals and pairs have been recaptured and released more than once. Eight pairs split up on release, four stayed together, and the outcome of one pair is uncertain. Each pair that remained together in the wild during the breeding season produced pups. Four litters were produced in the wild, two in 1988 and two in 1990. Seven different adults were involved (one female produced litters in 1988 and 1990). Only one pup survived from each of the 1988 litters. One of the adult females that whelped in 1988 died shortly thereafter. Her uterus contained six placental scars. The other female was also believed to have given birth to more than one pup. Of the two 1990 litters, one pup is believed to have survived from one litter and three from the other litter (as of mid-December 1990). Parasites are the suspected cause of pup deaths (Phillips et al., in preparation) although, because of a high water table, suitable denning and rendezvous sites are thought to have been scarce.

Sixteen red wolves have died: seven adult males, three adult females, two male pups, and four female pups. Five of these wolves were killed by vehicles, five drowned, two were killed by other red wolves, one suffocated from a raccoon kidney lodging in his trachea, one died from a uterine infection, one was shot, and one died from pleural effusion and internal bleeding. Survival of wolves in the island releases has generally been good, although two adult females and one female pup have been killed by alligators on Bull's Island. One adult female on Horn Island died of pancreatic cancer after release (M. K. Phillips, personal communication).

A small number of released wolves on the Alligator River National Wildlife Refuge have been observed often, especially along highways. In an attempt to reduce vehicle collisions, the North Carolina Department of Transportation has erected red wolf crossing signs. Local radio stations air public service announcements that alert motorists to the presence of wolves along selected highways (Phillips et al., in preparation).

Synthesized Results of Previous Studies and Discussion

In the following section, some of the major questions and issues in wolf relocations are examined in light of the studies previously summarized.

Captive Wolves Versus Wild Wolves

Captive wolves used in the Isle Royale introduction and Alaska experiment did not display the wildness or fear of humans that seems essential for survival in the wild. Wolves that had been maintained in captivity associated humans with food after release. Reintroduced and translocated wild wolves generally avoided humans, and most proved capable of obtaining food in the new environment. The red wolf project has had no option but to use captive-produced wolves. Even though captive-raised red wolves were acclimated with minimal human contact, some have not displayed much fear of humans. Improvements have been made toward resolving this problem by releasing young wolves that have limited experience with humans and through the island projects that allow young wolves to get some experience in the wild before being moved to the permanent release site on the Alligator River National Wildlife Refuge.

Hard Release Versus Soft Release

Hard-released adults showed no inclination to stay at the release site more than a few days whether captive-raised or wild, and some left within hours. Adult wolves not acclimated to their release site will not stay. The first inclination of most hard-released wolves apparently was to return home. Holding the Michigan wolves for 1 week at the release site was insufficient to prevent this. Wolves have the ability to orient movement in the general direction of home and are capable of homing if the distance is not too great and if significant barriers do not exist. There was considerable variation in the time wolves took to actually leave the release sites, independent of type of release. Pups lingered longer than adults and traveled away more slowly. A period of confusion seemed to precede movement away from release sites.

Age of Wolves

Pups were much more likely than adults to stay in the vicinity of the release site and somewhat more likely to remain together. Three 1-year-old wolves in Montana showed a comparable tendency. In Minnesota, the survival rate of pups was higher than that of adults, but the pup sample was small; all 3 of the radio-tagged pups and at least 4 of 45 ear-tagged pups survived the winter following release, although apparently alone. Pups that are older when released must have better survival odds than younger ones, although the number of pups that have been relocated is too small to show that relation.

Group Cohesion

Released adult wolves tended to separate. Even with a short acclimation at the release site, most have separated. The only instance known of relocated gray wolves remaining together was the reintroduction to Michigan where three of four wolves did so. Released pups (littermates) showed the strongest tendency to remain together, but sample sizes were small. The Michigan effort offers the only instance in which we can be fairly certain that two wolves—pair-bonded in the wild, subsequently captured, and then released together—stayed together after release. It is likely that some of the other wolves released in Minnesota and possibly Montana were mated pairs; still no cohesion was seen. A higher rate of cohesion was seen with red wolves, which were all acclimated before soft release, yet about twice as many pairs split up as stayed together. The sudden (hard) release of family members appeared to create an every individual for him- or herself situation.

Feeding Behavior

Nonacclimated captive wolves approached humans for food and scavenged considerably. Wild wolves are already experienced at killing prey and seemed to have little trouble transferring their predatory ability to another locale. How some wild wolves fed themselves during periods of extensive movement was not clear, but some indication of scavenging was noted. The small amount of data on pups is contradictory. The Minnesota translocations indicated that pups were successful in providing for themselves, but did not indicate how they did so. Some scavenging was certainly involved. The two pups that starved in Montana probably were in a food-poor area relative to the Minnesota pups. In the red wolf project, captive wolves made the transition to killing for themselves after a few weeks in the wild. No reintroduction or translocation has been done in which wolves experienced with one prey were moved to an area devoid of that prey. (Such a reintroduction—or translocation—would not be prudent.)

Affinity for Humans

The strongest relation depended on whether released wolves were captive-raised or wild. Captive-produced gray wolves apparently approached humans in every case observed. This behavior produces public relations problems and often results in the wolves being killed. The association between humans and food is difficult to break for captive-produced wolves. That problem was mostly solved in the red wolf program's approach, but a few animals in that project did not demonstrate the desired wariness around people, and some wandered into towns. Nonetheless, this has not been a major problem, because the introduced animals are closely monitored, and project personnel intervene to remove wolves from problem situations wherever possible. Translocated wolves seem to resettle in areas that resemble their former territory. Because most translocated wolves are taken from areas with livestock, those wolves are more conditioned to living around humans. Therefore, they are not reluctant to resettle in such areas and possibly even seek them out.

Homing Tendency

Thirteen (10%) of the 131 reintroduced or translocated gray wolves were known to have returned to their place of capture or holding facility. Several others apparently attempted to home. Some were physically unable to home because of insurmountable barriers; monitoring of most of the Minnesota wolves was insufficient to detect homing if it occurred. Both captive-raised and wild wolves tried to return home. No animals released as pups have been known to home. They seemed to lack the orientation ability or the inclination. Older adults, particularly breeding animals, seemed to demonstrate the strongest desire and ability to return home. Ability to home was inversely related to the distance relocated. Limited data suggest that wolves have trouble homing if moved more than 64 km, although one homed a distance of 282 km, possibly using unique auditory cues (sounds of aircraft). If a wolf homes successfully once, the task is probably easier the second time, as suggested by a Minnesota wolf's success. Homing tendency seemed to be strongest soon after release and weaker in subsequent weeks. The rate at which it wanes is variable.

Causes of Death

Causes of mortality were many, as is true for nonrelocated wolves. These case histories have indicated cause of mortality in 26 gray wolves, besides those that were taken in wolf control activities (approximately 17): 14 were shot or trapped, 4 were killed by automobiles, 3 starved, 3 were killed by other wolves, and 1 died of a capture injury. Among the Minnesota wolves, the role of shooting and trapping was likely much higher than data indicated because of the reporting bias resulting from wolves being legally protected. Fates of many Minnesota wolves were unknown due to ear-tagging for identification rather than conducting postrelease monitoring through radiotelemetry.

A major part of wolf mortality in Minnesota in recent years was human-caused (Mech 1977; Fritts and Mech 1981; Berg and Kuehn 1982; Fuller 1989). Vehicle strikes and accidents played a larger role with red wolves. The vehicle strikes in the red wolf release area related in part to dense vegetation that made road travel much easier for wolves and partly to their lack of experience in the wild, including the conditioning to avoid automobiles. Such a problem could be predicted for any release of wolves that are not raised in the wild. Accidents were less frequent for the relocated wild wolves, but still are a potential problem for any wolf wandering or released outside familiar habitat. In the Michigan study, the wolves traveled a great deal during the day, making them more vulnerable to shooting. Extensive travel over unfamiliar terrain likely makes wolves more vulnerable to traps.

Survival

Relocation of any type undoubtedly stresses wolves. Any time animals are captured, anesthetized, transported, and released into new surroundings, the chances of mortality are increased. Nonetheless, in the studies reviewed, being handled and relocated was not in itself a major mortality cause. Significant capture-related injuries were infrequent in the Minnesota work and were not believed to be a significant factor affecting survival. Confusion, extensive travel, extra travel during daylight, unfamiliarity with terrain, and other factors would seem to be more of a detriment to survival than the data reveal. Survival rates of the translocated Minnesota wolves were comparable to those of nontranslocated wolves. The death of the adult male in Montana was the result of a capture injury, and the starvation deaths of the two Montana pups were from being translocated. The cannibalism of a radio-collared pup at a Minnesota release site resulted from the animal being released with adults from a different pack. The nine wolves released in Alaska and Michigan had a high rate of mortality with humans as a major cause. The red wolf program demonstrates clearly that not all released wolves will survive.

Does Translocation of Problem Wolves Work?

If the primary objective of a translocation is to prevent individual wolves from further depredating either at their original site or a future site, then the translocations to date seem to have been fairly successful. The actual number of translocated wolves that depredated again could not be determined. The best minimum estimate is the number recaptured at farms experiencing wolf depredations: 16 (14%) of 114. The radio-collared Minnesota wolves tended to travel through areas where potential for conflicts was high, and they may have been attracted to livestock (possibly livestock carrion) or to characteristics of the habitat similar to where they were originally captured. Three of 17 were recaptured at farms following reports of depredations or harassment. Two of four Montana wolves that survived the translocation experience depredated again.

Problem wolves that are translocated probably are more tolerant of humans than wolves with territories in more pristine areas. An alternate explanation is that avoidance of resident wolves could have forced them into marginal wolf habitat. Whatever the reason, translocated wolves, during their extensive movements, at least created the opportunity for additional wolf–human conflicts, yet may have become involved in few. The adult female translocated in Montana conformed to this generalization precisely. This animal resettled in an area with livestock, encountering them frequently, yet fed on natural prey. Translocated wolves moved great distances away from their release sites. Permanent relocation to a targeted site is not a reasonable goal of wolf translocations unless a different release process is used, such as a long holding period in a large enclosure.

Another measure of success in translocations is whether or not the animal survives and once again becomes a functioning member of the wolf population. The translocations described in this paper indicated that wolves were able to form associations with other wolves. Some of the Alaska transplants associated with wild wolves, as did 5 of 16 radioed wolves in Minnesota. Translocated wolves were capable of establishing or reestablishing themselves as members of the breeding population. Three Minnesota wolves found mates and reproduced in the first breeding season following translocation. The Montana female bred and produced pups in the first breeding season after her translocation.

Conclusions

The experiences to date in reintroducing and translocating wolves are limited. Nonetheless, they do provide some general findings that can be used in the planning of future efforts with the gray wolf.

The strongest variable influencing the outcome of wolf relocation was whether captive-born or wild-captured wolves were used. Whether captive or wild wolves should be used has been debated previously (Klinghammer 1979). Experience has shown that attraction to humans is a major problem with captive wolves that have not undergone proper acclimation. Using wild wolves seems to have many advantages over using captive-born wolves in reintroductions, although the results of the red wolf project show that it is possible to raise and condition captive wolves to make their reintroduction successful. However, no compelling reason exists to do so if wild wolves are readily available. Henshaw et al. (1979) concluded that gray wolves raised in captivity should not be used as transplant stock. In a survey of reintroductions of various species, Griffith et al. (1989) found that reintroductions involving exclusively wild-caught animals were more likely to succeed than those of exclusively captive-raised animals. However, wild wolves for reintroductions should not be taken from areas near farms and ranches, towns, human residences, or any area where they could have become acclimated to humans or vestiges of civilization. Those wolves may have a tolerance of humans that could predispose them to locate near people, where the potential for conflicts is highest. Ideally, wolves used in reintroductions should avoid or be fearful of people, their machines, and their dwelling places.

Also, we should assume that, unless held temporarily in pens, wolves will not remain where released. None of the adult relocated gray wolves showed any attachment to their release site. Most tried to return home, and many have the ability to orient and travel homeward. If they fail to reach home, they will eventually begin to mimic the movement patterns of lone wolves, essentially searching for a mate and a territory. Although wolves are capable of traveling great distances (Fritts 1983), limited data suggest that most have difficulty homing if the distance they are moved is greater than 64 km. Evidently, the original territory is vitally important to wolves—perhaps of most importance to dominant–breeding wolves. Abandonment of offspring by adults attempting to home strongly illustrates the latter point. Pups that are hard-released in a translocation will leave their release site more slowly and not travel as far as adults. Attempts to return home may be more of a problem with wild wolves than with captive wolves that have been properly conditioned. Each of the previous releases of wild wolves was essentially a hard release with little or no holding time at the release site. A soft release with a long acclimation would offer a major opportunity to improve this outcome. Several weeks or months of acclimation at the release site in a large enclosure may be necessary. Such an approach has been used successfully with captive red wolves but is yet to be tried with wild gray wolves.

The tendency for groups of released wolves to split up is another major feature of prior reintroduction and translocation experiences. That the Michigan wolves stayed together (3 of 4) following release after only 1 week at the release site may have been atypical.

Most adult wild wolves can survive after being relocated; relocated adults and pups in Minnesota survived comparably to resident wolves. Humans were the main cause of mortality to date. Ability of wild wolves to survive and reproduce in new surroundings need not be a major concern. Nonetheless, wolves of all ages will be more vulnerable to most forms of mortality in their new, unfamiliar surroundings; some mortality should be expected.

Translocated wolves may travel extensively and well outside the intended area. Predicting where a translocated wolf will settle is impossible. However, a reasonable hypothesis from the available data is that they will tend to settle in a locale that resembles their original area. The problem wolves that end up being translocated are more likely to be members of the population that is more tolerant of civilization in the first place. Nonetheless, the known instances of translocated wolves that have returned to their capture site or been involved in more killing of livestock has been low. Most translocated wolves survive, and some have been known to reproduce. Therefore, translocation seems to be a reasonably viable control technique.

Reluctance to remain in the release vicinity is more of a problem in reintroductions than in translocations. However, if pups and adults are translocated together, the tendencies to leave the area and go their own way are important problems in each type of relocation. Differential ability of adults and pups to feed themselves should receive strong consideration in selecting the release site in translocations. Since pups are usually abandoned by parents in a hard release, they should be in an area of adequate small prey that pups can capture, or in an area with ample carrion. Supplemental feeding may be necessary to maximize survival potential of pups. Again, the best strategy is probably a soft release with a lengthy holding period, but the cost of that effort is easier to justify for a reintroduction than for a management translocation.

Reintroductions and translocations differ in that translocations are one-time events in which measures should be taken to give the translocated wolves the highest opportunity to survive. Reintroductions, on the other hand, have the broader objective of establishing a viable self-sustaining population, and the success or failure need not depend on results of a single release. The opportunity exists to repeat the release process until the problems that can plague small releases (seen in the case histories) and small populations are overcome and a self-sustaining population is finally established. Success of reintroductions is related to the number of individuals released (Griffith et al. 1989). According to a model for Yellowstone National Park, a moderately high probability of failure exists if the initial inoculum consists of fewer than 10 wolves; approximately 30 wolves were needed to assure success (Boyce 1990). Clearly, the probability of success of a reintroduction program would be greatly enhanced by multiple and sequential releases over a few years. During the course of such a program, the results of individual releases would be improved by building on the experience gained in previous ones—as is occurring in the red wolf program. Multiple releases over time should be assumed in reintroduction planning.

All reintroduced and translocated wolves should be radio-collared (Mech 1979; Fritts et al. 1985) and, if possible, fitted with capture collars (Mech et al. 1984, 1990; DelGiudice et al. 1990; Peek et al. 1991). The best information we have on this subject was obtained by use of radiotelemetry. Valuable information was lost from the Minnesota translocations because most wolves were not radio-collared, and those that were collared were not located as often as desired. If available, these data might well change the conclusions about some aspects of wolf relocation. At this point in the history of wolf relocations, we must learn as much as possible from each new experience and apply that knowledge to the next one. Capture collars offer a new dimension to reintroductions and translocations. Wolves fitted with capture collars before release can be remotely anesthetized, recaptured, and returned if they leave the intended area—several times if necessary. Once the wolves have settled into a territory and the need for recapture seems to be small, the capture collars could be replaced with standard telemetry collars that offer longer battery life, and monitoring of radio signals could become less frequent as data needs change. If monitoring of radio signals by poachers is a concern, telemetry systems that can be turned off and on by remote control should be used (Mech et al. 1990).

Based on previous work, we should be prepared to deal with the following scenarios: (1) adult pairs separating after release; (2) extensive movement outside the target area in the few weeks after release as wolves try to return home or explore their new environment; (3) mortality from expected and unexpected causes; and (4) wolves behaving differently from wild wolves in their original environment. Variations in behavior of individual wolves (which has been noted in numerous studies of captive and wild wolves) is a factor in making the outcome of reintroductions difficult to predict.

Many modern attempts to reintroduce wildlife have failed. Experiences with reintroduction suggest that the technique is not as universally applicable as it would seem at first glance (Conant 1988; Nielsen 1988). Numerous factors must be carefully considered; planning and preparation must be as meticulous as reasonably possible (Nielsen 1988; Kleiman 1989). Even so, anticipation of every problem is almost impossible, and unexpected turns of events should be anticipated (Booth 1988; Rathbun and Benz 1991). Thus, we should not be surprised if reintroductions and translocations of wolves in the northern Rockies do not go predictably. While planning as thoroughly as possible, our mindset must be to expect the unexpected.

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Possible Effects of a Restored Gray Wolf Population on Grizzly Bears in the Greater Yellowstone Area

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Abstract. A review of the literature and contact with scientists in other countries revealed little evidence that sympatric gray wolf (*Canis lupus*) and grizzly bear (*Ursus arctos horribilis*) populations have any significant demographic effect on each other. References exist in the literature about mortalities to both species because of interactions, but these instances are rare. No evidence was found in the literature of effect on survival or reproduction to populations of either species due to interspecific interactions. Interactions are apparently mediated by the age and sex of participants, the location, reason for interaction, and behavioral experience of the animals involved. No patterns emerged regarding the outcome of interactions.

Grizzly bears (*Ursus arctos horribilis*) have been listed as threatened in the contiguous 48 states under the Endangered Species Act since 1975. The Yellowstone grizzly population has been isolated from adjacent populations to the north for approximately 60 years. The Yellowstone grizzly population was reduced during the early 1970's to perhaps less than 150 animals due to closure of the open-pit garbage dumps that once attracted a significant portion of the population. The current population is estimated to be at least 200, although exact numbers are not known. Increasing numbers of females with cubs have been noted in recent years. Intensive recovery efforts have been in progress for the Yellowstone and other populations in the contiguous 48 states since 1981.

The gray wolf (*Canis lupus*) was eliminated, through predator control, from Yellowstone National Park by the 1920's (Murie 1940:16). Weaver (1978) reported two wolf sightings in the 1930's. Increasing impetus exists both within the scientific community and the public to reintroduce the wolf to Yellowstone National Park to restore some measure of ecological completeness. Such reintroduction efforts are directed by the requirements of the Endangered Species Act (1969).

Compared to grizzly bears, the wolf is a highly efficient predator that some laypersons fear could seriously deplete other animal populations. Since 1975, millions of dollars have been spent on grizzly bear research and management directed toward recovery from threatened status. This paper examines the possible interactions between the Yellowstone grizzly bears and wolves to predict the effects of a proposed wolf restoration project on the existing grizzly bear population.

Methods

We reviewed scientific and popular literature from North America and scientific literature from Europe for records concerning interactions between wolves and bears. Twenty-three Soviet scientists and wildlife managers were contacted by letter for information on records of interactions between wolves and brown bears (*Ursus arctos*). From the 23 contacted, we received 8 detailed responses.

Historical Perspective

Gray wolves and grizzly bears coexisted for centuries in and around the Yellowstone area. Wolf and grizzly bear remains have been found in deposits in Lamar Cave—the wolf bones were below a level carbon-dated at 960 years B.P. (Hadley 1989). Incidents are recorded of interaction between wolves and grizzly bears in the Yellowstone area. Relative numbers of the two species before human encroachment are difficult to estimate.

All predators were controlled by whatever means were available before Yellowstone National Park was established and during its early years. During the 1870's and through the mid-1880's, market hunting of wild game existed inside and outside the park (Houston 1982:11). This market hunting likely lowered densities of prey species for resident wolves. The Superintendent's Report for 1877 stated that "many carcasses were strychnine-poisoned for wolf, coyote and wolverine in 1874–75" (National Park Service, 1878 unpublished report). Haines (1977:80) stated that, "coyotes, wolves, cougars, wolverines, and bears were shot on sight by employees and visitors, prior to the era of army management."

By 1914, after a quarter century of U.S. Army protection of large game animals, wolves had increased noticeably in northern Yellowstone

National Park, and concerted efforts to exterminate them resulted in a minimum of 136 wolves killed in dens, trapped, shot, and poisoned within the park from 1914 to 1926 (Weaver 1978:9).

The original relation between wolves and grizzly bears is difficult to assess. Wolves may have been present in greater numbers than was evident. Mech (1970:9) stated, "Anyone who has spent much time in wolf country will verify that the wolf is one of the wildest and shyest animals in the northern wilderness. Many an experienced woodsman has lived a lifetime without even glimpsing a wolf in its natural surroundings." Early efforts at extermination may have had a far greater effect on wolves than on bears. Most of the efforts directed at killing wolves—whether to protect furbearer trap lines or, later, for wolf hides—took place through strychnine poisoning in winter when bears were hibernating. Wolves were also hunted in areas surrounding the park; bounties were paid on 80,730 wolves in Montana between 1883 and 1919 (Lopez 1978:183). Government agents killed 413 wolves in Montana from 1918 to 1930. The last known remnant wolf was killed in 1945. In Wyoming and South Dakota, 508 wolves were killed between 1918 and 1923 (Weaver 1978:20).

Known Interactions

Grizzly bears and wolves still coexist over vast areas of Canada, Alaska, and Eurasia. Some insight into probable interactions between these species in Yellowstone can be gained from published observations.

Pulliainen (1965) stated that bears and wolves do not often occupy the same regions in Eurasia and that bears in Finland decreased as wolves increased. However, his distribution maps for Finland did not support this contention, and his statements on interactions between the two species are unclear. Fedosenko (personal communication) believes that Pulliainen was mistaken because the species do coexist throughout much of the former Soviet Union. Mech (1970:283) believed that declines in bear populations where wolves are also present could be explained by other factors.

In the Soviet Union, Lavov (personal communication) notes an inverse relation between high wolf and high brown bear numbers in Byelorussia. However, he discounts the effect of either species on the direct mortality of the other in the Berezina Reserve. From 1950 to 1970, Lavov saw only one brown bear, a 3-year-old, killed by wolves and "a few" instances of bear fur in scat of wolves.

Kaal (personal communication) states that wolves and brown bears cohabit basically the same biotype in Estonia, in the former Soviet Union, with a few problems. Schevchenko (personal communication) has conducted field investigations in the Carpathian Mountains along the Romanian border for 20 years without noting any conflicts between brown bears and wolves.

Frkovic et al. (1987a, 1987b) compiled 40 years of mortality records for brown bears and wolves in Yugoslavia, where both species coexist in significant numbers. Although they do report an unknown category for cause of death, they mention no mortalities attributable to interspecific interaction.

Noting that "there are no sharp antagonistic or competitive relationship(s) between gray wolves and brown bears in the Soviet Far East," Eugene (personal communication) writes, "but there is no competition because of high general biomass of prey objects. There are more than 250 wild ungulates per one wolf in the South of the region." For Yellowstone National Park's 100 wolves, the wolf/ungulate ratios would be roughly 1:223 (winter) and 1:356 (summer; Singer 1990a).

Van Ballenberghe (1987) cited Haber (1987) as reporting wolf/moose ratios of 1:17–26 in the Savage wolf pack territory in Denali National Park and Preserve, Alaska, from 1970 to 1973. Fall moose (*Alces alces*) calf/cow ratios were high in spite of the low moose/wolf ratios. When the Savage pack declined to two to three wolves, moose calf survival remained relatively low. Brown bear predation may have been responsible for persistently low recruitment of moose calves to adults during 1974–82. In 1973 the bear/moose ratio in Denali was 1:8. Here, then, is a case where low ratios of prey to both wolves and bears would seem to produce maximum competition, even potential population depression of one or the other, yet that has not been observed.

Haber (1987), reporting on wolf–bear trade-offs in Denali National Park, concluded "that [brown–grizzly] bear numbers, distribution, and seasonal shifts have changed little since 1966." Haber cited other long-time observers at Denali who believed that little change in bear numbers occurred since at least the 1920's and 1930's.

To our knowledge, no documented instances exist where wolves and brown bears have negatively influenced each other on a population basis in either Canada or Alaska.

Direct Interactions

Murie (1944) summarized grizzly–wolf relations in Mount McKinley National Park (now Denali) as follows:

> As a rule grizzlies and [gray] wolves occupy the same range without taking much notice of each other, but not infrequently the grizzlies discover wolf kills and unhesitatingly dispossess the wolf and assume ownership. This loss is usually not a serious matter to the wolves, for if food is scarce, wolves will generally consume kills before bears find them. In the relationship existing between the two species, the wolves are the losers and the meat-hungry bears are the gainers.

Murie (1944) also described several skirmishes where no damage was sustained by either species.

Ballard (1982:77) summarized his observations on wolf–bear interactions in the Nelchina Basin, Alaska, as follows:

> My observations indicated that [gray] wolves do occasionally kill bears. The result of brown bear–gray wolf encounters, therefore, may be an additional source of natural mortality not previously documented for either predator species. Whether it is a significant source of mortality for either species remains unknown.

From 1966 to 1974, Haber (1987) recorded 36 wolf–bear interactions within wolf pack territories in Denali. Of the 36 interactions, 19 took place at ungulate carcasses; wolves won 9 of the 19. Of the 36 interactions, 17 were not at carcasses. In those instances, wolves harassed the bears or tried to take cubs, and the bears retreated.

Lent (1964) observed a wolf and a grizzly bear sharing the same carcass. Hornbeck and Horejsi (1986) documented a 4-year-old female grizzly bear displacing three or four wolves from a moose kill. They found the bear reluctant to leave the kill though the wolves were active and howling within 300 m of the bear.

Paquet and Carbyn (1986) recorded three instances of wolves digging up and killing cubs of hibernating American black bears (*Ursus americanus*) in Riding Mountain National Park, Manitoba, Canada, but they believed that it was not a common phenomenon, since over 2,000 wolf scats collected in this area did not contain any evidence of bear remains. Pimlott and others (1969:63) recorded an instance of a black bear killing an adult wolf in Algonquin Provincial Park, Canada, but they believed that there was probably little competition between the two species.

Steven Fritts, U.S. Fish and Wildlife Service, has collected 70 unpublished wolf–bear interactions from several sources and has consented to let us summarize them (Table). The results (Table) show no discernible harm to grizzly bears or wolves because of these interactions. The result of each interaction may be mediated by complex factors including age, sex, and reproductive status of both species; prey availability; hunger and aggressiveness of both species; numbers of animals; and previous experience in interacting with the other species—or any combination of these.

On the average, direct interaction between wolves and grizzly bears seems to be a standoff. Given the high degree of individuality in both species; this is not surprising. All serious confrontations seem to be in defense of food or young. No evidence exists that the occasional direct confrontation has any effect on the population of either species.

Table. Summary of unpublished wolf–grizzly bear (*Canis lupus–Ursus arctos*) interactions (data courtesy of S. Fritts).

	Interaction type[a]															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	**Total**
Occurrences	7	2	2	1	3	15	2	5	9	4	5	8	3	2	2	70
Winner																
Bear	2	—	1	1	—	3	—	—	—	—	—	8	3	—	1	19
Wolf	—	1	—	—	3	6	—	5	1	—	5	—	—	2	—	23
Neither	—	5	1	—	—	—	3	1	—	8	—	—	—	—	—	18
Both	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1	2
?	—	—	—	—	—	—	3	1	—	—	4	—	—	—	—	8
Numbers																
B:W	2	—	—	1	—	5	2	—	2	4	—	2	—	—	1	19
W:B	3	1	—	—	3	5	—	3	6	—	5	3	3	1	1	34
B = W	2	1	2	—	—	5	—	2	1	—	—	3	—	1	—	17
Site																
Feeding	7	2	2	1	3	2	—	5	3	—	5	8	3	2	1	44
Wolf den	—	—	—	—	—	4	—	—	—	—	—	—	—	—	—	4
Rendezvous	—	—	—	—	—	2	—	—	1	—	—	—	—	—	—	3
Other	—	—	—	—	—	7	2	—	5	4	—	—	—	—	1	19
Females with cubs																
Occurrences	2	—	—	—	—	5	2	—	1	3	—	2	—	—	1	16
Bear wins	2	—	—	—	—	3	—	—	—	—	—	2	—	—	1	8
Wolf wins	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1
Neither wins	—	—	—	—	—	1	1	—	1	—	—	—	—	—	—	3
?	—	—	—	—	—	—	1	—	—	3	—	—	—	—	—	4

[a] Bear–wolf interaction types: 1 = bear feeding, wolf in area, no bear reaction; 2 = wolf feeding, bear in area, no wolf reaction; 3 = bear and wolf feeding on same kill at same time; 4 = bear feeding on wolf kill, wolf not present; 5 = wolf feeding on bear kill, bear not present; 6 = bear–wolf fight or chase; 7 = wolf stalking bear; 8 = wolf feeding on bear; 9 = wolf and bear in same area; 10 = other, information not specific; 11 = wolf displaces bear from kill; 12 = bear defends kill from wolf; 13 = bear displaces wolf from kill; 14 = wolf defends kill from bear; and 15 = bear kills animal wounded by wolf.

Indirect Interactions

The most significant indirect interaction between wolves and grizzly bears is probably in competition for food. While wolves must kill prey and depend entirely on meat, grizzly bears can subsist on vegetation and eat meat opportunistically. Elk (*Cervus elaphus canadensis*) would be the most abundant prey species for wolves in Yellowstone National Park (Singer 1990a). Elk make up a significant portion of the diet of grizzly bears in Yellowstone (Mattson et al. 1991). Grizzly bears consume large amounts of elk in early spring, both as carrion and by preying on winter-weakened individuals. Grizzly bears are also efficient predators on newborn elk calves and commonly prey on adult bull elk during and after the rut. A few grizzly bears have learned to kill adult elk during the summer months. Depending on the size of the prey resource and the numbers of both predators, some competition related to elk is possible.

The most severe competition would likely be in spring after bears come out of the den, when competition would be for available carrion and winter-weakened animals. Reduction in elk numbers due to wolf predation may also be possible. Grizzly bears use approximately 34% of the available carrion not adjacent to open roads within Yellowstone National Park on the northern range (Green 1989) and 30–100% of available carrion not adjacent to open roads and recreational developments in the Firehole–Gibbon area of the park (Henry and Mattson 1988; Green 1989). Grizzly bears compete with other scavengers for elk carcasses in both areas, and the addition of wolves could intensify this competition. In the Firehole–Gibbon area, grizzly bears use bison (*Bison bison*) carcasses 3 times as much as elk carcasses. No competition exists for bison carcasses because other scavengers are apparently unable to get through the tough hide. We assume wolves could open bison carcasses and thus would compete directly with grizzly bears for winter-killed bison carrion.

The numbers of wolves that the Yellowstone area could support, their distribution, and their effects on the prey base are conjectural at this point. Singer (1990b) considers the number of ungulates present within Yellowstone National Park to be adequate to sustain a minimal recovered population of 100 wolves, even considering the many predators in the ecosystem. Boyce (1990) estimated that average elk numbers may be reduced by 15–25% if wolf recovery occurs. Garton and colleagues (1990) modeled the potential effect of a restored wolf population on the northern elk herd in the park. They projected that 9 packs of 75 wolves would decrease the northern elk population by 10% or less. Fifteen North American experts (Koth et al. 1990) expected that, 10 years after wolf reintroduction (assuming a wolf population of 10 packs of 10 wolves each), wolves would reduce elk and bison populations parkwide by less than 20%.

We are uncertain about the importance of spring carrion to the grizzly population. Yellowstone is unique among North American grizzly habitats because large amounts of carrion and winter-weakened ungulates are usually available. Most grizzly populations do well without the abundance of carrion now available in Yellowstone. On the other hand, Yellowstone does not have the abundance of alternative spring foods found in other areas; the Madison–Firehole area is impoverished in spring foods not related to carrion. The high-quality nutrition provided by carrion may also help compensate for minimum midsummer fruit crops in Yellowstone. Bears in northern Yellowstone may derive some limited benefit from usurping wolf kills. It is not known whether the availability of wolf ungulate kills would compensate for reduced winter-killed carrion as a result of potential wolf reduction of ungulate numbers.

Available evidence suggests that direct interaction between wolves and grizzly bears has minimal effect on either species. This is not surprising considering the historic coexistence of these animals throughout most of their range. Serious confrontations seem to be in defense of food or young. We find no evidence that these occasional events have any population effect.

A question remains on the effect of wolves restored into an ecological system from which they have been absent for 50–80 years. Filonov (1980) analyzed 25–30 years of data from nine nature reserves in the former Soviet Union. When wolves were greatly reduced or eliminated, disease and starvation among prey species substituted for wolf predation. According to Filonov (1980), "In Darvinsky Reserve, as a result of the great reduction in wolves, moose losses from wolf predation were reduced by 14 times, but at the same time, bear predation increased 3-fold and mortality caused by diseases by more than 10 times. When wolf numbers increased, moose losses from predation decreased 1.5 times and mortality from diseases ceased." Filonov concluded that "even local extirpation of predators such as the wolf does not change the level of natural mortality rate much, but it does influence population structure and the physical condition of the prey. Therefore, extirpation of large predators in nature reserves is not beneficial."

Fifteen North American experts agree that changes in behavior and distribution of ungulates as a result of wolf restoration will be minor (Koth et al. 1990). To the extent that this change affects overwinter mortality and subsequent carrion availability, it may have some effect on the grizzly bear population. Several correspondents from the Soviet Union noted the limited effect of wolves on brown bears because bears are omnivorous and can use other foods if wolves change the availability of protein sources.

Some grizzly bears in the Yellowstone area may be more dependent on ungulates than are many brown bear populations in the Soviet Union. Restoring wolves to the Yellowstone area could have the greatest effect on the grizzly bears dependent on ungulates. However, Haber (1988) documented large bear populations throughout northeastern British Columbia, and bears prey heavily on ungulates where wolves are present. Singer (1987) documented that, during 1984 and 1985 in Denali, grizzly bears killed 22 collared caribou (*Rangifer tarandus*) calves while wolves killed only 8, demonstrating that predatory grizzly bears compete with wolves most successfully for newborn calves. Since the slight changes anticipated in ungulate distribution and availability to bears will be gradual with increasing wolf numbers, it is reasonable to assume that grizzly bears could adapt to those changes.

In summary, available information suggests little if any effect on population numbers from wolf–bear interactions. We expect some initial change in bear–ungulate relations, but change would be gradual and grizzly bears are likely to suffer minimal effects.

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Distribution of Beaver in Yellowstone National Park, 1988–1989

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Abstract. In 1988–89, we surveyed riparian habitat in Yellowstone National Park to determine presence and distribution of beaver (*Castor canadensis*). Forty-two reliable observations of at least 26 individual beaver were collected during the survey. These observations should not be construed as a population estimate. We identified 43 stream segments or lakes with signs of present beaver activity, 82 sites with signs of previous activity, and at least 26 stream segments or lakes with both present and previous activity. One hundred forty lodges were located; half (71) of these were thought to be active. We believe that at least 13 streams or stream segments in the southeastern, southwestern, and northwestern portions of the park are continuously occupied by beaver. This baseline information provides a conservative estimate of occupied beaver habitats in Yellowstone National Park in 1989–90. The information may be used by other researchers investigating riparian systems and in predicting potential effects of gray wolves (*Canis lupus*) on secondary prey species such as beaver. We recommend monitoring river segments and pond sites on a periodic basis to assess changes in the status of beaver in Yellowstone National Park.

Relatively little monitoring or research has been done on beaver (*Castor canadensis*) in Yellowstone National Park. In the earliest days of the park's history, park naturalist M. P. Skinner made notes on the beaver. The first detailed study of beaver and their activity in the park was done in 1921 and 1923 (Warren 1926). That study was concentrated in the northern portion of the park, particularly in the Tower Junction–Yancey's Hole region near the Yellowstone River. Warren concluded that beaver were overstocked in Yellowstone and that available aspens (*Populus tremuloides*), a favored food for beaver, were being destroyed faster than they were being replaced in forests accessible to beaver. In 1953 and 1954, Jonas (1955) studied beaver in the Camp Roosevelt region near Tower Junction and collected information from more widespread drainages throughout the park. He concluded that the beaver population was unstable and had been for 30–40 years. He attributed this instability largely to a lack of preferred foods due to marginal habitat and xeric conditions, the "overpopulation of beavers" in the 1920's mentioned by Warren, and an "overpopulation of elk" in the 1950's (Jonas 1955).

From 1970 to 1979, the relations between ungulates and plants were studied on the northern range of the park (Houston 1982). Houston noted that beaver occurred throughout the northern range in the 1970's, but that most colonies in the park seemed to be ephemeral and that the "available evidence does not support earlier interpretations of competitive exclusion of beaver by elk" (Houston 1982). Fullerton (Yellowstone National Park, unpublished data) surveyed beaver habitat to establish some baseline information and speculated on patterns of colony persistence. She noted apparently persistent colonies in seven areas, from stream courses a few miles long to extensive riparian regions encompassing major portions of townships.

In 1986, the park increased its efforts to understand the ecology of Yellowstone's northern range. Questions were raised concerning the condition of riparian zones and the status of beaver. Recently, scientists have expressed interest in this topic for several reasons: Some observers believe that beaver, aspens, and willows (*Salix* spp.) are declining in the park because of high numbers of ungulates, particularly elk (Chase 1986); others have alleged that beaver no longer occur in the park (Teer 1988).

In 1988, the National Park Service and the U.S. Fish and Wildlife Service were mandated by Congress to analyze four major questions relating to proposals for wolf (*Canis lupus*) reintroduction into Yellowstone National Park. One of the mandates was to assess the potential effects of wolves on prey. Beaver are an important secondary food source for wolves in some areas, including western Canada; Isle Royale, Michigan; and the Alaska Peninsula (Mech 1970). In southern Ontario, beaver were one of three primary summer prey species for wolves (Pimlott 1967), and another study found that beaver gradually became the most important prey as deer (*Odocoileus* spp.) declined (Voight et al. 1976). Updated information on Yellowstone's beaver is thus timely to include in future wolf–prey analyses.

In 1988, the National Park Service began a survey to document presence and distribution of beaver in the park and to develop an appropriate monitoring scheme for assessing changes in the status of beaver. The objectives of the initial phase of the survey were to identify places with present or recent beaver activity and to assess the likelihood that those sites could support long-term versus highly intermittent beaver activity. Where evidence of beaver presence was identified, the objective was to follow up with more intensive observation and to identify the number of individuals in the colonies. However, we recognized that this probably would not be accomplished until after at least two seasons of field survey. Here, we summarize results from the sampling survey only.

Study Area and Methods

The study area was not confined to the ungulate winter range but was parkwide. Five major rivers drain the park (Fig. 1). The Yellowstone River drains the eastern half of the park. From its source in Wyoming's Teton Wilderness, the upper Yellowstone meanders for 23 km through the Thorofare region in the park's southeastern corner to the southeastern arm of Yellowstone Lake. The gradient is nearly level, and the river is bordered by tall willows and numerous ponds. Nine tributaries flow into the upper

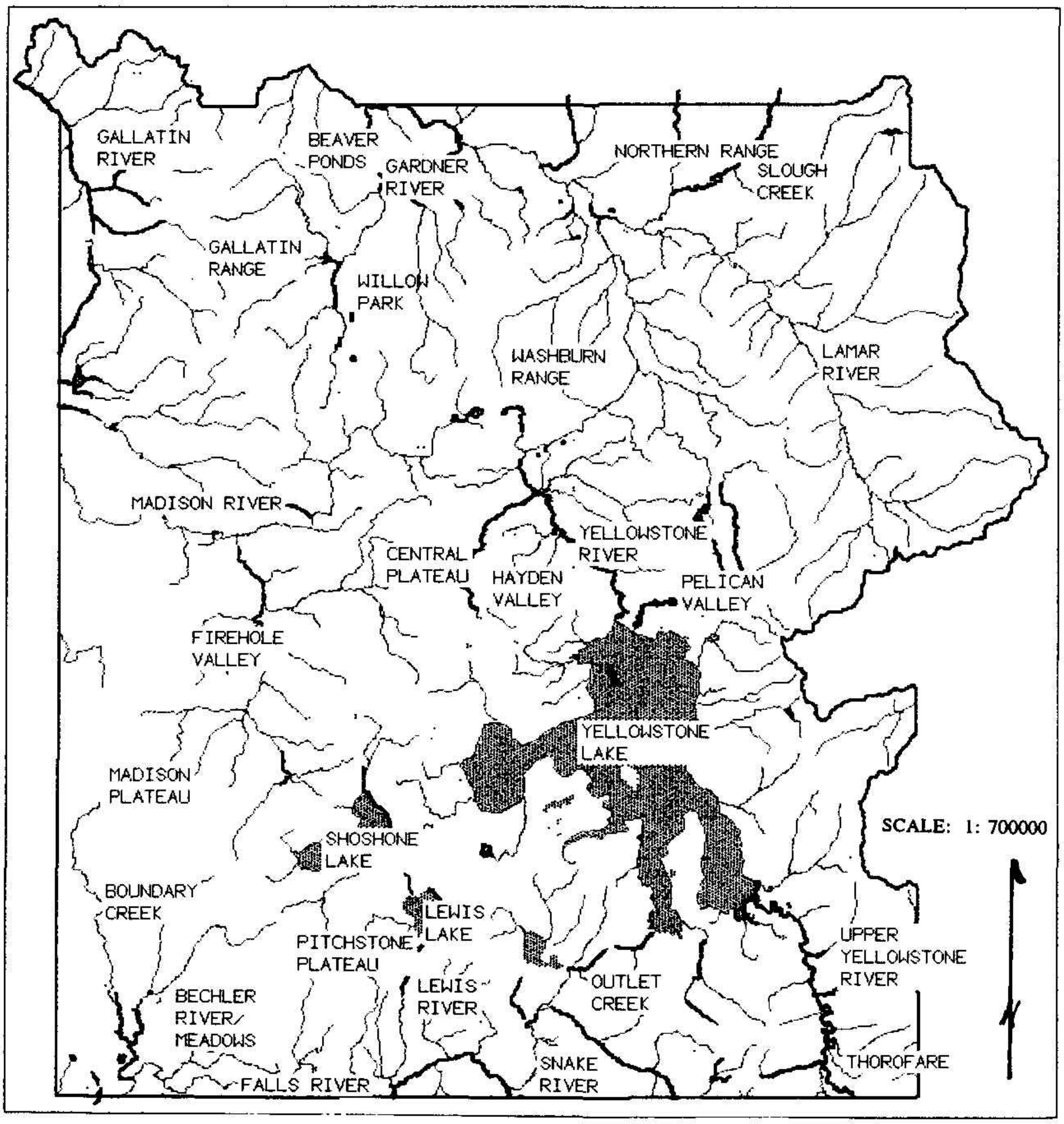

Fig. 1. Streams and lakes surveyed for beaver presence in Yellowstone National Park, 1988–89.

Yellowstone. Where the Yellowstone River flows into Yellowstone Lake it forms a broad, marshy delta with extensive willows and cottonwoods (*Populus* spp.). Of 124 known tributaries to Yellowstone Lake, beaver activity has been observed on only a few in recent years (R. Gresswell, U.S. Fish and Wildlife Service, personal communication). The river flows northward out of Yellowstone Lake at Fishing Bridge, passes through the sagebrush and the grasslands of Hayden Valley in the central portion of Yellowstone, then drops over two waterfalls in the Grand Canyon of the Yellowstone River. Here the character of the river and its riparian zone changes considerably as it continues northward around the Washburn Range and into the lower elevations of the park. The Lamar River and several other major tributaries drain the higher ridges of northeastern Yellowstone and the park's northern ungulate winter range. Aspens occupy 2–3% and riparian shrubs about 0.4% of the northern range (Houston 1982). The Gardner River and its tributaries drain the eastern side of the Gallatin Range; the Gardner joins the Yellowstone near the park's northern entrance at Gardiner, Montana.

The Madison River and its tributaries drain the west-central portion of the park, including the Central and Madison plateaus and the geyser basins in the Firehole Valley. Much of this area is dry, covered by lodgepole forest, and punctuated by thermal features. The lower 6.5 km of the Madison River valley support the only noticeable communities of willows, cottonwoods, or aspens in these riparian zones. The Gallatin River drains the western side of the Gallatin Range in the northwestern corner of the park. Along the park border, the riparian zone has extensive areas of willows, grasses, and sagebrush (*Artemesia* spp.) on a mild gradient.

The southwestern corner of Yellowstone receives the most snowfall in the park and retains much of that moisture in wet meadows until late summer. The Falls River and its major tributaries, the Bechler River and Boundary Creek, drain the Madison and Pitchstone plateaus into southeastern Idaho. The Bechler Meadows are a mixture of grassland, wet meadows with tufted hairgrass (*Deschampsia caespitosa*) and sedges (*Carex* spp.), and isolated stands of conifers. Aspens are present but not abundant. The rivers are bordered by extensive willow zones with occasional alder (*Alnus* spp.) present. Between the Pitchstone Plateau and Yellowstone Lake, the Lewis and Snake rivers drain Lewis and Shoshone lakes and the south-central portion of Yellowstone Park into Jackson Hole. These valleys contain occasional willow and aspen communities within a high-elevation coniferous forest.

Using information from known beaver observations in recent years and from previous beaver surveys, we identified routes along lakes and stream segments to survey in 1988–89. The park maintains a file of wildlife observations dating back to at least the 1940's, although the observation records for beaver apparently disappeared from the files in approximately 1986. Thus, we relied on information from experienced park staff and other reliable observers to determine points of recent beaver activity. These reference points were prioritized based on our preliminary assessment of known available beaver habitat. To better identify potential habitat and areas for ground survey, two aerial surveys were made in August 1989, covering the eastern and western halves of the park. Active areas were positively identified by green leaves or shoots on beaver dams or lodges, although bank dens, caches in rivers, and some other signs of activity were undoubtedly not observed. Large lodges were easily seen from an airplane, though we could not accurately determine whether lodges were active. Based on all available information, lakes or stream segments were identified and prioritized for ground survey. Stream segments included tributaries to major rivers where gradient and riparian cover type suggested that the area could support beaver. Major rivers, such as the Snake and Yellowstone, were divided into surveyable segments based on topographical barriers (such as Yellowstone Lake and the Grand Canyon of the Yellowstone River).

Ground survey methods involved walking or horseback riding along the prioritized streamcourses and pond or lake sites. We used a canoe to survey the lower 3.2 km of the Yellowstone River delta. As time permitted, we watched lodges and dams in the early morning and evening hours to observe beaver. The activities—classified as present, recent, or old—were documented on field data sheets. Present and recent activities were noted on topographical maps and later computerized into the park's geographic information system using Universal Transverse Mercator (UTM) coordinates (Fig. 2). Present and recent activities were identified by distinct fresh cuttings, wood chips, shoots with green leaves, fresh mud on lodges and dams, or a beaver sighting. Recent activity was estimated to be no more than several years old; here, no positive sign of beaver activity could be determined during the survey year, but other signs—such as old leaves remaining on shoots and dams still holding water—were subjectively evaluated as to the age of abandonment. Old activity was characterized by obvious abandonment of the site, indicated by collapsed beaver lodges, grayed tree stumps or cut logs, and barely evident or long-breached dams. Active areas that also showed signs of old activity were recorded as sites with long-term beaver presence.

Time and staff constraints, combined with the large number of riparian habitats that were identified as potential beaver habitat, required us to survey from May to October. Ideally, all habitats would have been surveyed in late summer or fall, when beaver are more active in repairing lodges and caching food. Thus, this survey provides at best a conservative estimate of occupied beaver habitats in Yellowstone in 1989–90. However, we targeted those habitats that were most likely to be occupied by persistent colonies for fall survey.

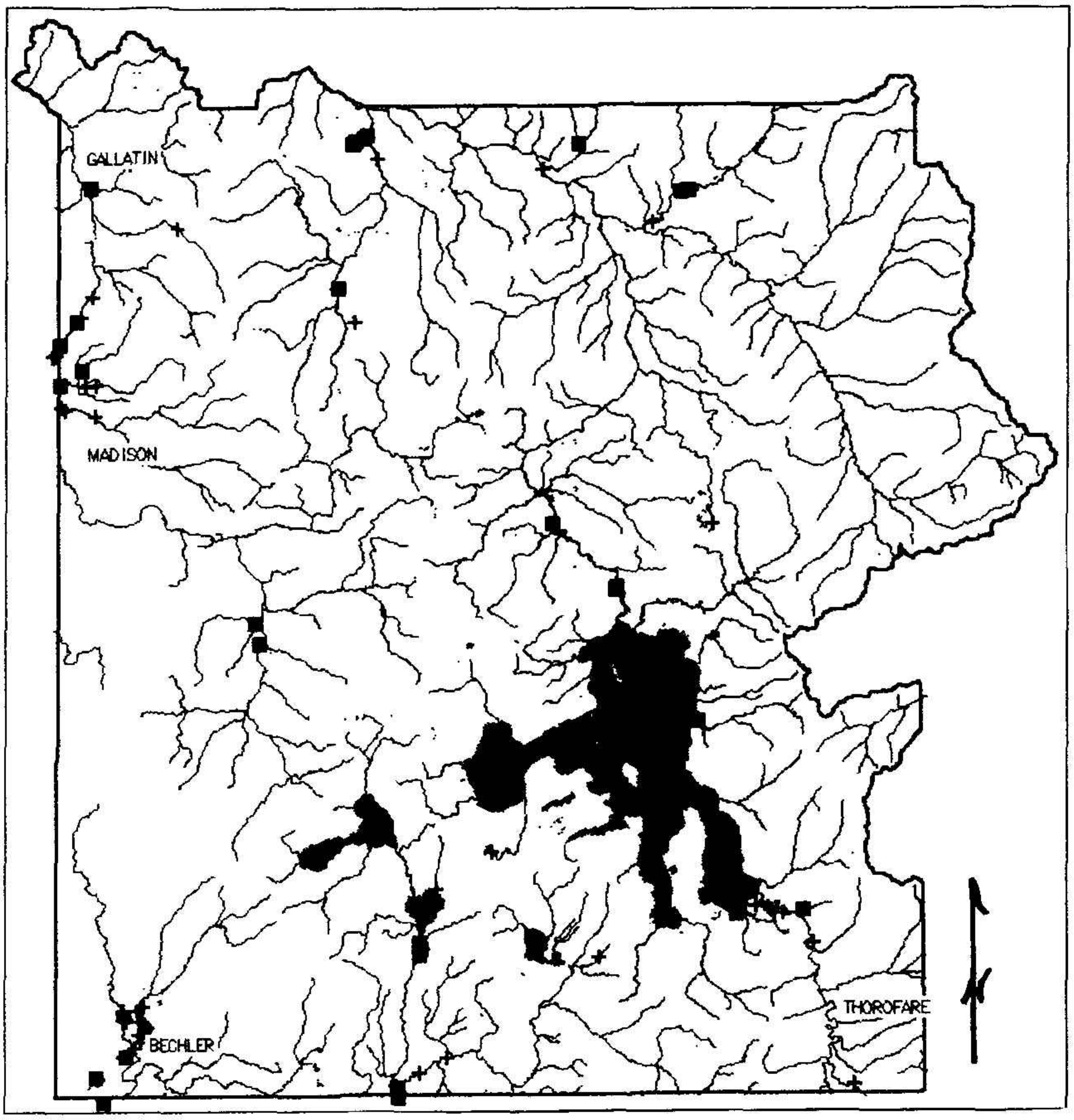

Fig. 2. Active signs and sightings of beaver in Yellowstone National Park, 1988–89: + = active sign; ♦ = sighting.

Results

During the survey, 42 sightings of beaver were reported throughout the park by reliable observers (Fig. 2). These sightings represented a minimum of 26 individual beaver and represented a biased sample based on access and proximity to park trails and roads. Between May 1988 and October 1989, a two-person crew surveyed 460 km of riparian habitat (Table). One hundred eight lakes and stream segments were visited in the 5 major river drainages across Yellowstone National Park (Fig. 1).

Table. Distribution of beaver (*Castor canadensis*) sign in Yellowstone National Park, 1988–1989.

Drainage	Streams and lakes surveyed	Kilometers of river traveled	Beavers sighted	Sighting locations	Active lodges
Yellowstone	61	272	20	11	23
Madison	25	58	6	3	17
Gallatin	3	37	1	1	3
Snake	13	68	6	3	6
Falls	6	25	9	2	22
Total	108	460	42	20	71

One hundred forty lodges were located; half (71) of these were thought to be active, 8 were characterized as recently abandoned (1–5 years ago), and 61 were thought to be occupied by beaver more than 5 years ago. Other signs of current activity—such as dams, canals, fresh caches, wood chips, and beaver tracks—were documented.

Dams were included in 71 areas of past and present activity—29 looked active, 8 seemed to be recent, and 34 were distinctly old dams. As found in other areas (Easter-Pilcher 1987), not all beaver colonies build dams. Not all locales with current signs of beaver were represented by active dams. Most of the dams found were on small creeks (<3 m wide) and rivulets, such as those running into the Gallatin and Lewis rivers. Larger creeks and rivers had few dams, although lodges, caches, bank dens, and other signs were commonly found. This is not surprising for fast-moving streams such as the Snake River and Slough Creek, which typify many park rivers that have substantial seasonal water-level fluctuations.

At least 27 lakes, streams, or stream segments had signs of present and old activity, indicating persistent occupation by beaver. Ten stream segments had multiple areas of beaver occupation or a number of lodges spread over 4–9 km of waterway.

Discussion

Signs of numerous, persistent beaver colonies typified by abundant lodges, caches, cuttings, and dams were found in the upper Yellowstone River–Thorofare region, the Bechler region, lower elevations of the Gallatin River drainage, and portions of the Madison River drainage near West Yellowstone, Montana. With the exception of the Bechler River drainage, these findings are consistent with the findings of Fullerton (Yellowstone National Park, unpublished data). Along the Bechler River and Boundary Creek, we found approximately one active lodge per 0.8 km of river and also identified lodges associated with dams or ponds. The Gallatin and Madison drainages had numerous ponds, often associated with several lodges and dams. Willow communities were present and vigorous, and aspen or other hardwoods were present nearby. As expected, these areas were outside the park's predominant rhyolitic plateaus in broader, flat valleys. Each of these areas receives considerably more snowfall than does the drier northern range along the lower Yellowstone River.

Moderately persistent beaver activity was found on the Yellowstone River just downstream from Yellowstone Lake, Slough Creek, the Gardner River, the Beaver Ponds and Slide Lake north of Mammoth Hot Springs, Obsidian Creek in Willow Park, and along the Snake and Lewis rivers. These areas were characterized by some combination of present, recent, and old activity, evidenced by cuttings, lodges, dams, and canals. We suggest that these sites are somewhat ephemeral, supporting perhaps only one colony of beaver at a time over 5 to 10 years. Hardwoods and willow communities were not abundant, if present at all; however, we did not survey aquatic and riparian vegetation, which form the diet of beaver. Thus, as the available food source in the area is depleted, beaver may be forced to move to other areas. For example, we hypothesize that beaver may move between the Gardner River and nearby ponds and lakes (such as Slide Lake). Beaver may also move around Shoshone Lake and its tributaries colonizing different parts of the lakeshore in different years; a similar pattern may exist on Lewis Lake.

Some additional sites appear to represent isolated pockets of beaver activity, either in ponds, such as Harlequin Lake, or in stream stretches that have the only beaver activity for miles. During the aerial survey, we identified some of these isolated colonies such as those on Outlet Creek south of Yellowstone Lake and on Broad Creek north of Pelican Valley. These isolated colonies were typically located at higher elevations than the more persistent beaver sites. We classify both the moderately persistent and the more isolated sites as marginal beaver habitat; however, we predict that these sites will likely continue to support intermittent beaver use over the long term.

Thirty-two lakes or stream segments not known to be currently occupied by beaver had signs of past beaver activity. Twenty-two of these were surveyed on the ground; 10 were observed only from the air. Caution must be used in comparing the number of currently active sites with previously active areas, because the latter represents an accumulation of activity that occurred over decades. The rate of decay of old dams and lodges varies significantly due to the differing nature of the habitat, the structures built, and the flooding characteristics of the associated riparian zones. The overall impression gained from aerial observations was that old beaver activity did not exceed the amount of current activity. It appeared that old dams, lodges, and other signs remained visible for many years after abandonment.

During the ground surveys, we found beaver colonies in areas that seemed to offer suitable habitat, as expected. Suitable habitat did not necessarily require aspen, but beaver colonies with persistent activity in Yellowstone usually were associated with either sizeable willow or aspen communities. In some sites, aquatic vegetation such as the pond lily (*Nuphar polysepalum*), seems to be the major food for beaver. We surveyed several areas in which aspen was present, but beaver did not seem to be using it in these sites. No sign of cut aspen stumps was observed, nor were any aspen shoots or leaves observed on lodges in these areas, which were surveyed in fall. The risk associated with leaving cover adjacent to the watercourse to reach the aspen may have been unacceptable to the beaver. However, in another survey area, beaver regularly cut aspen and moved them across a busy highway, despite making themselves vulnerable to predators and traffic.

We undoubtedly missed some signs of beaver activity, both in surveyed and unsurveyed locations. Particularly on large rivers not suited for beaver dams, we observed some bank dens but likely failed to see others. We emphasize that an abundance of beaver signs does not mean an abundance of beaver (Townsend 1953; Hay 1958; Swenson et al. 1983; Easter-Pilcher 1987). However, beaver signs do reflect current animal presence and distribution.

Summary and Conclusions

In 1988–89, Yellowstone National Park had beaver present and active in at least 27 lakes or stream segments. These locations varied from a single pond or lake to lengthy riparian zones with evidence of multiple beaver colonies. Almost all the active sites showed signs of long-term beaver presence. We classify as high-quality beaver habitat at least 13 of the streams or stream segments in the northwestern, southwestern, and southeastern portions of the park. These are Thorofare Creek, Trapper's Creek, the upper Yellowstone River, the lower Madison River, Duck Creek, Cougar Creek, Campanula Creek, the Gallatin River, Fan Creek, the Lewis River, Boundary Creek, the Bechler River, and Wyoming Creek. The sites are characterized by a permanent watercourse with a low-to-moderate gradient, low seasonal water-level fluctuation, and more persistent aspen or willow communities than the northern and central portions of the park. We predict that these sites are likely to be continuously occupied by beaver, although beaver may not be present in all years or in consistent densities over time. Other tributaries to the major rivers in this group are likely to be periodically or persistently occupied; long-term monitoring may result in adding streams to the list.

Other sites vary in terms of the water regime, nearby vegetative cover types, and their likely ability to support relatively stable versus ephemeral beaver colonies. Tributaries to the Snake River and the Yellowstone River north of the lake are mostly steep, rocky, and show high water-level fluctuations. On the Snake River, we saw one recently active lodge that in mid-July was 2–3 m above the level of the river. Such large fluctuations limit the size and persistence of beaver colonies (Retzer et al. 1956).

Should wolves reoccupy Yellowstone, Singer (1990) predicts that the major prey species will be elk (*Cervus elaphus*), bison (*Bison bison*), mule deer (*Odocoileus hemionus*), and moose (*Alces alces*), depending on prey availability and the predator's dietary preference. Singer suggests that wolves may limit (at least temporarily) numbers of more vulnerable and less abundant prey. In southeastern Alaska, Smith et al. (1987) concluded that although deer was the main prey for wolves, other food such as beaver, salmon, and human garbage supplemented wolf diets when deer were less available.

Based on the results of our preliminary survey, we suggest two hypotheses regarding potential effects of wolves on beaver in Yellowstone National Park: Beaver are so widely dispersed and outnumbered by an available ungulate prey base that effects of wolf predation on this secondary prey species would be minor; and wolves have the potential to strongly affect individual beaver colonies where they are widely dispersed and located in marginal habitat, such as on the northern range.

Beaver were observed in sufficient numbers and distribution to indicate that, other site influences remaining about equal, they are in no imminent danger of extinction in Yellowstone National Park. We suggest that beaver along the western and southern borders should not be highly vulnerable to wolf predation; however, beaver colonies on the northern range and in other areas such as Hayden Valley may be vulnerable due to their low densities.

Easter-Pilcher (1987) found that food availability, water depth, stream width, slope distance between low and high watermarks, vertical water fluctuation, and the presence of a confluence were positively correlated with beaver colony size. We propose using a more comprehensive stream survey system, such as that developed by Rosgen (1985) or Beier and Barrett (1987) to assess potential beaver habitat based on characteristics of Yellowstone's streams. At a minimum, aerial surveys should be done in September and October approximately every 5 years to identify areas of potential beaver activity throughout the park. However, aerial surveys are not sufficient to determine active versus abandoned beaver sites. We recommend that streams and lakes with previous or potential beaver activity be surveyed on the ground approximately once each decade. All present and historic beaver observations and activity records should be entered into a geographic information system to maintain a long-term data base to assess changes in the status of beaver in Yellowstone National Park.

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Using Pop-II Models to Predict Effects of Wolf Predation and Hunter Harvests on Elk, Mule Deer, and Moose on the Northern Range

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Abstract. The effects of establishing a gray wolf (*Canis lupus*) population in Yellowstone National Park were predicted for three ungulate species—elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and moose (*Alces alces*)—using previously developed POP-II population models. We developed models for 78 and 100 wolves. For each wolf population, we ran scenarios using wolf predation rates of 9, 12, and 15 ungulates/wolf/year. With 78 wolves and the antlerless elk harvest reduced 27%, our modeled elk population estimates were 5–18% smaller than the model estimate without wolves. With 100 wolves and the antlerless elk harvest reduced 27%, our elk population estimates were 11–30% smaller than the population estimates without wolves. Wolf predation effects were greater on the modeled mule deer population than on elk. With 78 wolves and no antlerless deer harvest, we predicted the mule deer population could be 13–44% larger than without wolves. With 100 wolves and no antlerless harvest, the mule deer population was 0–36% larger than without wolves. After wolf recovery, our POP-II models suggested moose harvests would have to be reduced at least 50% to maintain moose numbers at the levels predicted when wolves were not present. Mule deer and moose population data are limited, and these wolf predation effects may be overestimated if population sizes or male–female ratios were underestimated in our population models. We recommend additional mule deer and moose population data be obtained.

POP-II population models (Bartholow 1988) were developed for elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and moose (*Alces alces*) on Yellowstone's northern range (Mack and Singer 1993). Hunters harvest substantial numbers of northern range ungulates when they leave

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the boundaries of Yellowstone National Park. Average annual harvests, 1980–89, were 1,512 elk, 532 mule deer, and 31 moose. These POP-II models incorporated observed classification data and the effects of observed hunter harvests to estimate ungulate population sizes (Mack and Singer 1993). Additional mortality due to predicted wolf (*Canis lupus*) predation is easily incorporated into POP-II models, and the results are useful in assessing what effects wolves may have on elk, mule deer, and moose on the northern range. In this paper, we estimate the effects that a recovered wolf population may have had on elk, mule deer, and moose populations on Yellowstone's northern range if wolves had been introduced there in 1980. We also examine what effects modifying observed hunter harvests would have on the ungulate populations in the presence of wolves.

Other models investigating wolf predation on elk incorporate actual elk counts or slightly corrected estimates (Boyce 1990; Garton et al. 1990). We used POP-II models to predict the effects of wolf predation on northern range ungulates for the following reasons: (1) our ungulate population models were based on observed hunter harvest and classification data (the stochastic variables in our models); (2) we were able to easily incorporate three different wolf predation rates into the ungulate population models; (3) we were able to rapidly alter hunter harvests in various model scenarios because the POP-II models are user-friendly; and (4) we found the models were simplistic.

Our models do not include the potential functional responses of wolf predation on the ungulate populations. Our models do not account for density-dependent reproductive mechanisms or density-dependent mortality factors that ungulate populations may exhibit with wolf predation. While we do propose some alternatives that modify hunter harvests, we do not examine the wide range of alternatives the Montana Department of Fish, Wildlife, and Parks could use in modifying hunter harvests. These weaknesses may exaggerate the effects of wolf predation on northern range ungulate populations, particularly when a high wolf population, high wolf predation rate, and declining ungulate population are combined in the same model scenario. These weaknesses preclude using our models for predicting long-term fluctuations in wolf–prey population dynamics. However, we predicted wolf predation effects on elk 4 years into the future. Under these restricted conditions, use of POP-II models may be desirable because they are simple and strongly dependent on observed field conditions.

The large fires of 1988 burned extensive areas of ungulate summer range and approximately 32% of the entire northern winter range (Singer et al. 1989). During the first severe winter following the fires, the elk population declined as much as 40% (because of increased harvests and winterkill) and mule deer declined about 19% (Singer et al. 1989). The fires are predicted to increase production (Lyon and Stickney 1976), protein content, and digestibility of forage (Spalinger et al. 1986), although some of the positive effects on grasses and forbs may only last for 1–3 years (Hobbs and Spowart 1984; Wood 1988). After 1990, ungulate populations are predicted to increase because of combinations of increased bodyweight and survival, reduced calf vulnerability to predators, and reduced winterkill (Singer et al. 1989). Because of the predicted benefits to the elk population following the 1988 fires, we created a postfire elk–wolf model extending to 1994. If the elk population does not increase according to our model assumptions, our postfire elk population results could be invalid. Mule deer and moose were not modeled under a postfire scenario because the existing data on these species are incomplete, and the population dynamics and biology of these species inhabiting the northern range are not well understood (Mack and Singer 1993).

Study Area and Methods

The 1,000-km^2 study area consists of the northern elk winter range. Houston (1982), Despain (1991), and Singer (1991a) describe the climate, vegetation, geology, and landownership of the area.

Models

The POP-II elk, mule deer, and moose models used observed hunter harvest and classification data (young/100 adult females and males/100 adult females) to estimate population numbers. Additional mortality to the ungulate populations was incorporated as an age-specific overwinter mortality rate. The basic mortality rates provided for high young mortality and low adult mortality. Specific assumptions and detailed descriptions of the elk, mule deer, and moose models are described in Mack and Singer (1993). For the elk–prefire scenario, model simulations began in 1975 and ended in 1989. The elk–postfire scenario extended from 1975 to 1994. The mule deer and moose models extended from 1975 to 1989.

Elk–Postfire Scenario

We modeled the postfire-scenario elk population to reflect the benefits of the 1988 fires. Although several unknown and unquantified ecological factors associated with the 1988 fires may indeed be beneficial to the elk population, the reproductive and overwinter mortality responses we predicted are hypothetical. However, the values we used in our predictions were within the range of values observed during the 1980's. We predicted reproduction would increase from 26 calves/100 cows in 1990 to 36 calves/100 cows in 1992 and then slightly decrease to 34 calves/100 cows in 1993 and 1994. Overwinter mortality was reduced 40% from the average used for the high population prefire scenario.

Wolf Numbers

Beginning in 1980, we used an initial wolf population of 2 pairs of wolves in each of 3 years for a total of 12 wolves. We assumed these wolves experienced no mortality, and they increased at a high rate. We used 1.8 as the rate of increase (Boyce 1990). This rate of increase was higher than the one shown in Garton et al. (1990) and represents optimistic conditions of high pup and adult survival.

We modeled 2 wolf population scenarios of 78 and 100 wolves. For each of these wolf populations, we used 3 predation rates: 9, 12, and 15 ungulates/wolf/year. Our choice of 78 wolves is the average number of wolves that Garton et al. (1990) and Singer (1991b) estimated would inhabit the northern range. Between 50 and 150 wolves were expected to inhabit Yellowstone National Park (Boyce 1990; Koth et al. 1990; Singer 1991b). Therefore, we believe that more than 100 wolves inhabiting Yellowstone's northern range is unlikely. After the wolf populations reached their maximum number of 78 or 100 wolves, density-dependent factors (natural- and human-caused) were assumed to regulate natality and mortality and maintain the wolf population at the predefined maximum.

Wolf Predation

We predicted annual wolf kills based on published literature of wolf kill rates. Mech (1970) predicted one wolf killed 15 deer/year in Minnesota but recent data suggests 1 wolf killed the equivalent of 17 adult-sized white-tailed deer (*Odocoileus virginianus*)/year (L. D. Mech, personal communication). Fuller (1989) suggested one wolf killed 19 deer/year in Minnesota. Of this total, 11 were fawns and 8 were adults. These wolf predation rates occurred in deer-dominated systems and would be lower in elk-dominated systems.

Carbyn (1983) estimated 1 wolf killed 14 ungulates/year in Riding Mountain National Park in Canada. The approximate ungulate ratios in Riding Mountain National Park were 100 elk/24 deer/50 moose. Recent studies have shown the wolf predation rate ranging from 10 to 17.5 ungulates/wolf/year in Riding Mountain National Park (P. Paquet, personal communication). The wolf kill composition was 53% elk, 39% deer, and 7% moose; based on average ungulate population ratios, these percentages included slightly more deer than what would be expected on Yellowstone's northern range. Wolves avoided carrion in Riding Mountain National Park (P. Paquet, personal communication), possibly because they learned to avoid poison bait stations.

The wolf predation rate for the Nordegg, Alberta, area in Canada was 14 ungulates/wolf/year, and J. R. Gunson (Alberta Fish and Wildlife Division, Edmonton, personal communication) believed his estimates of predation rates were biased upward because he extrapolated mid- to late-winter predation rates to the whole year. A multiungulate prey base exists in the Nordegg area and includes elk, mule deer, moose, bison (*Bison bison*), bighorns (*Ovis canadensis*), and feral horses (*Equus caballus*). Average prey size is similar to Yellowstone's northern range. Gunson (personal communication) noted that the Nordegg area had very little carrion but that wolves in Yellowstone would probably always eat some carrion, suggesting the predation rate in Yellowstone would be lower than in the Nordegg area.

Because of the variable nature of wolf kill rates (Vales and Peek 1993), we used predation rates of 9, 12, and 15 ungulates/wolf/year. Our predation rates are near the low and moderate kill rates used in Vales and Peek (1993) of 6.6 and 13.4 elk killed/wolf/year.

Wolves may engage in surplus killing (Eide and Ballard 1982; Carbyn 1983; Miller et al. 1985). We compensated for surplus wolf kills by increasing the kill 10% for adult and subadult ungulates, as did Boyce (1990).

Relative Species Abundance and Vulnerability

Species composition of the wolf kill was calculated according to species abundance and vulnerability to wolves. Elk should be the primary prey species for wolves on the northern range (Boyce 1990; Garton et al. 1990; Singer 1991b). Therefore, relative abundance and vulnerability of mule deer, moose, pronghorn (*Antilocapra americana*), bison, and bighorns is expressed relative to elk (Table 1).

After correcting for availability, mule deer were killed from 1.3 to several times more often than elk in the Rocky Mountain parks of Canada (Cowan 1947; Carbyn 1974). However, we believe northern range mule deer will only be available to wolves 75% of the year (9 of 12 months). About 96% of the herd migrates north of the park each winter—near the town of Gardiner and adjacent to human settlements—where they will be less available to wolves (Singer 1991b). Based on these factors, we estimated that mule deer would be 1.1 times more vulnerable than elk. Moose were killed 0.7 times as often as elk in a Manitoba, Canada, study (L. N. Carbyn, P. Paquet, and D. Meleshko, unpublished manuscript). In snow, pronghorns are predicted to be 1.5 times more vulnerable than elk (Telfer and Kelsall 1984); however, pronghorns will be less available to

Table 1. Predicted relative abundance and vulnerability of ungulates inhabiting the northern range in comparison to elk (*Cervus elaphus*).

	Relative abundance			
Species[a]	Estimated population	Abundance ratio	Vulnerability[b]	Abundance vulnerability ratio
Elk	19,000	100.0	1.00	100.0
Mule deer	4,000	21.0	1.13	24.0
Moose	600	3.0	0.70	2.1
Pronghorn	600	3.0	1.00	3.0
Bison	500	2.6	0.70	1.8
Bighorn	300	2.0	0.30	0.6

[a] Elk = *Cervus elaphus*; mule deer = *Odocoileus hemionus*; moose = *Alces alces*; pronghorn = *Antilocapra americana*; bison = *Bison bison*; bighorn = *Ovis canadensis*.
[b] Vulnerability in comparison to elk, with elk having a vulnerability of 1.

wolves because they winter near Gardiner, Montana, and on private lands north of Yellowstone National Park (Singer 1991b). Therefore, we consider pronghorn and elk as having equal vulnerabilities (1:1). Bison are probably 1.2 times more vulnerable than elk in deep snow (Telfer and Kelsall 1984), but bison may be harder to kill than elk in shallow snows because of their large size and group defense of calves (Carbyn and Trottier 1987, 1988). We predict bison will be 0.7 times as vulnerable as elk on the northern range because of relatively shallow snows. After correcting for availability, bighorns were killed 0.2 to 0.4 times as often as elk in the Rocky Mountain parks of Canada (Cowan 1947; Carbyn 1974). For our model, we estimated bighorns to be 0.3 times as vulnerable as elk. From these species-abundance and vulnerability values, we calculated abundance/vulnerability ratios (Table 1).

Age–Sex Class Vulnerability

Wolves prefer preying on young of the year, adult male, and old adult ungulates (Mech 1966; Pimlott et al. 1969; Peterson 1977; Carbyn 1983). Mortality sensor radio collar studies have shown neonates to be more vulnerable to predators than previously believed (Franzmann et al. 1980; Miller et al. 1985; Bergerud and Elliot 1986; Ballard et al. 1987; Singer 1987). From these data, we estimated age–class vulnerability of young of the year/adult females to be 2:1, and the vulnerability of adult males/adult females to be 1.3:1. For each ungulate species, these age–sex vulnerabilities were then used with the POP-II estimated age–sex structure to predict the number of subadults, adult males, and adult females in the wolf kill each year. These age-specific kill rates (Tables 2 and 3) were applied to respective POP-II ungulate population models each year, 1980 through 1989, to obtain the model outputs.

We predicted wolves would kill between 534 and 1,141 elk per year during the postfire scenario (Table 4). The same age–sex vulnerabilities—plus the average POP-II estimated ratios (1990–94) of 32 calves/100 cows and 25 bulls/100 cows—were used to calculate the age–sex composition of the wolf kill for elk for the postfire scenario model (Table 4).

Human Harvest of Elk, Mule Deer, and Moose

Elk-Prefire Scenario

We used two different harvest levels in the elk–wolf models. We first modeled wolf predation effects on elk using observed hunter harvests. Second, we reduced the hunter harvest, beginning in 1980, by limiting the general season antlerless harvest to 25 elk in district 316 (7% reduction) and 100 elk in district 313 (20% reduction). We limited the late hunt antlerless harvest in district 313 to 875 elk. For any year the antlerless harvest was exceeded in a district, we proportionally reduced the hunter harvest of adult cows and subadults (Table 5). These modifications reduced the antlerless harvest from an observed average of 994 elk/year (which

Table 2. Hypothesized wolf (*Canis lupus*) predation on elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and moose (*Alces alces*) according to species and age–sex composition for a maximum population of 78 wolves.

			Species composition[a]				Age–sex composition[b]								
							Elk			Deer			Moose		
Year	Wolves	Ungulates as prey	Elk	Deer	Moose	Other	B[c]	C	Ca	B	D	F	B	C	Ca
9 Ungulates per wolf per year															
1980	4	36	27	7	1	1	6	14	7	1	3	3	0	1	0
1981	11	99	75	18	2	4	14	41	20	1	9	8	0	1	1
1982	24	216	164	39	4	9	24	77	63	1	18	20	1	2	1
1983	43	387	294	71	6	16	50	139	105	2	43	26	2	3	1
1984	78	702	534	128	11	29	111	252	171	2	59	67	3	6	2
1985	78	702	534	128	11	29	98	222	214	10	59	59	2	5	4
1986	78	702	534	128	11	29	93	266	175	12	57	59	3	6	2
1987	78	702	534	128	11	29	85	249	200	14	56	58	3	5	3
1988	78	702	534	128	11	29	90	300	144	18	83	27	2	5	4
1989	78	702	534	128	11	29	106	310	118	9	70	49	3	5	3
12 Ungulates per wolf per year															
1980	4	48	36	9	1	2	8	19	9	1	4	4	0	1	0
1981	11	132	101	24	2	5	19	55	27	1	12	11	0	1	1
1982	24	288	219	53	4	12	32	103	84	2	24	27	1	2	1
1983	43	516	393	94	8	21	67	185	141	3	56	35	2	4	2
1984	78	936	712	171	15	38	148	336	228	2	80	89	4	8	3
1985	78	936	712	171	15	38	130	297	285	13	79	79	3	7	5
1986	78	936	712	171	15	38	124	354	234	16	77	78	4	8	3
1987	78	936	712	171	15	38	113	333	266	19	75	77	4	7	4
1988	78	936	712	171	15	38	120	400	192	24	111	36	3	7	5
1989	78	936	712	171	15	38	141	414	157	11	94	66	4	7	4

Table 2. *Continued.*

							Age–sex composition[b]								
		Ungulates	Species composition[a]				Elk			Deer			Moose		
Year	Wolves	as prey	Elk	Deer	Moose	Other	B[c]	C	Ca	B	D	F	B	C	Ca
15 Ungulates per wolf per year															
1980	4	60	46	11	1	2	10	25	11	1	5	5	0	1	0
1981	11	165	125	30	3	7	24	67	34	2	15	13	1	1	1
1982	24	360	274	66	6	14	40	129	105	3	30	33	2	3	1
1983	43	645	491	118	10	26	83	232	176	3	71	44	3	5	2
1984	78	1,170	890	213	19	48	185	420	285	3	99	111	5	10	4
1985	78	1,170	890	213	19	48	163	371	356	17	98	98	4	9	6
1986	78	1,170	890	213	19	48	155	443	292	20	96	97	5	10	4
1987	78	1,170	890	213	19	48	141	416	333	23	94	96	4	9	6
1988	78	1,170	890	213	19	48	150	500	240	31	138	44	4	9	6
1989	78	1,170	890	213	19	48	176	517	197	14	117	82	5	9	5

[a] Calculated from an abundance–vulnerability ratio of 100 elk/24 deer/2.1 moose/5.4 others.

[b] Calculated from the POP-II estimated young per female and adult male per female ratios (Mack and Singer 1993) and the age–sex class vulnerability of 2 young/1.3 adult males/1 adult female.

[c] B = bulls or bucks; C = cows; Ca = calves; D = does; F = fawns.

Table 3. Hypothesized wolf (*Canis lupus*) predation on elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and moose (*Alces alces*) according to species and age-sex composition for a maximum population of 100 wolves.

			Species composition[a]				Age–sex composition[b]								
							Elk			Deer			Moose		
Year	Wolves	Ungulates as prey	Elk	Deer	Moose	Other	B[c]	C	Ca	B	D	F	B	C	Ca
9 Ungulates per wolf per year															
1980	4	36	27	7	1	1	6	14	7	1	3	3	0	1	0
1981	11	99	75	18	2	4	14	41	20	1	9	8	0	1	1
1982	24	216	164	39	4	9	24	77	63	1	18	20	1	2	1
1983	43	387	294	71	6	16	50	139	105	2	43	26	2	3	1
1984	78	702	534	128	11	29	111	252	171	2	59	67	3	6	2
1985	100	900	685	164	14	37	126	285	274	13	75	76	3	7	4
1986	100	900	685	164	14	37	119	341	225	15	74	75	4	7	3
1987	100	900	685	164	14	37	109	320	256	18	72	74	3	7	4
1988	100	900	685	164	14	37	115	385	185	23	107	34	3	6	5
1989	100	900	685	164	14	37	136	398	151	11	90	63	4	7	3
12 Ungulates per wolf per year															
1980	4	48	36	9	1	2	8	19	9	1	4	4	0	1	0
1981	11	132	101	24	2	5	19	55	27	1	12	11	0	1	1
1982	24	288	219	53	4	12	32	103	84	2	24	27	1	2	1
1983	43	516	393	94	8	21	67	185	141	3	56	35	2	4	2
1984	78	936	712	171	15	38	148	336	228	2	80	89	4	8	3
1985	100	1,200	913	219	19	49	167	381	365	17	101	101	4	9	6
1986	100	1,200	913	219	19	49	159	454	300	21	98	100	5	10	4
1987	100	1,200	913	219	19	49	145	427	341	24	97	98	4	9	6
1988	100	1,200	913	219	19	49	154	513	246	31	142	46	4	9	6
1989	100	1,200	913	219	19	49	180	531	202	15	120	84	5	9	5

Table 3. *Continued.*

			Species composition[a]				Age–sex composition[b]								
							Elk			Deer			Moose		
Year	Wolves	Ungulates as prey	Elk	Deer	Moose	Other	B[c]	C	Ca	B	D	F	B	C	Ca
15 Ungulates per wolf per year															
1980	4	60	46	11	1	2	10	25	11	1	5	5	0	1	0
1981	11	165	125	30	3	7	24	67	34	2	15	13	1	1	1
1982	24	360	274	66	6	14	40	129	105	3	30	33	2	3	1
1983	43	645	491	118	10	26	83	232	176	3	71	44	3	5	2
1984	78	1,170	890	213	19	48	185	420	285	3	99	111	5	10	4
1985	100	1,500	1,141	274	24	61	209	476	456	22	126	126	5	12	7
1986	100	1,500	1,141	274	24	61	199	567	375	26	123	125	6	12	6
1987	100	1,500	1,141	274	24	61	181	533	427	30	121	123	5	12	7
1988	100	1,500	1,141	274	24	61	192	641	308	39	178	57	5	11	8
1989	100	1,500	1,141	274	24	61	226	663	252	18	151	105	6	12	6

[a] Calculated from an abundance–vulnerability ratio of 100 elk/24 deer/2.1 moose/5.4 others.

[b] Calculated from the POP-II estimated young per female and adult male per female ratios (Mack and Singer 1993) and the age–sex class vulnerability of 2 young/1.3 adult males/1 adult female.

[c] B = bulls or bucks; C = cows; Ca = calves; D = does; F = fawns.

Table 4. Hypothesized wolf (*Canis lupus*) predation on elk (*Cervus elaphus*) according to age–sex composition for maximum populations of 78 and 100 wolves, 1990–1994.

			Age–sex composition[b]		
Wolf population	Predation rate[a]	Elk as prey	Bulls	Cows	Calves
78	9	534	88	272	174
	12	712	118	362	232
	15	890	147	453	290
100	9	685	113	349	223
	12	913	151	465	297
	15	1,141	189	581	371

[a] The predation rate is expressed as ungulates per wolf per year.
[b] The age–sex composition was calculated from the 1990–94 average predicted classification ratios of 25 bulls/100 cows/32 calves and an age–sex class vulnerability of 2 young/1.3 adult males/1 adult female.

Table 5. Actual hunter harvest of antlerless elk (*Cervus elaphus*) and the hunter harvest reduced 27% for use in the elk–wolf (*Canis lupus*) predation models.

	Hunter harvest of antlerless elk						Reduced antlerless elk harvest[a]					
	District 316		District 313		Late hunt		District 316		District 313		Late hunt	
Year	C[b]	Ca	C	Ca	C	Ca	C	Ca	C	Ca	C	Ca
1980	21	0	21	1	42	16	21	0	21	1	42	16
1981	31	10	21	1	422	100	19	6	21	1	422	100
1982	22	7	17	0	681	232	22	3	17	0	653	222
1983	0	0	38	28	815	396	0	0	38	28	590	285
1984	24	0	51	4	742	291	24	0	51	4	629	246
1985	36	6	53	9	728	205	21	4	53	9	683	192
1986	23	8	305	64	566	206	16	6	83	17	566	206
1987	41	6	76	12	148	56	22	3	76	12	148	56
1988	4	0	98	9	1,846	458	4	0	92	8	701	174
1989	26	4	400	44	326	58	22	3	90	10	326	58
Mean	26.6		125.2		833.4		19.6		63.2		631.5	

[a] Harvests were proportionally modified when the antlerless harvest exceeded 25 in Montana hunting district 316, 100 in Montana hunting district 313, and 875 for the late hunt.
[b] C = cows (adult female elk); Ca = calf elk.

included a total of 84 illegal kills for 1982 and 1983 of unknown sex and age) to 714 elk/year, reducing the antlerless harvest 27%. Bull harvests were unchanged.

Elk–Postfire Scenario

We ran two options in the elk–postfire scenario. For our first option, we ran the elk model without wolf predation and used the same average observed hunter harvest during 1984–89 (423 bulls, 916 cows, and 240 calves) for the hunter harvest during 1990–94. Our second option included wolf predation, and we used the same reduced antlerless harvest of 27% as in the elk–prefire scenario. The 1984–89 average reduced antlerless harvest of 601 cows and 168 calves was used for the antlerless harvest from 1990 through 1994. The bull harvest remained at 423 from 1990 through 1994.

Mule Deer

Three options for hunter harvests of mule deer were modeled. First, we modeled wolf predation on the mule deer population using the observed mule deer harvest. Second, we modeled wolf predation while limiting the antlerless harvest to 50. Finally, we modeled wolf predation and eliminated the antlerless harvest but used the observed buck harvest.

Moose

Three options for hunter harvest of moose were modeled. First, we used the observed moose harvest. Second, we reduced the bull and antlerless harvest by half. Third, we eliminated the antlerless harvest and only used the observed bull harvest.

Results

For comparative purposes, all ungulate population scenarios having no wolf predation were modeled with observed and unmodified ungulate harvests. Throughout the remainder of the text, these scenarios are identified as elk, mule deer, or moose populations without wolf predation.

Wolf Predation Effects on Elk

Prefire Scenario

The elk population declined during 1988–90 without wolf predation and declined much more rapidly during this period when wolf predation, at populations of 78 and 100 wolves, was added to the existing elk harvests (Figs. 1 and 2). When antlerless elk harvests were reduced 27% and the wolf population was 78, the elk population in 1989 was estimated to be 5 to 18% smaller than the elk population without wolf predation (Fig. 3). With the same reduced antlerless elk harvest and a wolf population of 100, the estimated 1989 elk population was 11–30% smaller compared to the elk population without wolves (Fig. 4).

Postfire Scenario

Under the postfire scenario with unmodified elk harvests and no wolves, the population was estimated to increase from 17,420 in 1989 to about 21,300 animals in 1994. For 78 wolves and the antlerless elk harvest reduced 27%, we estimated the elk population recovered from its downward trend in the late 1980's under wolf predation rates of 9 and 12

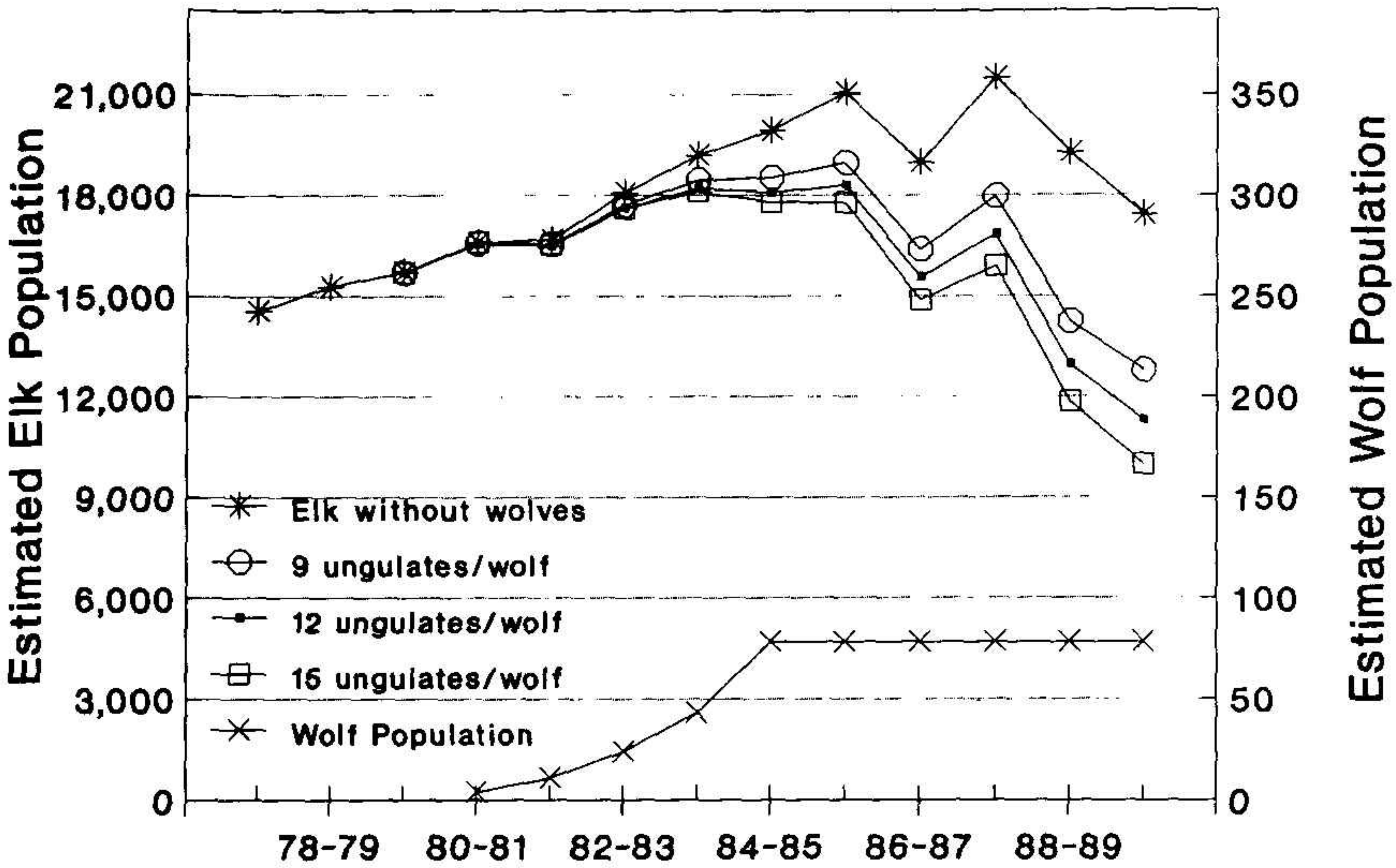

Fig. 1. Estimated elk population trends on Yellowstone's northern winter range, 1980–89, in which elk harvests were unmodified. Scenarios include elk without wolves and a maximum of 78 wolves having predation rates of 9, 12, and 15 ungulates/wolf/year.

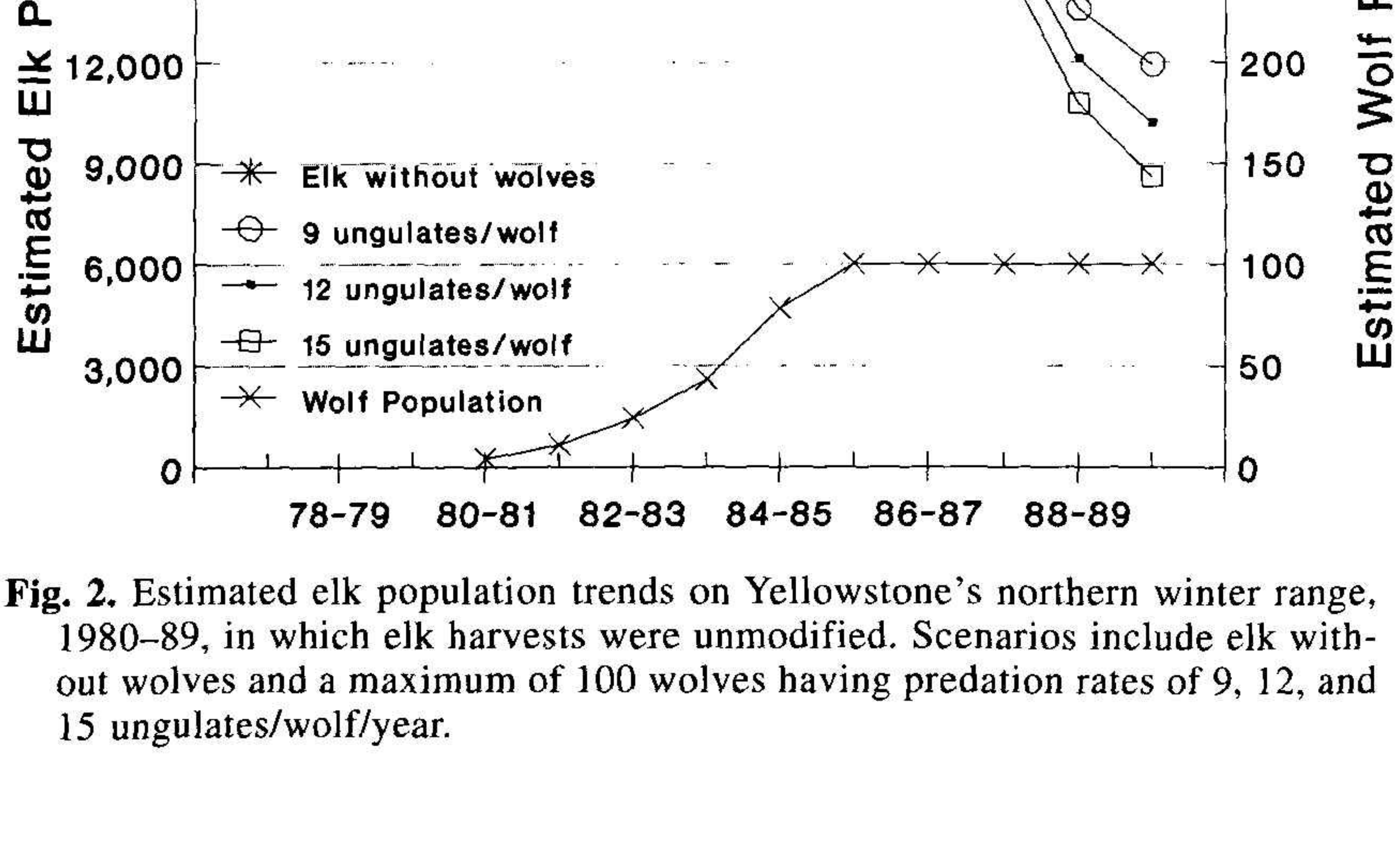

Fig. 2. Estimated elk population trends on Yellowstone's northern winter range, 1980–89, in which elk harvests were unmodified. Scenarios include elk without wolves and a maximum of 100 wolves having predation rates of 9, 12, and 15 ungulates/wolf/year.

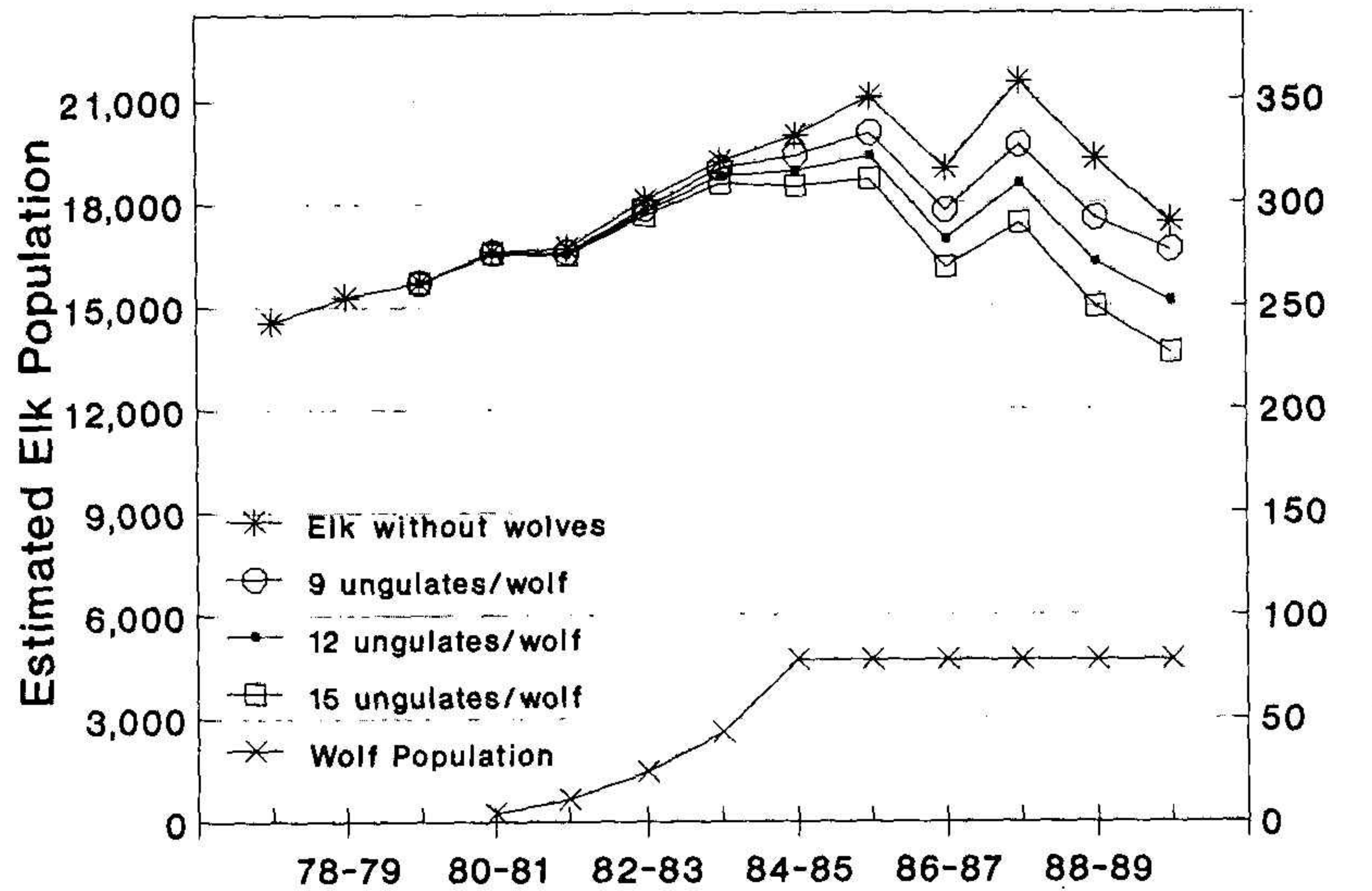

Fig. 3. Estimated elk population trends on Yellowstone's northern winter range, 1980–89, in which antlerless harvests were reduced 27% for the wolf predation scenarios. Scenarios include elk without wolves and a maximum of 78 wolves having predation rates of 9, 12, and 15 ungulates/wolf/year.

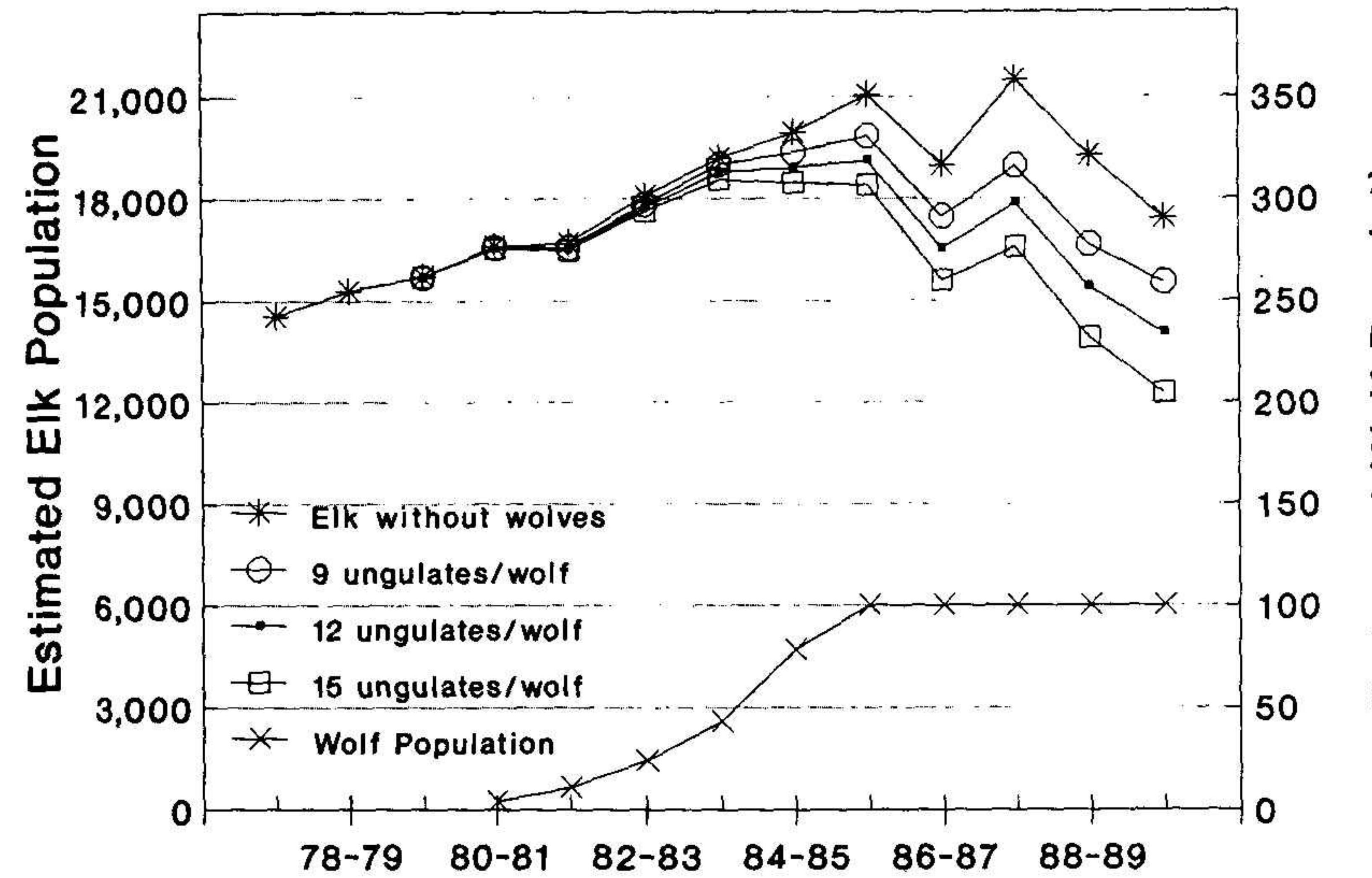

Fig. 4. Estimated elk population trends on Yellowstone's northern winter range, 1980–89, in which antlerless harvests were reduced 27% for the wolf predation scenarios. Scenarios include elk without wolves and a maximum of 100 wolves having predation rates of 9, 12, and 15 ungulates/wolf/year.

ungulates/wolf/year (Fig. 5). The elk population decreased slightly with a wolf predation rate of 15 ungulates/wolf/year (Fig. 5). For 78 wolves and predation rates of 9, 12, and 15 ungulates/wolf/year, our estimates suggested the 1994 elk population would be 5% (20,287 elk), 23% (16,446 elk), and 41% (12,561 elk) lower, respectively, compared to our predicted populations without wolves. For 100 wolves and the antlerless elk harvest reduced 27%, our estimates showed the elk population increased with a wolf predation rate of 9 ungulates/wolf/year and was about stable with a wolf predation rate of 12 ungulates/wolf/year (Fig. 6). The elk population rapidly declined when 100 wolves killed 15 ungulates/wolf/year (Fig. 6).

Wolf Predation Effects on Mule Deer

Observed Harvest

Wolf predation on mule deer—calculated for 78 wolves killing 9 ungulates/wolf/year (Table 2)—was entered into the POP-II mule deer model. The model ran to 1984 and then failed because too few bucks were available in the population to support hunter deer harvests and wolf predation during that year. In 1984, the predicted wolf kill of bucks totaled only two, so it was unlikely that wolf predation caused the model to fail. These results suggested that the modeled northern range mule deer population could

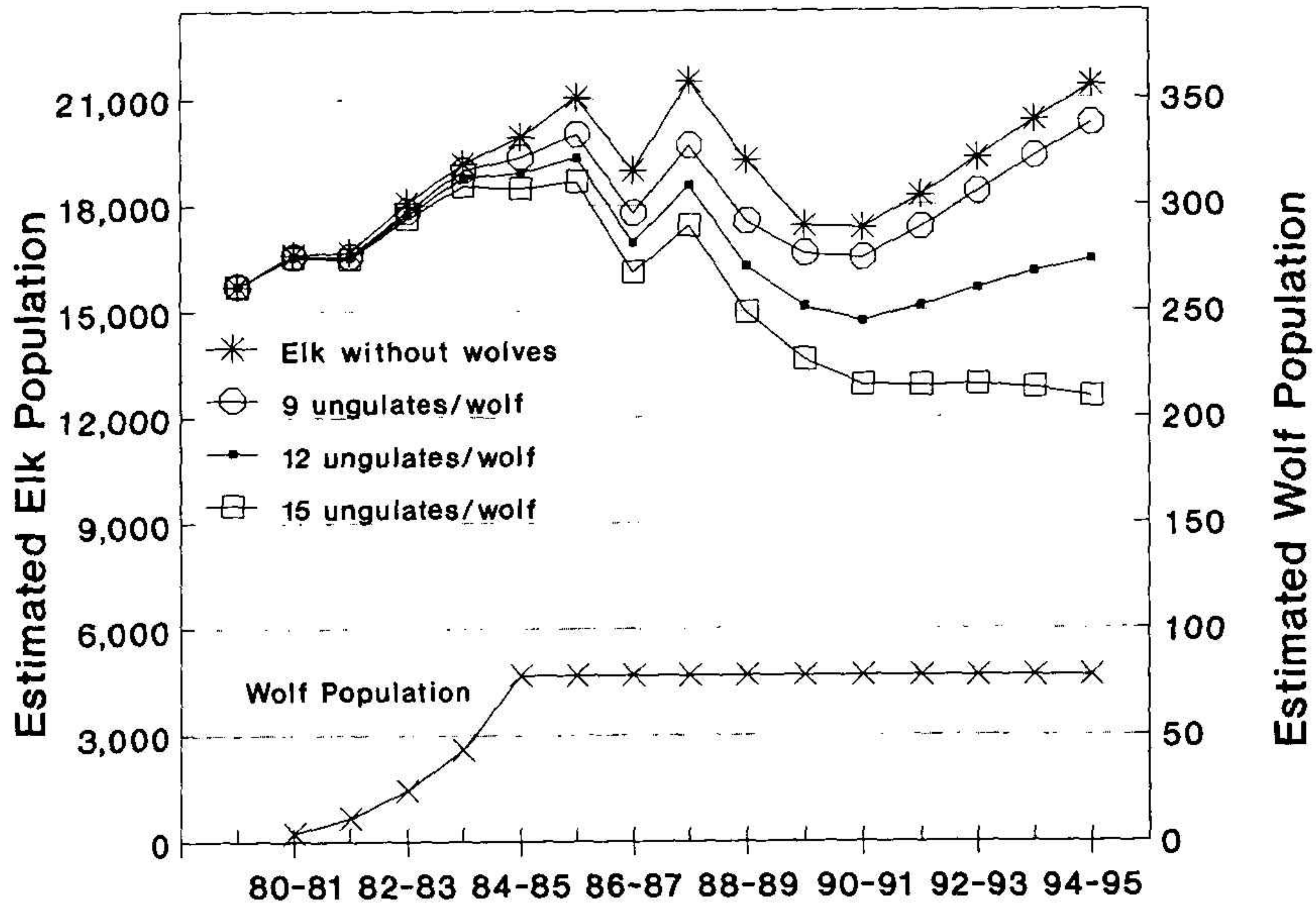

Fig. 5. Estimated elk population trends on Yellowstone's northern winter range, 1980–94, in which antlerless harvests were reduced 27% for the wolf predation scenarios. Scenarios include elk without wolves and a maximum of 78 wolves having predation rates of 9, 12, and 15 ungulates/wolf/year.

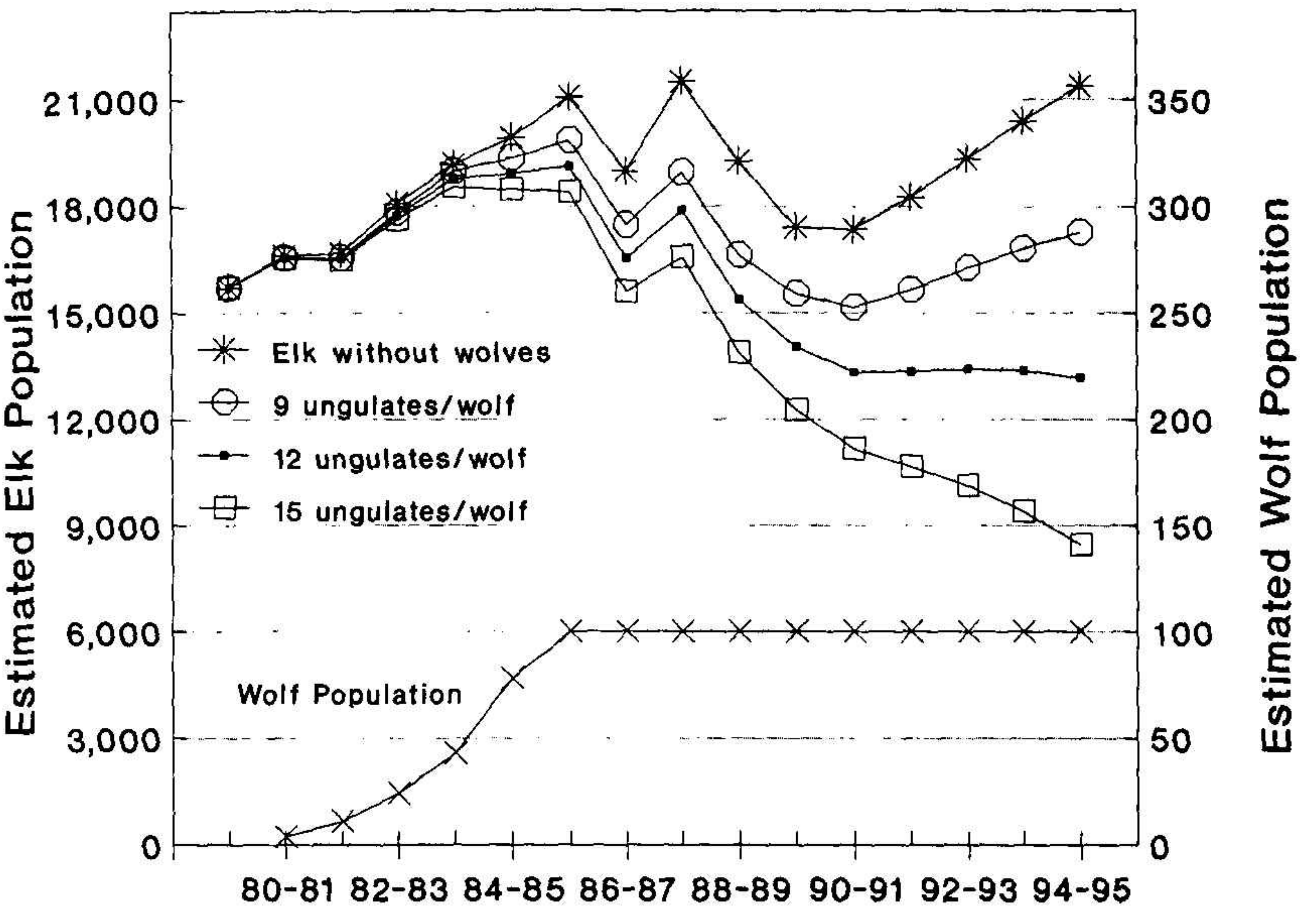

Fig. 6. Estimated elk population trends on Yellowstone's northern winter range, 1980–94, in which antlerless harvests were reduced 27% for the wolf predation scenarios. Scenarios include elk without wolves and a maximum of 100 wolves having predation rates of 9, 12, and 15 ungulates/wolf/year.

not support wolf predation and the observed mule deer harvest levels of the 1980's. A more likely explanation is that our mule deer model does not accurately describe the northern range mule deer population, particularly the buck population during the mid-1980's.

Reduced Antlerless Harvest

We reduced the average antlerless harvest 62% from the observed harvest of 122 antlerless deer/year. Only one scenario—78 wolves killing 9 ungulates/wolf/year—ran in the mule deer population model without failing. This wolf predation scenario predicted a 9% larger deer population compared to the population estimate without wolf predation. The remaining wolf populations and predation rates caused the model to fail because too few bucks were available to support the observed buck harvest and wolf predation.

No Antlerless Harvest

Eliminating the antlerless harvest allowed the northern range mule deer population to grow in the presence of wolves. For 78 wolves and the three predation rates, the modeled mule deer population ranged from 13 to 44% larger in the late 1980's compared to the estimated population with no wolf predation (Fig. 7). For 100 wolves and the three predation rates,

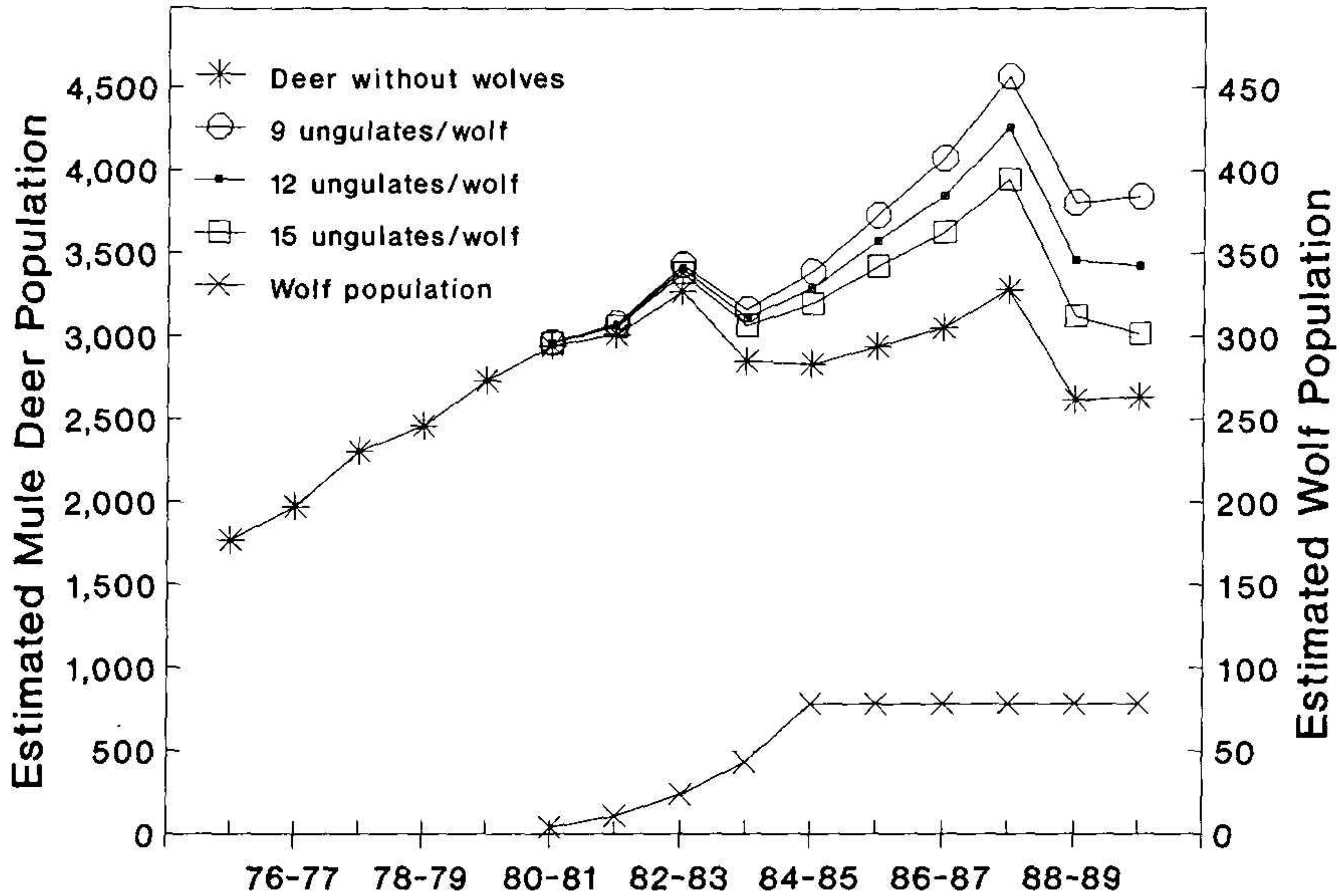

Fig. 7. Estimated mule deer population trends on Yellowstone's northern winter range, 1980–89, in which the antlerless harvests were eliminated for the wolf predation scenarios. Scenarios include mule deer without wolves and a maximum of 78 wolves having predation rates of 9, 12, and 15 ungulates/wolf/year.

the modeled mule deer populations ranged from 0 to 36% larger in 1989 compared to the modeled population without wolf predation (Fig. 8).

Wolf Predation Effects on Moose

Our initial models, combining wolf predation and the observed moose harvest for 1980–89, predicted that the moose populations declined and were unable to sustain added wolf predation (Figs. 9 and 10). A second option was modeled with hunter harvests of bulls and antlerless moose reduced by half for 1980–89 (Table 6). For 78 wolves and the three predation rates, our models predicted a 5% smaller to 12% larger population than what was observed with no wolf predation (Fig. 11). For 100 wolves and three predation rates, our estimates predicted a 13% smaller to 7% larger moose population compared to the moose population with no wolf predation (Fig. 12).

For 78 wolves, three predation rates, and no antlerless moose harvest, our models predicted only one less moose in the 1989 population compared to the estimates when the moose harvest was reduced by half. The same situation existed for the 100-wolf scenario with all three predation rates.

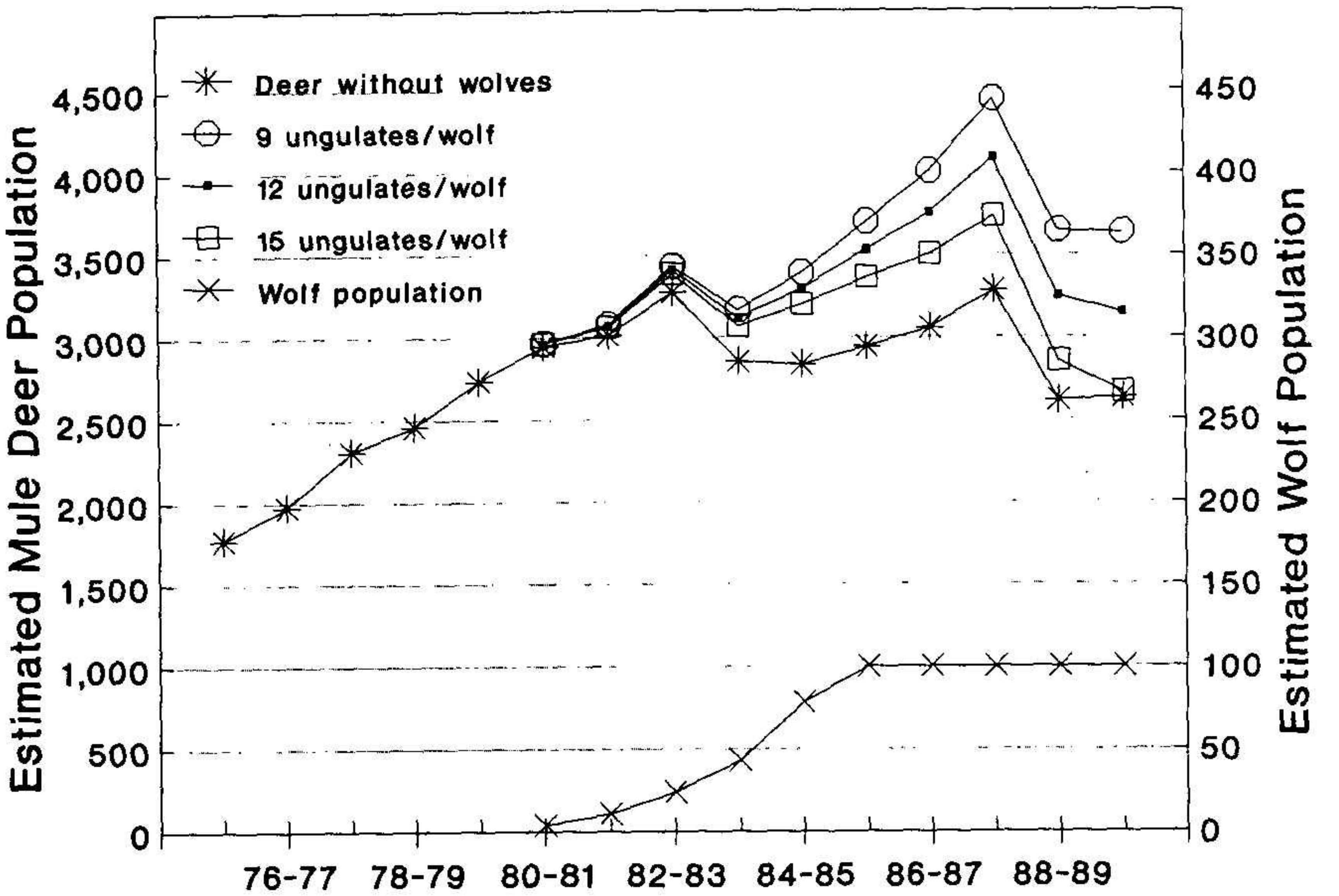

Fig. 8. Estimated mule deer population trends on Yellowstone's northern winter range, 1980–89, in which the antlerless harvests were eliminated for the wolf predation scenarios. Scenarios include mule deer without wolves and a maximum of 100 wolves having predation rates of 9, 12, and 15 ungulates/wolf/year.

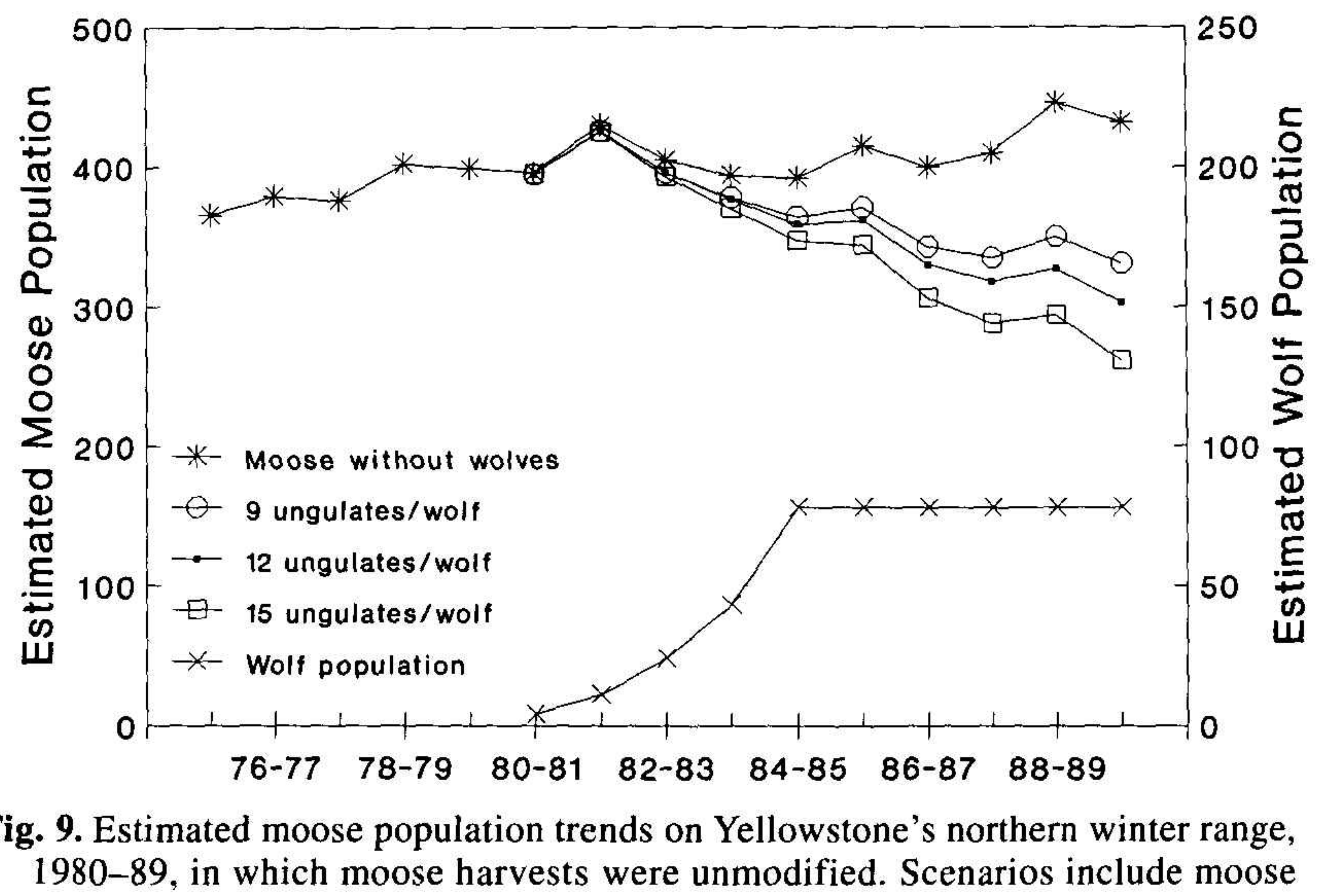

Fig. 9. Estimated moose population trends on Yellowstone's northern winter range, 1980–89, in which moose harvests were unmodified. Scenarios include moose without wolves and a maximum of 78 wolves having predation rates of 9, 12, and 15 ungulates/wolf/year.

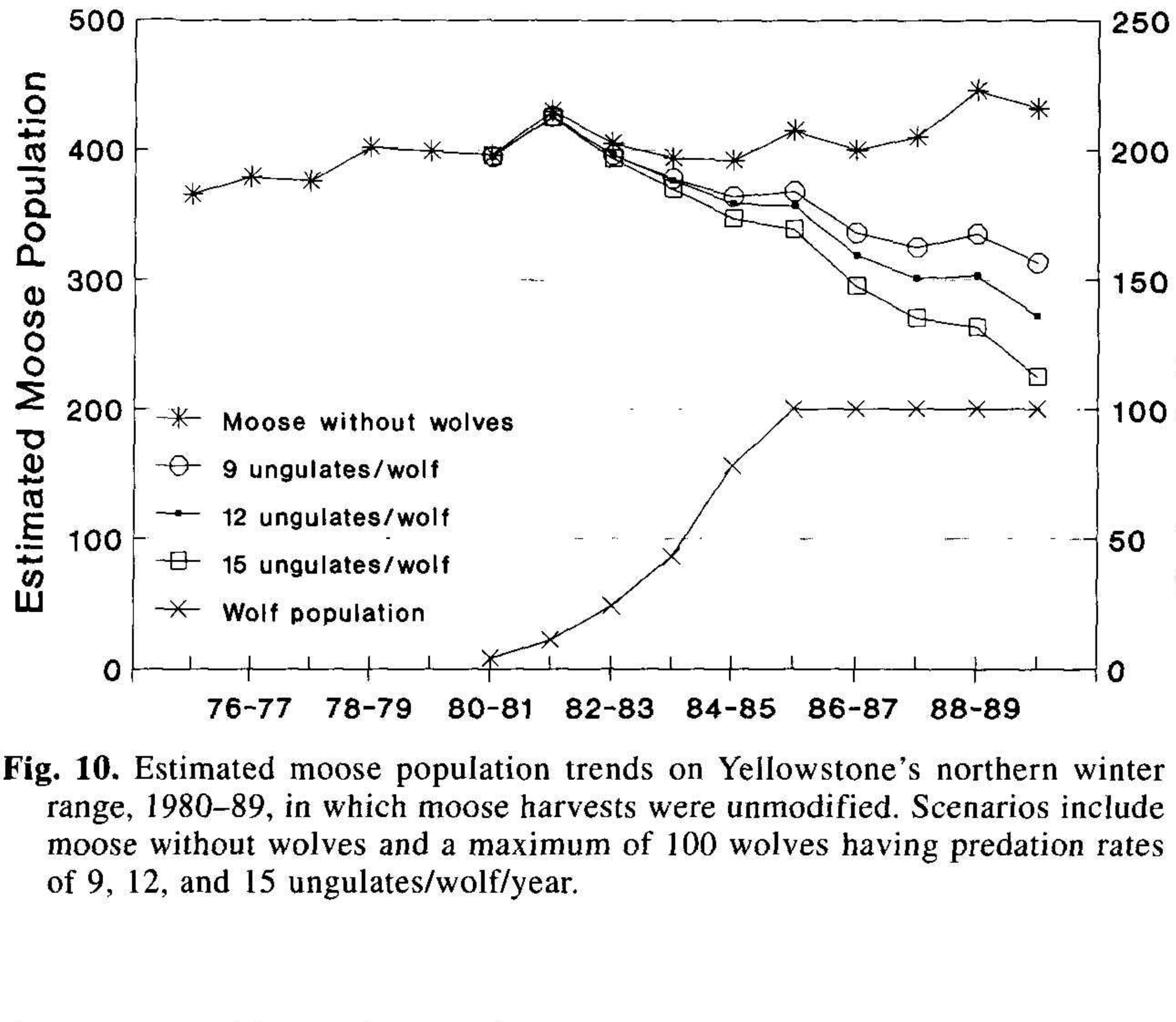

Fig. 10. Estimated moose population trends on Yellowstone's northern winter range, 1980–89, in which moose harvests were unmodified. Scenarios include moose without wolves and a maximum of 100 wolves having predation rates of 9, 12, and 15 ungulates/wolf/year.

Table 6. Actual hunter harvest for the northern range moose (*Alces alces*) population and reduced hunter harvest values used in the moose–wolf (*Canis lupus*) predation model.

	Hunter harvest			Hunter harvest reduced by half		
Year	Bulls	Cows	Calves	Bulls	Cows	Calves
1980	17	4	1	8	2	1
1981	23	5	0	12	2	0
1982	26	5	4	13	3	2
1983	27	3	2	13	1	1
1984	20	6	3	10	3	2
1985	21	5	3	11	3	1
1986	19	14	0	9	7	0
1987	19	12	1	10	6	1
1988	14	9	4	7	4	2
1989	23	14	1	11	7	0

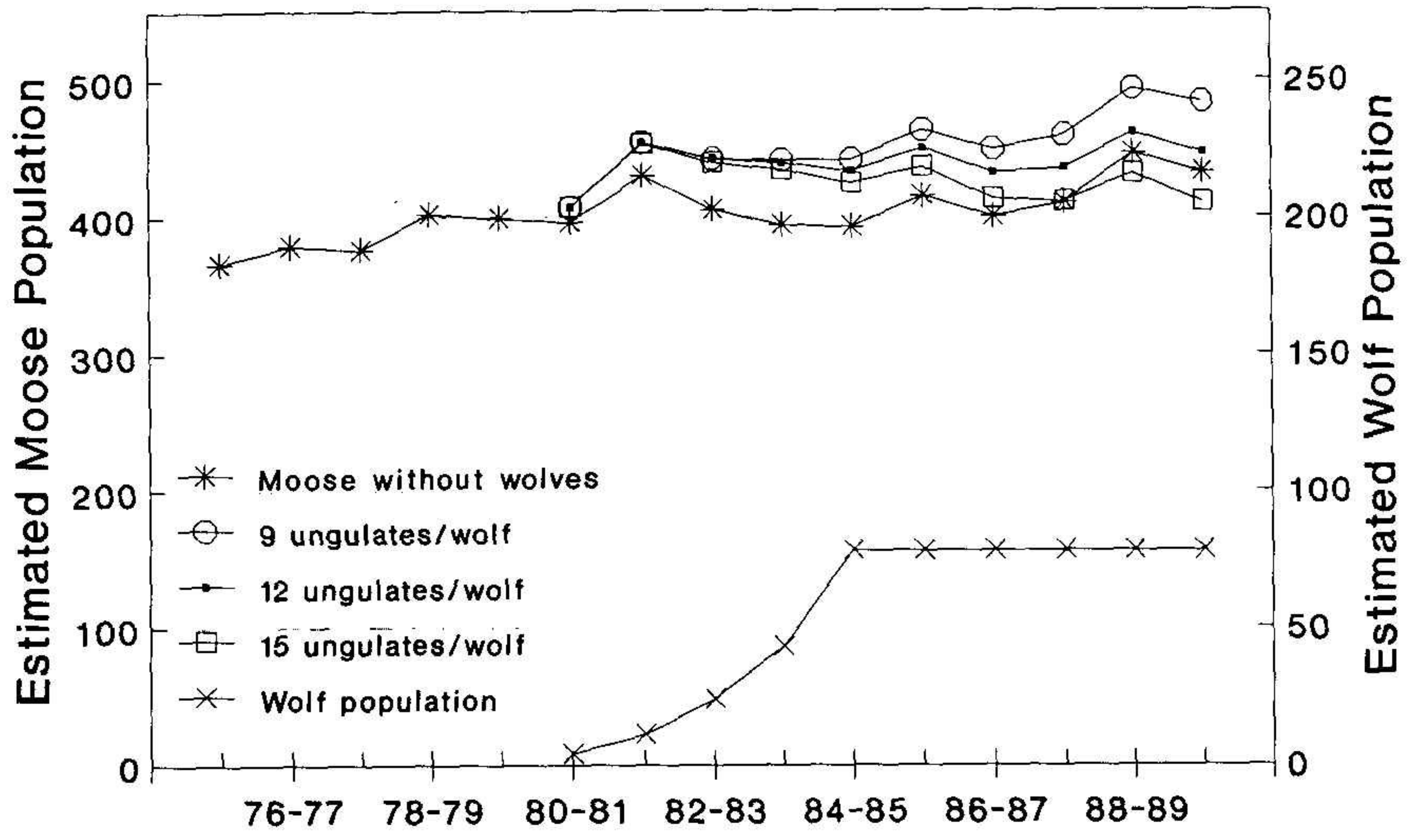

Fig. 11. Estimated moose population trends on Yellowstone's northern winter range, 1980–89, in which the moose harvests were reduced by half for the wolf predation scenarios. Scenarios include moose without wolves and a maximum of 78 wolves having predation rates of 9, 12, and 15 ungulates/wolf/year.

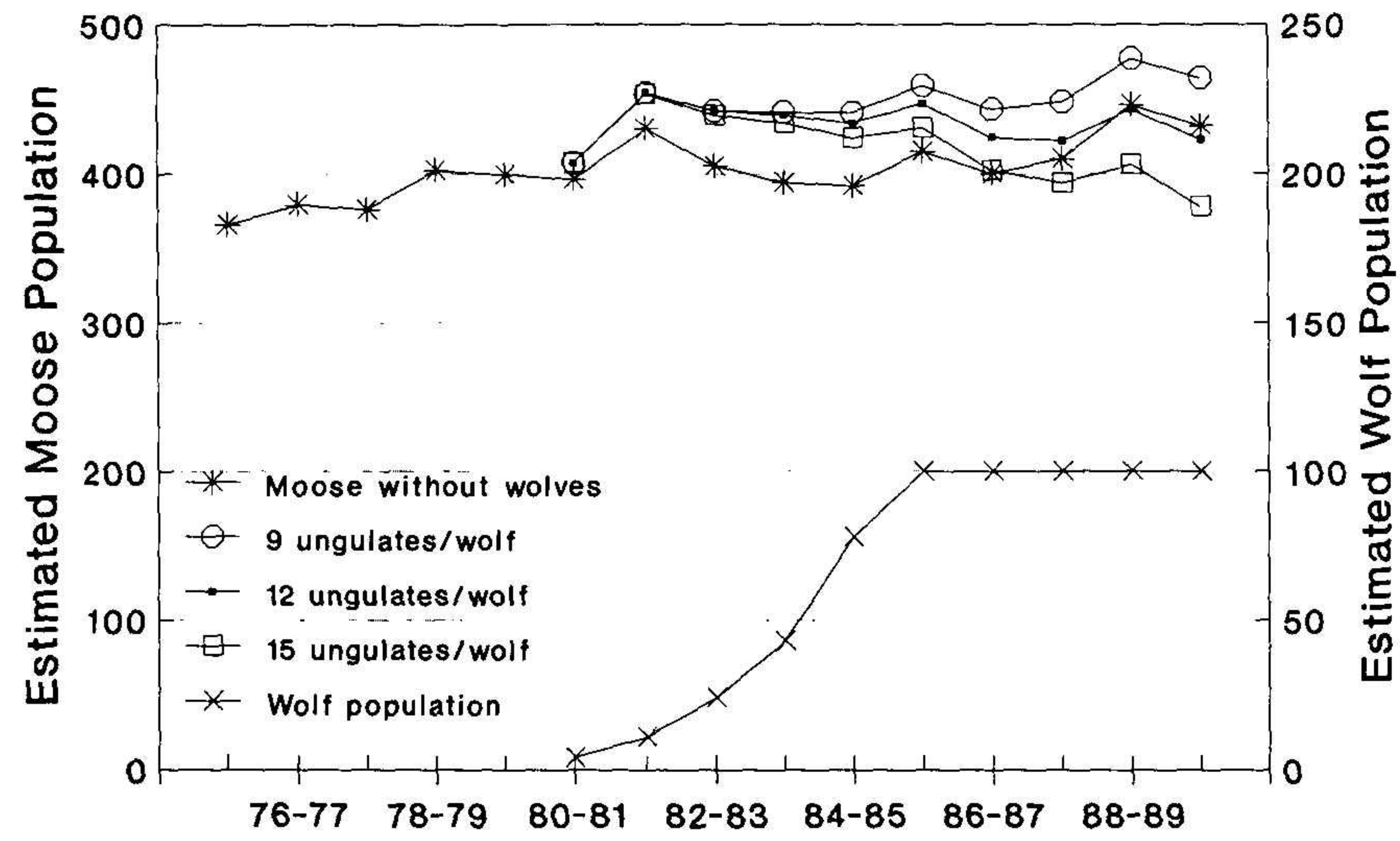

Fig. 12. Estimated moose population trends on Yellowstone's northern winter range, 1980–89, in which the moose harvests were reduced by half for the wolf predation scenarios. Scenarios include moose without wolves and a maximum of 100 wolves having predation rates of 9, 12, and 15 ungulates/wolf/year.

Discussion

Our models, with a population of 78 wolves, suggested that, when antlerless elk harvests were reduced 27%, 5–18% fewer elk would exist on the northern range with wolves. With 100 wolves and reduced antlerless harvests, we estimated 11% to 30% fewer elk. Boyce (1990) stated that "it does not appear necessary that wolf predation require that hunting opportunities be reduced." Boyce concluded that mean numbers of elk would be reduced 15–25% after wolf recovery, slightly higher than our predictions for 78 wolves but within the range of our predictions for 100 wolves. Boyce estimated a smaller late hunt harvest of elk (600 total) than we did (875 antlerless, approximately 925 total). Boyce based his lower harvest estimate on the reduced number of permits issued by the state of Montana in 1989–90 as a result of the fires and winterkills in 1988–89. However, permits were again increased in 1990–91, and we feel the higher harvest rate we used was realistic.

Garton et al. (1990) predicted that northern range elk would decrease less than 10% after wolf recovery. They estimated wolves killed about 1,500 elk each year, 1.3–2.8 times higher than any of our predictions at either 78 or 100 wolves. They included several responses in their model that might have accounted for the lower predicted effect on elk than our models predicted. These compensatory or functional responses included (1) increasing search rate by wolves with decreasing ungulate density; (2) decreasing survival rate of wolves with decreasing ungulate biomass; (3) declining pups per pack, percent pups in the population, pup survival, and wolf density; (4) increasing pack territory size with decreasing prey density; and (5) increasing elk survival and increasing elk pregnancy rate at lower elk densities.

The absence of functional and density-dependent responses in our models is apparent in our postfire elk–wolf models that extend to 1994. Of particular interest is the scenario of 100 wolves with a predation rate of 15 ungulates/wolf/year. Any one or combination of possible wolf responses could be invoked due to rapidly declining prey numbers, including (1) reducing the predation rate, (2) reducing wolf numbers by a number of different mechanisms, (3) changing to alternative prey sources, or (4) reducing or eliminating surplus killing. It would be difficult to predict when, in what capacity, and in what combinations wolves may employ these functional responses when faced with declining prey populations. Another factor not included in our models is that hunter harvests of elk, particularly antlerless elk, would likely decrease as the elk population decreased. Before 1990, our elk–wolf models used observed reproductive and harvest data but did not adjust for presumed density-dependent reproductive or density-dependent mortality responses that might occur when wolf predation was included. Houston (1982) presented evidence that elk calf survival on Yellowstone's northern range was density dependent during the 1970's. However, density dependence was not strongly demonstrated for other variables such as female age of sexual maturity, natality rate, and male survival (Houston 1982:68). Houston also pointed out the difficulty in determining density-dependent effects because of hunter harvests on the northern range elk herd. Without predator–prey functional responses, possible density-dependent responses, and hunter harvest responses, our elk–wolf models may exaggerate wolf predation effects on ungulate populations, particularly at high wolf populations, high wolf predation rates, high hunter harvests, and declining ungulate populations.

Wolf predation on ungulates resulted in reduced hunter harvests in some North American studies (Keith 1974, 1983; Gasaway et al. 1983; Gunson 1986). For the Gallatin elk herd, Vales and Peek (1993) predicted hunter harvests would need to be reduced 9–33% and restricted primarily to bulls if wolves were restored. When the antlerless elk harvest was reduced 27%, our elk–wolf models suggested a 5–30% reduction of the northern range elk population would occur due to wolf predation.

Compared to the mule deer population without wolves and with an unmodified hunter harvest, our POP-II models suggested that from 0 to 44% more mule deer would be on the northern range with wolves present if hunter harvests of antlerless deer were eliminated. The models indicated that hunter harvests play a more significant role in this population than the presence of wolves. Deer from this herd, particularly bucks, are heavily harvested by hunters (Mack and Singer 1993), and recently observed buck/doe ratios are 4 to 8 bucks/100 does. The modeled mule deer population is sensitive to minor increases in hunter harvest, and the sensitivity to any additional predation is not surprising. Mack and Singer (1993) speculated that both total deer numbers and buck/doe ratios are underestimated in the population model. Underestimates of deer numbers and buck/doe ratio variables would exaggerate the effects wolf predation would have on the mule deer population. A conservative antlerless deer harvest is recommended if a wolf population is established, at least until more deer population data can be gathered and evaluated.

Our POP-II models suggested moose harvests would likely need to be reduced after wolf recovery. Some moose populations sustain antlerless moose harvests even when combined with wolf or bear predation (Fuller and Keith 1980; Gasaway et al. 1983; Bangs et al. 1989). When the hunter harvest was reduced by half, our model estimates predicted a 13% smaller to 12% larger moose population compared to the scenario without wolves and an unmodified hunter harvest. When the antlerless moose harvest was eliminated and the antlered-bull harvest remained unchanged, the moose population estimates were nearly equal to the estimates with wolf predation and moose harvests reduced by half. Both harvest scenarios produced stable moose populations. When the antlerless moose harvest was eliminated in the model, the absence of any significant benefits to moose numbers might have been due to the observed low calf recruitment and the relatively high harvest of bull moose each year.

Wolf predation might be compensatory with other sources of moose mortality, or recruitment rates might increase as the moose population declines. The observed low calf ratios might be due to high rates of bear predation, either by grizzlies (*Ursus arctos*; Ballard et al. 1987) or black bears (*Ursus americanus*; Franzmann et al. 1980). Both species are common in moose habitats on the northern range. Wolf and bear predation on moose calves was compensatory in some situations (Filonov 1980; Van Ballenberghe 1987). However, Gasaway et al. (1983) found no compensatory reduction in mortality or compensatory increase in reproduction of moose calves in interior Alaska, and they warned, "Therefore, great caution must be exercised in harvesting ungulates in ecosystems where wolves are harvested lightly or are essentially naturally regulated."

With an established population of 78 to 100 wolves, our wolf–ungulate models proposed reducing antlerless harvests of elk, mule deer, and moose to maintain or increase those ungulate populations inhabiting Yellowstone's northern range. As we discussed earlier, our models do not include possible density-dependent population responses of ungulates or wolf–ungulate functional responses that may operate on the northern range. We do not propose how and to what degree these responses may occur, but if they do, ungulate populations may be larger than we predicted, and hunter opportunities and harvests may not be affected to the degree proposed in our models.

Management Implications

Our predictions suggested that with existing hunter harvests and no wolves, the northern range elk population would increase to about 21,000 animals by 1994. The Montana Department of Fish, Wildlife, and Parks is currently allowing late season hunts to reduce the northern range elk population. After wolf recovery, bull harvest levels can be maintained, but antlerless harvests may need to be reduced if wildlife managers want to stabilize the elk population at levels lower than those observed in the late 1980's. Managers need to establish population objectives for the northern range elk herd to help decide when and how much the antlerless elk harvests should be modified.

Our models suggest antlerless harvests of northern range mule deer and moose will have to be greatly reduced if wolves are introduced into Yellowstone National Park. However, population data are limited for both species, and wolf predation on mule deer and moose might be much lower than our predictions indicate if we underestimated population sizes or male/female ratios. We suggest obtaining better estimates of mule deer and moose population sizes and verifying age/sex ratio data.

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Potential Ungulate Prey for Gray Wolves

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Abstract. Data were gathered for six ungulate species that reside in or near Yellowstone National Park. If gray wolves (*Canis lupus*) are reintroduced into the Yellowstone area, their avoidance of human activities or their management by humans may determine their range. Therefore, the area of wolf occupation cannot be predicted now. We restricted our analysis to Yellowstone National Park and to the adjacent national forest wilderness areas. We included mostly ungulate herds that summer inside or adjacent to the park and that would probably be affected by wolves. Our wolf study area includes Yellowstone National Park and adjacent wilderness areas most likely to be occupied by wolves. We reviewed publications, park records, survey reports, and state fish and game surveys and reports for statistics on ungulate populations. These data provide an overview of ungulate populations and harvests. Each ungulate herd is described in detail. We restricted our analysis to 1980–89, because population surveys were more complete during that period and because population estimates of most ungulate populations had increased by the 1980's. We feel the higher estimates of the 1980's reflect more up-to-date techniques and are most representative of the situation into which wolves would be reintroduced.

Ungulate Populations and Harvest

Elk

Seasonal Ranges and Distribution

Portions of eight elk (*Cervus elaphus*) herds from our wolf study area spend summers in Yellowstone National Park (Figs. 1 and 2). Estimates from the eight elk herds summering within Yellowstone National Park ranged from 25,000 to 31,000 annually (Table 1). This estimate is based on the proportion of radio-collared elk (n = 386) in eight herds that migrate into the park each summer (see details in the Appendix). Roughly

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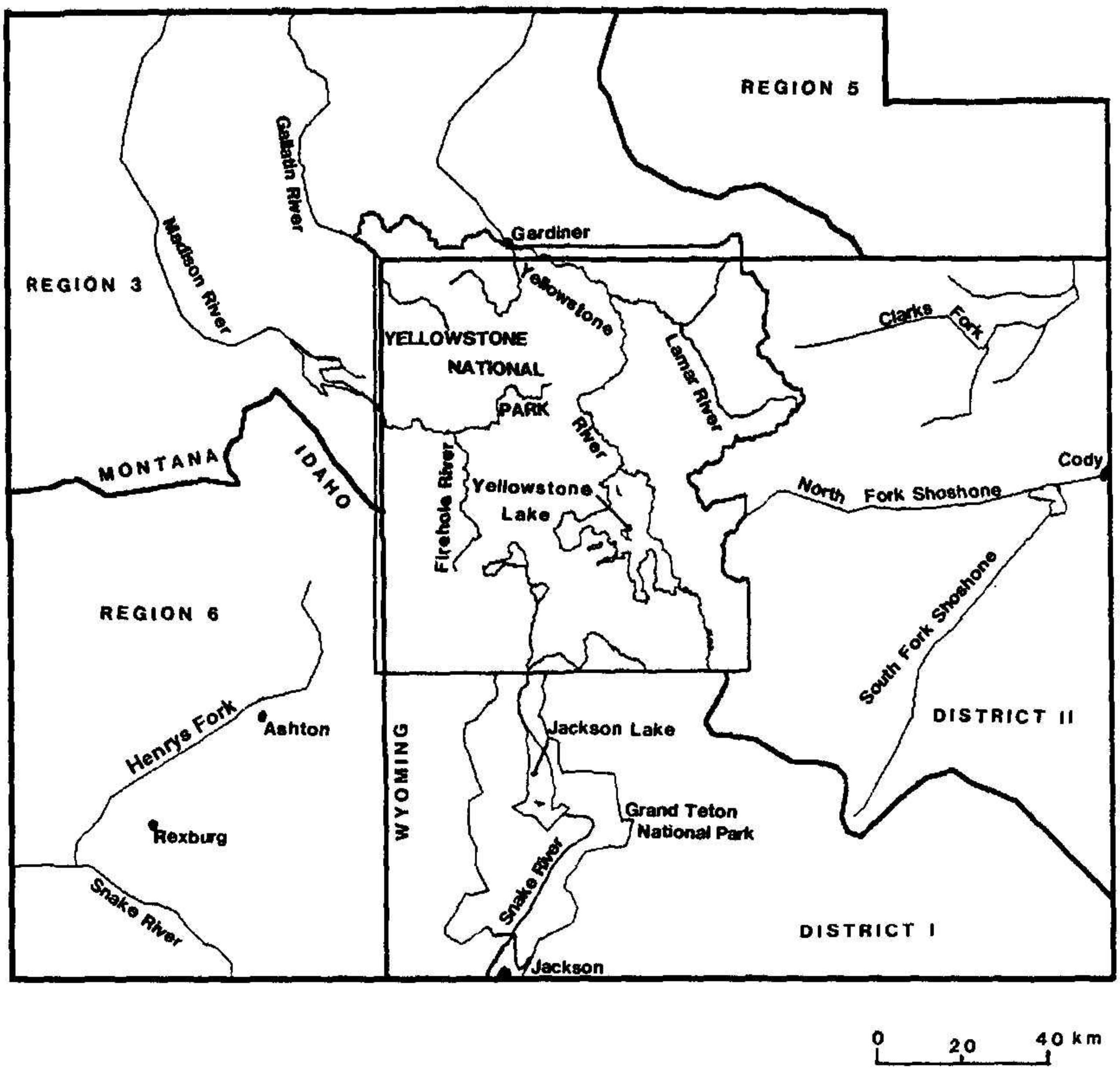

Fig. 1. Yellowstone National Park and wolf study area, including five state game management units in the three states surrounding the park.

58–63% of the elk in the eight herds summer within the boundaries of the park, while 37–42% occupy summer ranges within 40 km of the park boundary.

Elk occupy summer ranges within Yellowstone National Park from 138 to 160 days a year (38 to 44% of the time), when they would be most available to wolves. Fall migrations last from 19 days for the Jackson herd (Smith and Robbins, in preparation) to 27 days for the Sand Creek herd (Brown 1985). Spring migrations last 46 days for the Sand Creek herd (Brown 1985), and some calves are born en route to Yellowstone (Brown 1985; Smith and Robbins, in preparation). Calves born to these migrating cows probably will encounter fewer wolves than calves born in Yellowstone or immediately adjacent wilderness areas.

Elk outside the Yellowstone area may be less accessible to wolves during winter. Three elk herds spend the winters distant from the park and close to human population centers, such as the towns of Ashton or Idaho

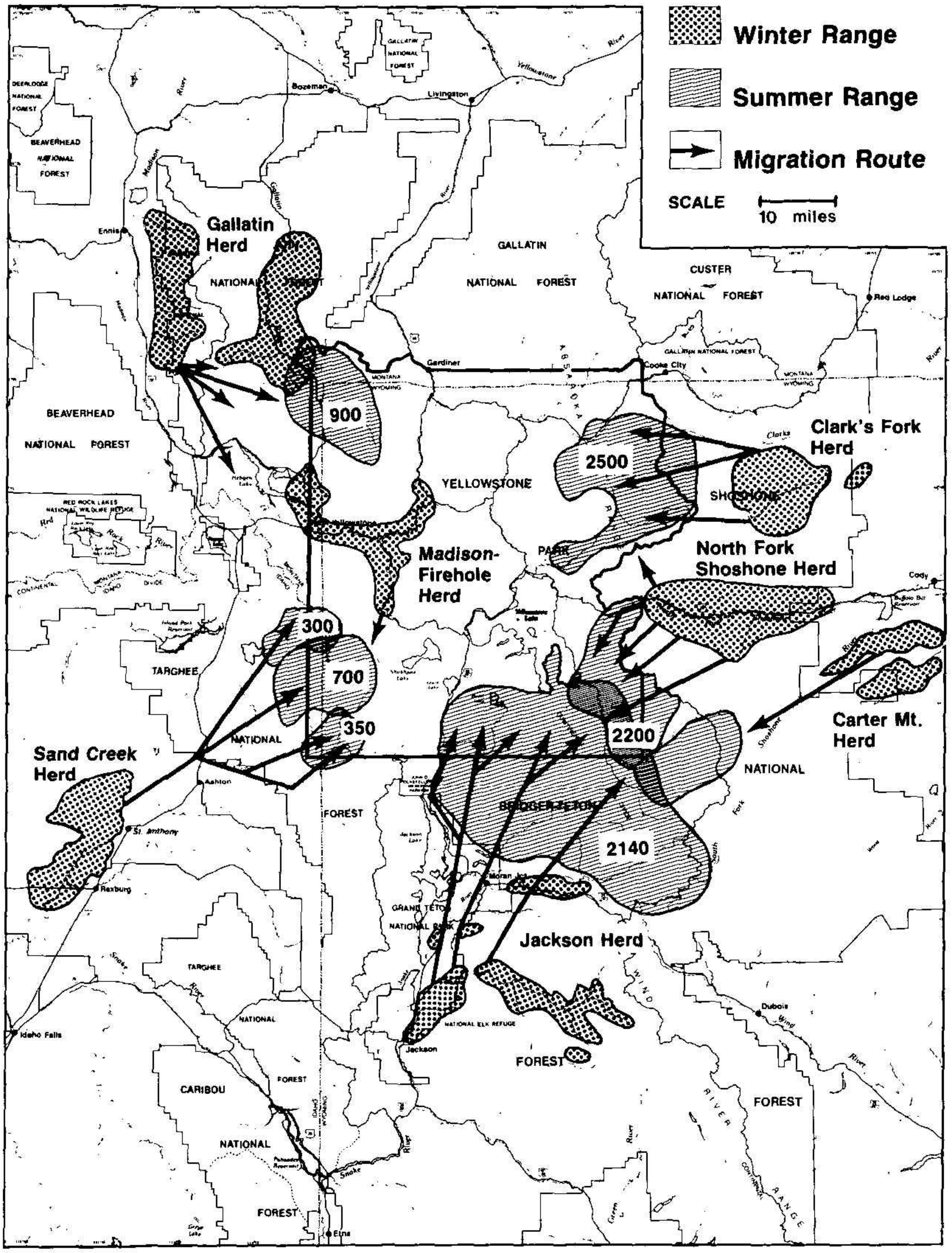

Fig. 2. The approximate winter range and those portions of summering areas in Yellowstone National Park for seven elk herds other than the northern herd. The numbers indicate the approximate numbers of elk from each herd that summer within the park.

Falls, Idaho; Jackson, Wyoming; or towns of the Bighorn Basin, Wyoming. The Carter Mountain, Jackson, and Sand Creek elk herds spend winters 48–64 km from the park boundary. Wolf activity is less likely on winter ranges near human population centers.

Table 1. Estimates of eight major elk (*Cervus elaphus*) herds summering in Yellowstone National Park, 1984–1988 (Cada 1970–75; Craighead et al. 1973; Taylor 1978–86; Rudd 1982; Brown 1985; Davidson et al. 1985, 1986; Yorgason et al. 1986; Boyce 1989; Lockman et al. 1989; Vore 1990; B. Smith, in preparation; D. Vales, unpublished report).

Herd	Herd size	Proportion of radio-collared[d] elk summering in Yellowstone	Sample size of collared elk	Estimated number of elk summering in Yellowstone	Mean number of elk wintering in Yellowstone	Years of radiolocation data	Days spent on summer range	Summer locations
Gallatin	1,850[a,c]	48	72	900	580[a]	1969–86	150	Gallatin Range, Specimen Creek
Sand Creek	4,900[b]	0.21	84	1,056[b]	0	1981–87	138	Bechler Meadows, Madison Plateau, Chick Creek
Jackson	16,000[b]	0.28	85	4,480	0	1978–82	150	Thorofare, Two Ocean Plateau, Big Game Ridge, and Chicken Ridge
Carter Mountain	2,550[b]	tr	0[d]	100+	0	1986–88	—	South Fork Shoshone
North Fork Shoshone	2,600[b]	78	18	2,020	0–500	1979–80	160	Signal Hills, Thorofare

Table 1. *Continued.*

Herd	Herd size	Proportion of radio-collared[d] elk summering in Yellowstone	Sample size of collared elk	Estimated number of elk summering in Yellowstone	Mean number of elk wintering in Yellowstone	Years of radiolocation data	Days spent on summer range	Summer locations
Clarks Fork	3,180[b]	0.83	18	2,600	0	1979–80	160	Upper Lamar, Pelican Valley, Mist Creek
Northern	21,000[b]	0.98	68	20,580	17,457	1985–88	140	All of Yellowstone Park
Madison–Firehole	800[a]	1.00	6	800	800	1965–66	—	Madison drainage, Madison Plateau
Total	—	—	—	32,536	16,837 19,337	—	—	—

[a] Count.
[b] Estimate.
[c] Vales and Peek (1993) concluded this number underestimates the herd size.
[d] No radiotelemetry studies were conducted on the Carter Mountain herd. Such a study is scheduled for 1990 (L. Roop, personal communication).

The Clarks Fork and North Fork Shoshone elk herds winter within 30 km of Yellowstone in remote areas where wolf activity is likely. Portions of four elk herds winter within the boundaries of the park. About 80% of the northern Yellowstone herd, nearly 100% of the Madison–Firehole herd, 31% of the Gallatin herd, and about 15% of the North Fork Shoshone herd winter in the park (Table 2). In the 1980's, 13,480–20,880 elk wintered in the park each year in these 4 herds.

Population Trends

During the past 20 years, population estimates for the 8 elk herds that summer in or near Yellowstone increased dramatically from about 30,000 elk to about 46,700 elk (Houston 1982; Brown 1985; Hurley et al. 1988; Boyce 1989; Lockman et al. 1989; Vales and Peek 1993; Appendix). Population estimates for the Sand Creek and the northern Yellowstone elk herds increased about fourfold during this period. The Jackson and Gallatin herds have remained relatively stable over these 20 years; both declined but then recently increased (Taylor 1986; Boyce 1989; Vales and Peek 1993). Only the Madison–Firehole herd may have declined over this period; recent counts showed 500 to 600 elk (Table 2), but 1970's counts showed 800–1,000 elk (Cole 1983).

Nine elk herds that summer in or near Yellowstone increased dramatically during the 1980's, including the small Targhee herd. Three herds had significantly increasing population rates of change (λ values ranged from 1.12 to 1.21)—the Targhee, North Fork Shoshone, and the Carter Mountain herds. The Jackson, northern Yellowstone, Clarks Fork, and Gallatin herds grew more slowly (1.02 to 1.07); the Sand Creek and Madison–Firehole herds did not grow appreciably during this period. Estimates for the minor Targhee herd increased dramatically, but a change in the estimation technique may have accounted for much of the recent increase (Lockman et al. 1989). At peak population levels in 1988, an estimated 51,327 elk comprised these 9 herds. Improved census techniques and counting effort may have contributed to some of the reported increases.

Harvests

Human harvests include ungulates legally taken for purposes of sport hunting in our wolf study area. Annual elk harvests for the herds residing in the wolf study area averaged 7,650 elk/year (Table 3). The effects of the harvest on population growth is greater when more adult cows are included in the harvest. Percent harvest of the various groups of elk are not entirely comparable because the extent of adult cow harvest varied from 24 to 45% of each herd's total harvest. Elk harvests ranged from 6 to 36% of the minimum population counts, but the elk herds are probably 20 to 40% larger than the reported herd sizes. Visibility corrections and population models suggest that 20 to 40% of the elk are missed during aerial counts (Samuel et al. 1988; Lockman et al. 1989; Mack and Singer 1993; Vales and Peek 1993). Population models or visibility corrections

Table 2. Estimated early winter elk (*Cervus elaphus*) populations for eight elk herds and one group of elk inhabiting the Yellowstone National Park area, 1980–1989.[a] Annual variations in counting conditions and effort may explain some of the variations in counts.

Year	Northern Yellowstone	Clarks Fork	North Fork Shoshone	Carter Mountain	Jackson	Sand Creek	Madison–Firehole	Gallatin	Targhee
1980–81	16,684	2,500	—	—	—	2,310	—	1,719	170
1981–82	18,075	2,600	1,800	2,000	15,533	2,327	—	1,682	170
1982–83	19,184	2,600	1,700	2,225	13,980	2,959	—	1,880	200
1983–84	19,930	2,550	1,700	2,400	13,293	2,287	—	2,068	215
1984–85	21,056	3,000	2,400	2,400	13,504	2,553	—	1,525	205
1985–86	18,982	3,000	2,400	2,050	14,431	2,269	588	2,297	215
1986–87	21,491	2,900	2,000	2,100	15,478	—	—	—	205
1987–88	18,267	3,334	3,131	3,047	16,509	2,815	560	—	440[b]
1988–89	18,919	3,666	2,945	3,101	16,093	2,441	476	—	490[b]
Average	1.02	2,905	2,259	2,202	14,852	2,495	541	1,862	256
λ^f	0.02	1.04	1.21	1.12	1.02	1.008	[c]	1.07	1.13
r^g	0.81[d,e]	0.04	0.08	0.05	0.02	0.008	—	0.03	0.12
Aerial counts as a probable proportion of actual population		—	—	—	0.80[e]	0.60[e]	—	0.80[e]	—
Distance (km) of winter range from park boundary	inclusive	32	8–13	48	48	20	48	inclusive	inclusive

[a] Adapted from Brown 1985; Rudd et al. 1988; Lockman et al. 1989; Mack and Singer 1993; Vales and Peek 1993; and aerial counts by the senior author.
[b] Change in technique for estimated elk likely explained large increases.
[c] Insufficient or questionable data to calculate λ.
[d] Probable percent of actual population calculated from aerial sightability (Lockman et al. 1989; Mack and Singer 1993; Vales and Peek 1993).
[e] Probable percent of actual population calculated from population models (Lockman et al. 1989; Mack and Singer 1993; Vales and Peek 1993).
[f] Finite rate of change.
[g] Rate of increase, slope of regression line of the log population counts.

Table 3. Estimated elk (*Cervus elaphus*) harvest for eight herds[a] inhabiting the Yellowstone National Park area, 1980–1989 (Brown 1985; Rudd et al. 1988; Lockman et al. 1989; Mack and Singer 1993; Vales and Peek 1993; and aerial counts by the senior author).

Year	Northern Yellowstone	Clarks Fork	North Fork Shoshone	Carter Mountain	Jackson	Targhee	Sand Creek	Gallatin
1980–81	247	532	257	—	3,748	70	962	284
1981–82	1,234	590	470	588	4,298	69	1,226	370
1982–83	1,804	859	610	477	3,548	57	1,036	284
1983–84	1,955	709	567	702	2,355	46	893	586
1984–85	1,419	646	666	866	1,561	46	685	346
1985–86	1,371	750	633	794	1,368	34	994	451
1986–87	1,595	600	376	455	1,254	30	1,531	—
1987–88	215	379	206	383	1,657	65	892	—
1988–89	2,773	884	546	424	2,756	74	1,236	—
Average harvest	1,401	661	481	586	2,505	54	1,050	912
Cows in harvest (%)	45	44	32	39	36	—	37	24
Estimated herd harvested (%)[b]	6	—	—	—	16	—	25	36

[a] Harvest figures for the Madison–Firehole herd are estimated at <1% annually and are not presented.
[b] Estimated herd sizes are from modeling efforts (Lockman 1989; Vales and Peek 1993; Mack and Singer 1993), which correct herd sizes upwards.

for the remaining elk herds were not attempted or were not yet complete (Hurley et al. 1989) at the time of this analysis. Therefore, for these four elk herds, we were unable to estimate the percentage of the elk herd that was harvested annually.

For elk herds with a high total rate of harvest and a high proportion of cows harvested—that is, the Sand Creek and Gallatin herds—Vales and Peek (1993) concluded that "...the presence of wolves means that hunter harvest will likely be confined to males most of the time." In situations where cow harvests or total harvests are less, the effects of wolves on hunter harvest are predicted to be much less (Boyce 1989). Following wolf recovery, both bull and cow harvests are predicted to be unchanged in the northern Yellowstone elk herd (Boyce 1993), although reducing the cow harvests by one-third in the northern herd was suggested to prevent elk declines following wolf restoration (Mack and Singer 1993). The proximity of an elk herd to its vegetation–ungulate ceiling (or ecological carrying capacity) will also influence the effect of human harvests or wolf predation (Theberge 1990), but the carrying capacity for the various elk herds is not well understood (Merrill and Boyce 1991).

Mule Deer

Seasonal Ranges and Distribution

Seven mule deer (*Odocoileus hemionus*) herds occur in our wolf study area. These deer populations would likely be preyed on at least in summer by wolves that live in the park and adjacent wilderness areas. Mule deer are known to migrate into Yellowstone each summer (Hurley et al. 1989; Kuck et al. 1989; Lockman et al. 1989; Singer 1991b; Appendix; T. Puchlerz, unpublished data); however, the mule deer winter ranges (Fig. 3) lie farther from the park boundaries and at lower elevations than the elk winter ranges (Table 4). From the park's boundaries, elk winter ranges lie an average of 22 km and deer winter ranges lie an average of 35 km. Several of the deer winter ranges are close to major towns such as Jackson, Cody, and Ashton. Wolves are much less likely to prey on mule deer than elk in winter because most deer ranges are close to human habitation. The Gallatin and northern Yellowstone mule deer winter ranges lie within or close to the park, and wolves are predicted to prey on those herds, especially in winter.

Population Trends

Approximately 15,531 mule deer occur in the 8 herds in our wolf study area. Populations increased significantly during the 1980's for the Targhee, Jackson, North Fork Shoshone, Clarks Fork, and Junipers–Sand Creek herds (λ = 1.11 to 1.37; Table 4). The South Fork herd grew more slowly (λ = 1.02), and the northern Yellowstone herd was stable. The total population estimates for the 8 herds increased by nearly 2,300 during

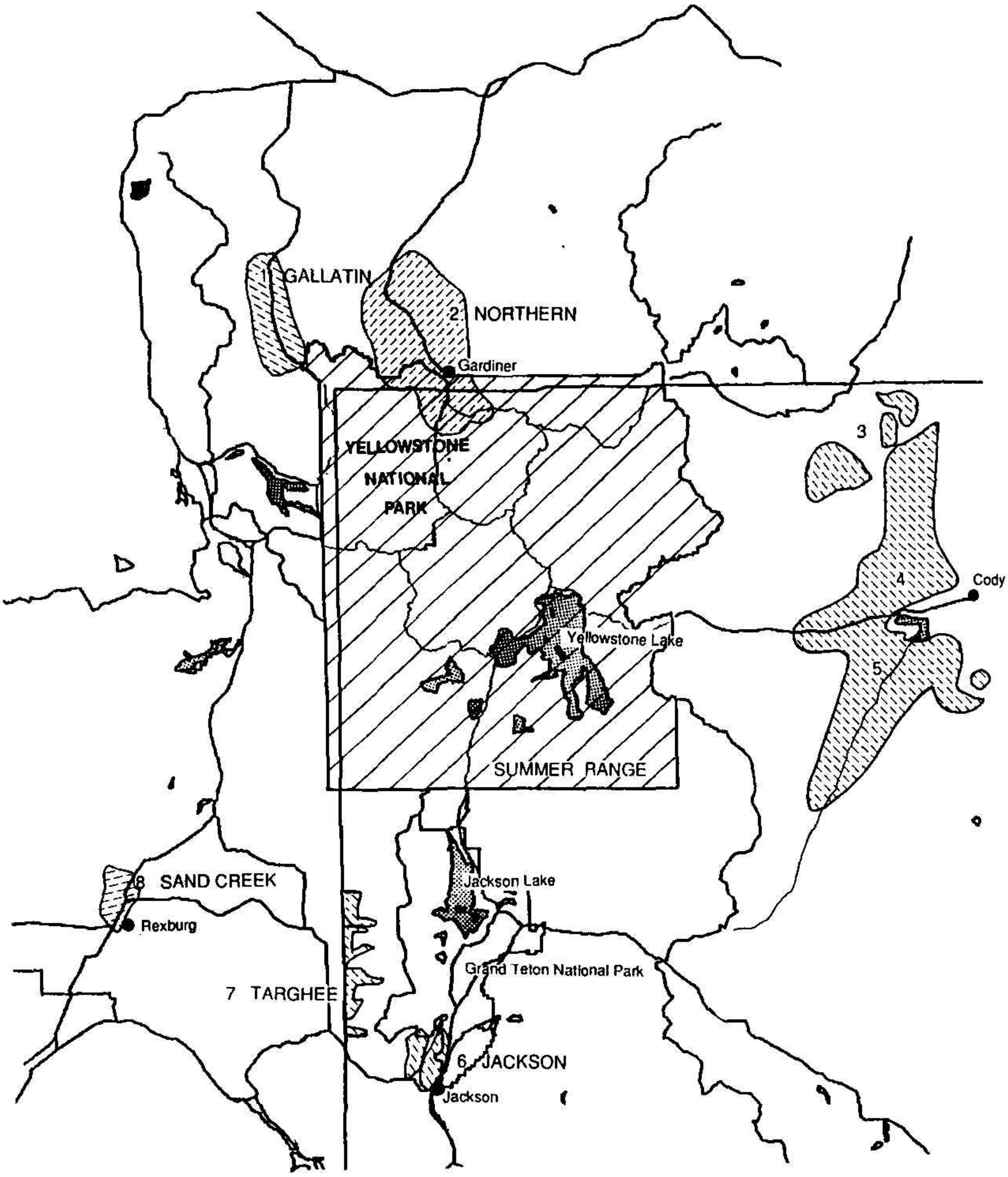

Fig. 3. Winter ranges for eight mule deer herds that summer in the Yellowstone area: *1* = Northern Yellowstone; 2 = Gallatin; *3* = Clarks Fork; *4* = North Fork Shoshone; *5* = South Fork Shoshone; *6* = Jackson; *7* = Targhee; *8* = Sand Creek.

the 1980's. Some of the most recent increases in estimates, like the Jackson and Clarks Fork herds, are largely the result of refined population harvest models (Hurley et al. 1989; Lockman et al. 1989). Recent population increases in mule deer in the Yellowstone National Park region are probably due to the milder winters of the 1980's (Singer 1991b). Ackerman (1989) and Mack and Singer (1991) concluded that about 35–40% of mule deer were missed on helicopter counts in the study area and that visibility of deer varied widely between counts. Therefore, mule deer numbers in Table 4 may be greatly underestimated.

Table 4. Annual trends in mule deer (*Odocoileus hemionus*) population size, 1980–1989, for seven deer herds that inhabit the Yellowstone National Park area (Foss 1987; Hurley et al. 1989; Kuck et al. 1989; Lockman et al. 1989; Mack and Singer 1993).

Year	Northern Yellowstone	Clarks Fork	North Fork Shoshone	South Fork Shoshone	Jackson	Targhee	Junipers–Sand Creek[a]
1980–81	2,944	3,000	950	4,125	—	550	—
1981–82	3,013	1,900	1,200	3,600	200	500	—
1982–83	3,274	5,000	2,675	6,150	230	550	1,443
1983–84	2,853	3,000	1,200	3,600	270	485	1,337
1984–85	2,835	4,000	1,400	4,800	275	510	1,983
1985–86	2,942	3,200	1,500	3,800	300	675	1,547
1986–87	3,057	3,900	1,600	4,300	325	770	—
1987–88	3,284	4,000	2,500	4,312	340	880	—
1988–89	2,617	6,699	2,500	4,800	700	1,000	1,684
Average	2,979	3,855	1,725	4,387	330	657	1,598
λ	0.99	1.21	1.22	1.02	1.37	1.22	1.11
r	—	0.08	0.09	0.01	0.13	0.08	0.05
Distance (km) of winter range from park boundary	0	32	48	27	48	24	16–48

[a] Partial counts only.

Harvests

Hunters kill an average of 3,406 mule deer each year from the 8 herds. Of these deer, an average of 22% of the total harvest (range 15–32%) are does, 77% (66–85%) are bucks, and 1% are fawns (Table 5). Mule deer harvests varied greatly between 1980 and 1989 in all the herds. A downward trend in harvests occurred in the Targhee and Jackson herds. We found no consistent long-term trends in the other herds.

Moose

Seasonal Ranges and Distribution

Moose live on 14 winter ranges in the Yellowstone area (Fig. 4, Table 6). Portions of each of the six wintering herds are known to summer within the park (Ritchie 1978; Trent et al. 1984; Alt and Foss 1987; Hurley et al. 1989; Lockman et al. 1989; Appendix; D. Tyers, Gallatin National Forest, Gardiner, Montana, unpublished data). The other eight moose herds may migrate near or into the park each summer, where they would potentially be killed by wolves. Six of the moose winter ranges are

Table 5. Annual trends in mule deer (*Odocoileus hemionus*) harvests, 1980–1989, for seven deer herds that inhabit the Yellowstone National Park area (Foss 1987; Hurley et al. 1989; Kuck et al. 1989; Lockman et al. 1989; Mack and Singer 1993).

Year	Northern Yellowstone	Clarks Fork	North Fork Shoshone	South Fork Shoshone	Jackson	Targhee	Junipers–Sand Creek	Gallatin[a]
1980–81	346	574	202	794	76	85	1,239	90
1981–82	593	637	399	879	142	107	1,114	101
1982–83	618	564	289	781	3	125	1,293	88
1983–84	786	671	202	816	11	105	762	93
1984–85	622	550	232	882	15	56	238	71
1985–86	512	747	217	960	12	25	1,207	114
1986–87	536	498	255	778	7	33	728	61
1987–88	413	460	217	694	7	61	632	—
1988–89	561	383	166	548	5	63	2,075	—
Does in harvest (%)	—	19	15	21	32	17	30	—
Average harvest	554	564	242	792	31	73	1,020	68

[a] Includes only hunting district 310, that portion of the Gallatin Valley closest to the Yellowstone National Park boundary.

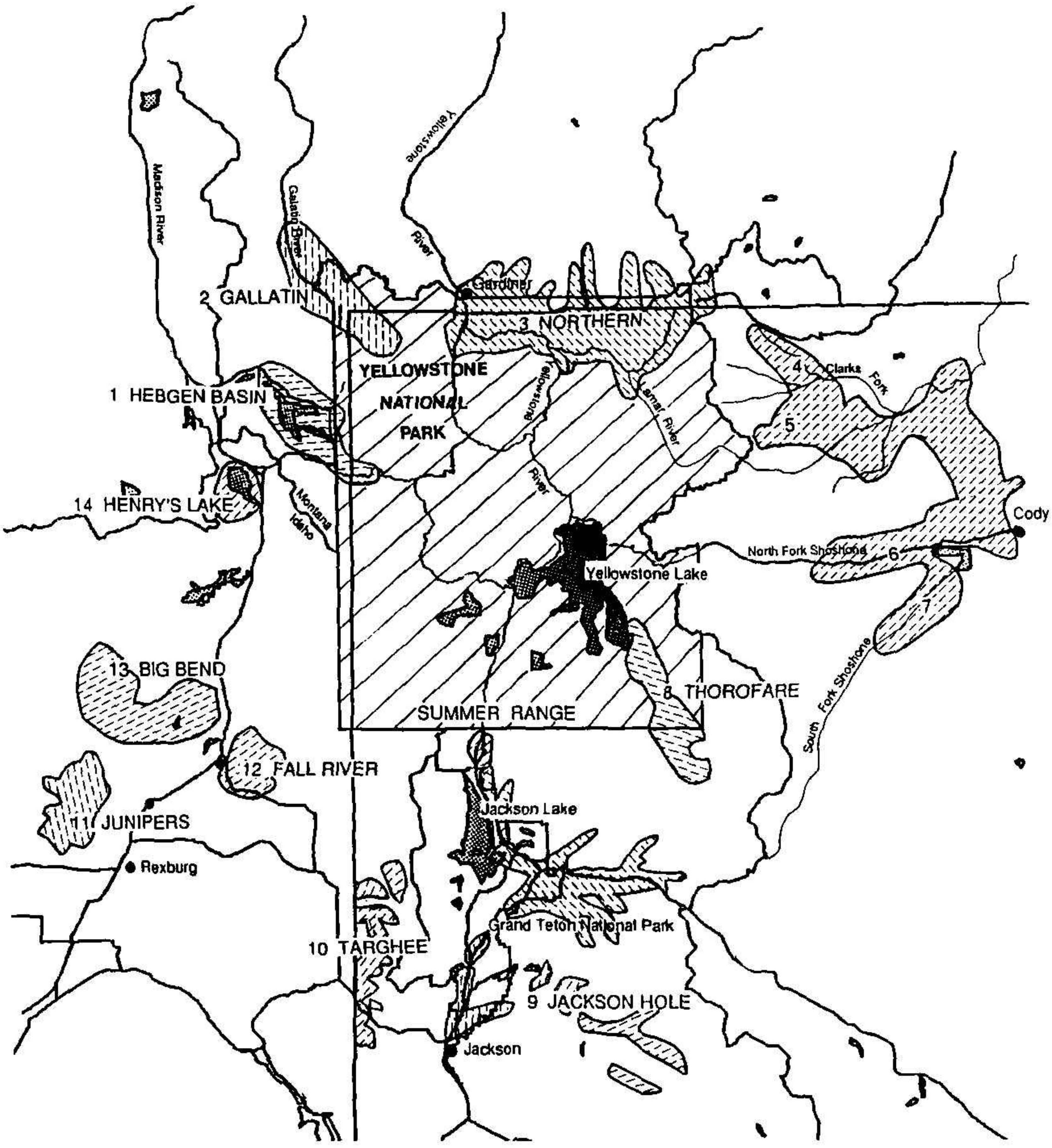

Fig. 4. Winter ranges for 14 moose herds in the Yellowstone area and moose summer range in Yellowstone National Park.

in or adjoin Yellowstone. Elk outnumber moose by a factor of 8 elk/1 moose in the Yellowstone study area, and moose are rated only 0.7 times as vulnerable to wolves as are elk (Singer 1991a). However, moose are ubiquitous in the study area, and on some of the higher elevations and deeper snow ranges (like Thorofare, upper Snake River, Targhee, upper Madison, and Buffalo River), elk outnumber moose by only 3–5:1. Moose will likely be significant prey for wolves on these deeper snow winter ranges. Therefore, we predict that moose will be a small component of the summer and winter diets of wolves, but moose may be an important factor to wolf occupation of the highest-elevation winter ranges.

Population Trends

Population estimates are available for only 6 of the 14 moose herds (Table 6). These 6 herds constitute about 4,000 moose. We conservatively

Table 6. Moose (*Alces alces*) population trends, 1980–1989, in and adjacent to Yellowstone National Park[a] (Ritchie 1978; Chu et al. 1988; Hurley et al. 1989; Lockman et al. 1989; Mack and Singer 1993).

Year	Northern	Jackson	Targhee	Fall River	Junipers–Big Bend	Henrys Lake
1980–81	396	2,200	130	151	172	65
1981–82	430	2,000	120	159	136	66
1982–83	405	1,800	125	138	353	61
1983–84	394	1,860	126	—	—	—
1984–85	392	1,830	126	—	—	—
1985–86	415	1,950	123	—	—	—
1986–87	400	2,030	145	—	—	—
1987–88	410	2,150	210	—	—	—
1988–89	446	2,300	300	217	372	224
Average	409	2,013	156	166	258	104

[a] No population estimates or counts were available for the Hebgen Basin, Gallatin, Sunlight Basin, North Fork Shoshone, South Fork Shoshone, or Thorofare herd units.

estimate that the remaining 8 herds total 1,500, and moose numbers in our wolf study area likely total 5,500. Most moose populations are apparently stable or increasing. Moose in the Yellowstone area use coniferous forests extensively, and aerial counts are probably underestimated. Through population models, Mack and Singer (1993) concluded that the northern Yellowstone moose herd was more than 2 times larger than previous estimates and more than 5 times larger than the highest aerial counts.

Harvests

Moose harvests in the 1980's averaged 545 moose annually in the study area (Table 7). Harvests in nine herds were bulls only, and harvests in the remaining five herd units were 75–86% bulls. Total legal harvests averaged less than 10% of the estimated moose populations. Since harvests are restricted predominately to bulls, we suspect that human harvests in most herds, with the possible exception of the northern Yellowstone, Gallatin, Jackson, and Targhee herds, are not significantly affecting moose populations. The effects of harvest on the four herds with cow harvests cannot be accurately determined until better population estimates exist (Mack and Singer 1993).

Bighorn Sheep

Seasonal Ranges and Distribution

Thirteen bighorn sheep (*Ovis canadensis*) herds winter in our wolf study area (Fig. 5). Many sheep migrate to mountain tops and high ridge lines in or near the park boundaries each summer (Houston 1982; Keating 1982; Hurley 1985; Irby et al. 1986; Hurley et al. 1989; Lockman et al.

Table 7. Moose (*Alces alces*) harvest trends,[a] 1980–1989, in and adjacent to Yellowstone National Park.

Year	Hebgen basin	Gallatin	Northern Yellowstone	Sunlight basin	North Fork Shoshone	South Fork Shoshone	Thorofare	Jackson	Targhee	Ashton, Idaho, moose[a] herds
1980–81	38	23	22	5	5	3	26	476	29	5
1981–82	43	29	28	5	4	5	25	450	22	7
1982–83	44	40	35	5	2	1	25	373	31	7
1983–84	42	34	32	5	3	4	23	317	29	42
1984–85	38	39	29	5	2	1	20	328	32	46
1985–86	42	34	29	5	4	5	20	214	40	57
1986–87	37	36	33	5	2	3	20	222	34	68
1987–88	—	—	32	5	5	4	24	229	43	68
1988–89	—	—	27	5	4	4	21	289	50	—
Average	40	33	29	5	3	3	22	322	34	35
Distance (km) of winter range from Yellowstone Park	adjoins	adjoins	adjoins	3	48	48	adjoins	adjoins	30	8–56[b]
Bull proportion of harvest	0.75	0.75	0.75	1.00	1.00	1.00	1.00	0.76	0.86	1.00

[a] Harvest statistics were not available separately for the Fall River, Junipers–Big Bend, Island Park, and Henrys Lake moose herd units in Idaho. The combined harvests for these four herds are presented.

[b] The Fall River moose winter range lies 8 km from Yellowstone National Park; Island Park winter range, 19 km; Big Bend winter range, 32 km; and the Junipers winter range, 56 km (Ritchie 1978).

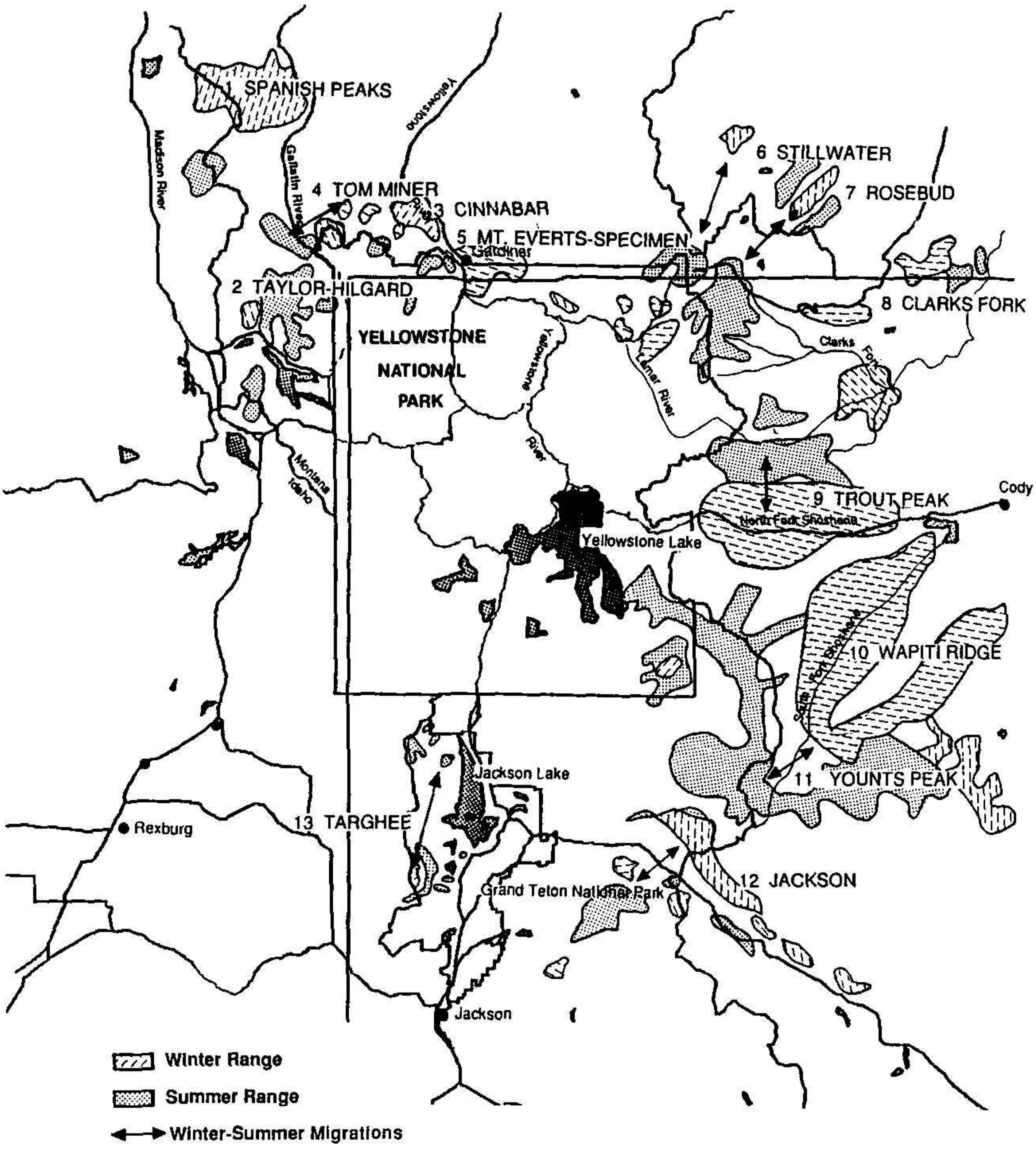

Fig. 5. Winter and summer ranges for 13 bighorn herds that occupy the Yellowstone National Park area.

1989; Appendix). Radiotelemetry studies of movements have been conducted on 5 of the 13 herd units.

Population Trends

Approximately 4,000 bighorn sheep reside in the Yellowstone area. Two larger populations east of the park in the study area—Trout Peak and Wapiti Ridge—increased during the 1980's, but most of the remaining herd units were stable or declined (Table 8). Bighorns are predicted to be only 0.3 times as vulnerable to wolves as elk and 0.15–0.23 times as vulnerable as mule deer (Singer 1991a). Bighorns will probably be a minor component of the wolf diet in places where elk or deer live.

Table 8. Bighorn (*Ovis canadensis*) population statistics in areas adjacent to Yellowstone National Park (NP) during the 1980's (Houston 1982; Keating 1982, 1985; Meagher 1982; Hurley 1985; Irby et al. 1986; Hurley et al. 1989; Lockman et al. 1989; M. Meagher, personal communication).

Herd	Estimated population size	Mean harvest[a] 1980's	Percent population change 1980's	Extent summer migration into Yellowstone NP	Distant (km) of winter range from Yellowstone NP
North of Yellowstone[b]					
Spanish Peaks (301)[c]	—	4	—	none	32
Taylor–Hilgard (302)	—	3	—	none	16
Cinnabar Mountain (300)	80–130	8	stable	most herd	13
Tom Miner (300)	80–100	2	declined	most herd	5–8
Mount Evert–Specimen Ridge (303)	136[d]	3	declined[e]	most herd	includes Yellowstone
Stillwater (500)	40–50	2	declined	none	48
Rosebud (501)	70–100		stable	possible	32
East of Yellowstone					
Clarks Fork	500	13	stable	a few	5–8
Trout Peak	500	19	+14	a few	13
Wapiti Ridge	1,000	28	+14	includes Yellowstone	includes Yellowstone
Younts Peak	900	31	stable	a few	13–24
South of Yellowstone					
Jackson	500	15	stable or slight decline	none	56
Targhee	100	2	stable	a few	24
Total	3,906–4,016+	130	—	—	—

[a] Harvest consists of 3/4–curl–or–larger rams.
[b] West of Yellowstone there were no nearby populations.
[c] Montana hunting district numbers in parentheses.
[d] Actual count of sheep from Mount Everts along the Yellowstone River to the Specimen Ridge area.
[e] Population reduced by a pinkeye epidemic in 1982 (Meagher 1982).

Harvests

In the 1980's, an average of 130 rams was harvested annually from the 13 bighorn herds inhabiting the Yellowstone area (Table 8). All harvests were restricted to rams with three-fourths or larger curl. These harvests of only mature males likely have little influence on bighorn populations.

Mountain Goats

There are 800–830 mountain goats (*Oreamnos americanus*) in our wolf study area, but less than 100 occur in areas wolves might occupy (Fig. 6). Mountain goats are not native to Yellowstone. The nearest native population occurs 97 km to the west of the park near Monida Pass. Mountain goats occupying the park area originated from three releases: near Spanish Peaks, Montana, in 1947 and 1950 (Peck 1972); in the Absaroka Mountains of Montana between 1942 and 1948 (Guenzel 1980); and in the Palisades and Black Canyon area of Idaho in 1969–71 (Hayden 1984; also see review in Laundre 1990).

Current estimates for goat populations are 300 in the Spanish Peaks area, a few in the Gallatin Mountains, 100 in the Absaroka Mountains area (including 8 to 10 near Wolverine Peak), 150 to 180 in the Beartooth Mountains in Wyoming, and 250 in the Palisades Mountains in Idaho (Table 9; Swenson 1985a; Laundre 1990). Mountain goats could expand into suitable habitats in Yellowstone at some time in the future (Laundre 1990). Laundre (1990) estimated that the park could support 100 to 500 mountain goats following their invasion of the area.

Pronghorns

Seasonal Ranges and Distribution

Only one pronghorn (*Antilocapra americana*) herd—the northern Yellowstone herd—occupies the Yellowstone area year-round (Fig. 7). Pronghorns from the northern herd winter near the town of Gardiner, Montana, along the boundaries of the park and on adjoining private lands (Houston 1982; Singer 1991b). Some pronghorns remain to summer on the winter range. Others migrate 10–30 km to summer ranges on the higher sagebrush grasslands of Gardners Hole, Antelope Creek, Specimen Ridge, and the Lamar Valley (Fig. 7; Houston 1982). In summer, pronghorns from the northern range will be available to wolves, as will a small number of Idaho animals that summer in the Duck Creek and Cougar Creek area of Yellowstone. Northern range pronghorns will be largely unavailable to wolves in winter due to their proximity to Gardiner, Montana, a human population center most wolves will likely avoid.

Pronghorns summer in Henrys Lake, Idaho; Jackson, Wyoming; and Cody, Wyoming (Fig. 7). But pronghorns migrate each winter to lower elevations out of the study area (U.S. Department of Agriculture and U.S. Department of the Interior 1987; H. A. Harper, Grand Teton National Park, unpublished report).

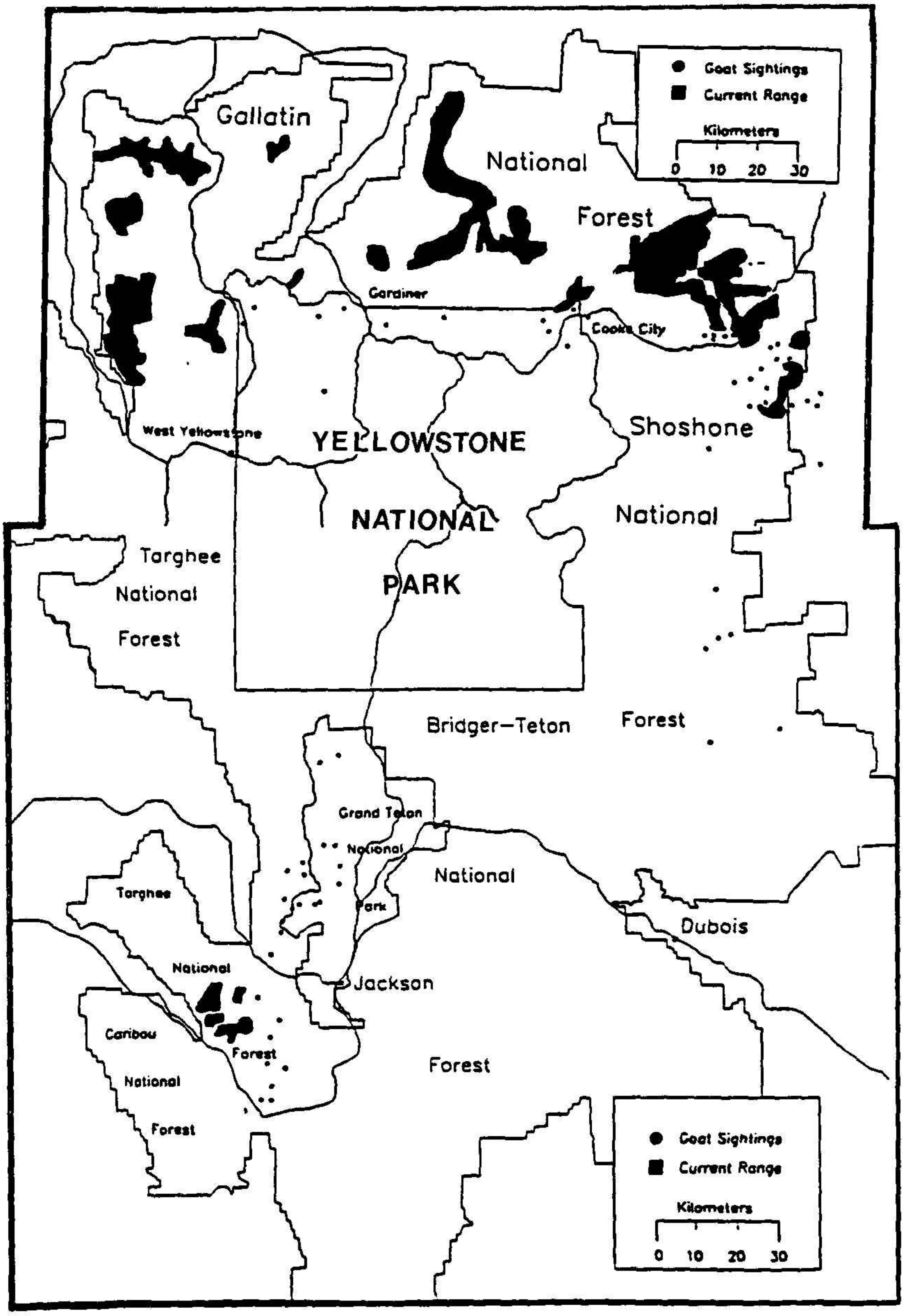

Fig. 6. Distribution and recent sightings of mountain goats on lands in and adjacent to Yellowstone National Park, 1987 (Laundre 1990).

Table 9. Non-native mountain goat (*Oreamnos americanus*) populations in areas adjacent to Yellowstone National Park (adapted from Laundre 1990).

Herd location	Estimated population	Distance (km) from Yellowstone National Park
North of Yellowstone		
Absaroka	100	0–24
Gallatin Range	(a few)	0–45
East of Yellowstone		
Beartooths	150–180	19
South of Yellowstone		
Palisades	250	80
West of Yellowstone		
Spanish Peaks–Hebgen Lake	300	10–24
Total	800–830	—

Population Trends and Harvests

Between 1930 and 1947, the number of pronghorns on the northern winter range varied between 500 and 800 (Houston 1982). Declining big sagebrush on the pronghorn winter range motivated park staff to artificially reduce pronghorn numbers during 1947–67 (Houston 1982). As a result of the reductions, counts declined to less than 200 during 1969–80 (Houston 1982; Scott 1987). Fawn ratios remained low at 38 ± 15 ($\bar{x}$ SD) fawns/100 does from 1967 to 1979 (Houston 1982). However, during the 1980's, pronghorns increased to nearly 500 animals. Fawn ratios after 1984 were higher than those for 1967–79. A total of 80 fawns/100 does was observed in November 1986, the highest recorded ratio since 1963 (Houston 1982). Pronghorn density on the 48-km^2 area of winter range increased from 3/km^2 in 1979 to 10/km^2 in 1988. Pronghorns declined about 27% following the drought of 1988 and the severe winter of 1988–89 (Singer et al. 1989).

Bison

Seasonal Ranges and Distribution

Four bison (*Bison bison*) herds occupy the study area. The Mary Mountain herd (1,500–1,800 animals), the Pelican Valley herd (300–500), and the northern range herd (300–700) inhabit the park. The Jackson Hole herd (80–150 animals) inhabits Grand Teton National Park and adjacent areas (Fig. 7; Meagher 1973, 1989; U.S. Department of Agriculture and U.S. Department of the Interior 1987). A handful of bison use the Bechler Meadows area of southwestern Yellowstone National Park.

All four bison herds migrate shorter distances (10–25 km) between seasonal ranges than the other ungulates. However, the northern herd ex-

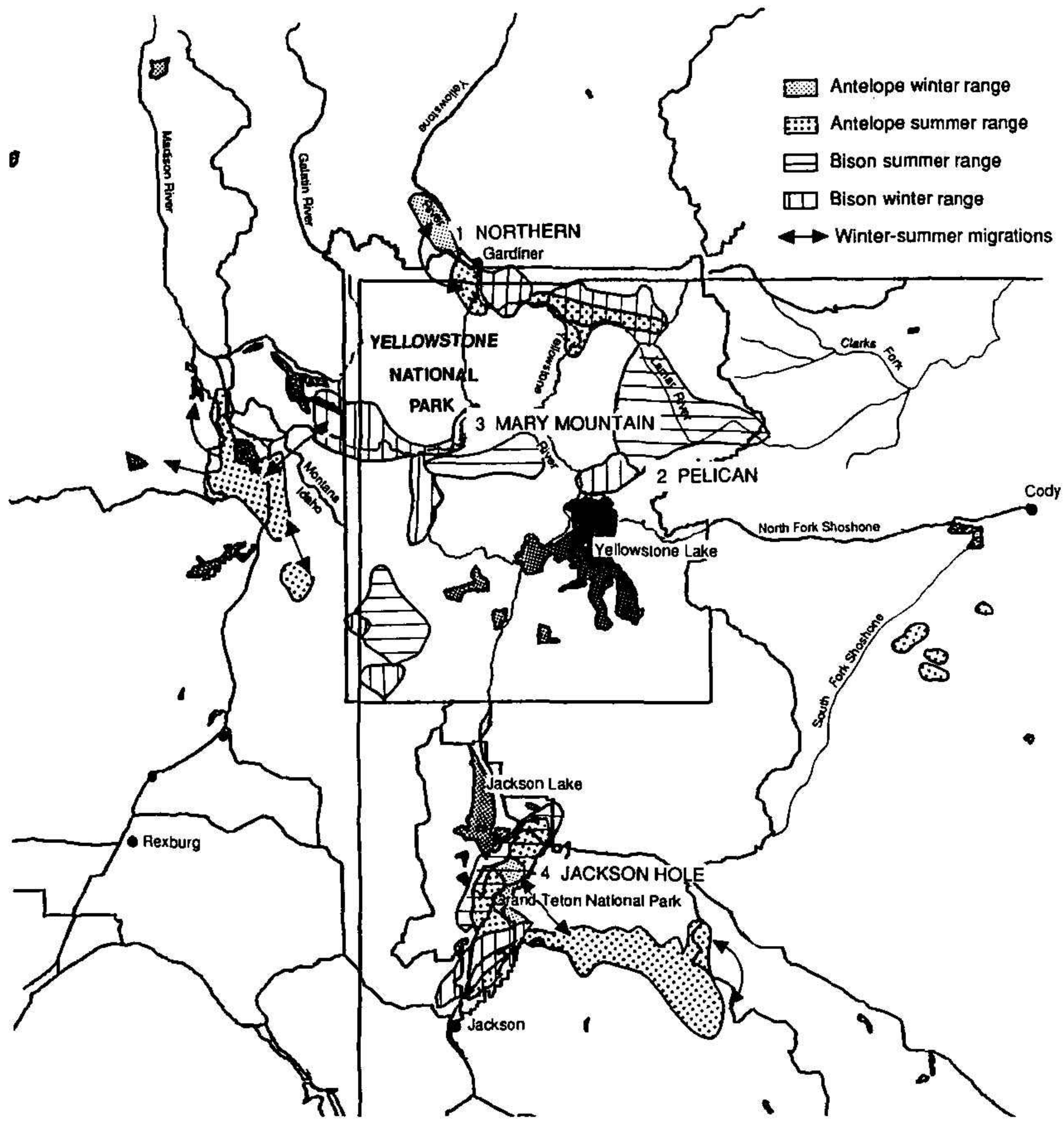

Fig. 7. Four winter–summer ranges used by bison in the Yellowstone National Park area: northern, Pelican, Mary Mountain, and Jackson. The northern antelope herd winters and summers in the Yellowstone National Park area; the other three antelope groups spend only summers in the park area.

tended its range and its migration during the 1980's (Meagher 1989) and has the potential for long annual migrations.

Population Trends and Harvests

Bison populations increased dramatically in the 1980's. The Mary Mountain herd increased about 33%—from 1,200 in 1980 to 1,600 in 1989 (Meagher 1989). The northern range herd increased 260% from an estimated 250 bison in 1980 to about 900 bison in December 1988. Immigration from the other park herds partially explained this increase (Meagher 1989). A hunt in Montana during 1988–89 reduced the northern range bison herd to about 300 by May 1989 (Meagher 1989), but recovery to 456 bison occurred by January 1991. The Jackson Hole bison herd grew rapidly during the 1980's, but due to conflicts with agricultural activities and with elk on feed grounds, a U.S. Fish and Wildlife Service plan calls for reducing the herd to less than 150 animals.

Bison are predicted to be 0.7 times as vulnerable to wolves as elk; however, bison vulnerability was predicted to be more variable than other ungulates (Singer 1991a). Where bison numbers are well below the ungulate vegetation ceiling and where snows are shallow (like on the Jackson Hole and northern Yellowstone winter ranges), bison are predicted to be infrequently killed by wolves due to the defensive behaviors of bison. However, chest heights and foot loading (weight/hoof unit area) suggest that bison will be vulnerable to wolves in deep snows (Telfer and Kelsall 1984), and bison are the primary prey for wolves in several parts of northern Canada (Oosenbrug and Carbyn 1983). Singer (1991a) predicted that 74 bison would be killed by wolves for every 100 elk on the higher, interior Yellowstone National Park winter ranges (e.g., Mary Mountain, Pelican, Bechler Meadows). Any wolves frequenting Pelican Valley in winter must survive almost exclusively on bison as prey.

Availability of Ungulates to Wolves

During winter, 7 ungulate species (totaling 80,800 animals) inhabit our wolf study area (Table 10). About 30,100 (37%) of these ungulates occur within the boundaries of the park each winter and would be available to wolves. About 43,650 (54%) ungulates inhabit the combined Yellowstone area and immediately adjacent national forest wilderness areas where they would be largely available to wolves in winter. The remaining 46% of the ungulates inhabit areas closer to human habitation, where we predict less wolf activity.

Elk dominate the ungulate fauna more within the park than in adjacent areas. Elk outnumber all other ungulates combined in Yellowstone by a ratio of 100 elk/40 other ungulates. The ratio in the combined Yellowstone National Park–national forest wilderness areas is 100 elk/56 other ungulates, while the ratio is 100 elk/76 other ungulates when considering the entire wolf study area (Table 10). Relatively more moose, mule deer, and bighorns occur outside the park. Mule deer availability increased 50% when wilderness areas were included, and deer availability was 5 times higher in the entire study area than within the boundaries of Yellowstone National Park (Table 10).

Winter wolf diets are predicted to be 70% elk in Yellowstone, 68% elk in the combined Yellowstone National Park–national forest wilderness areas, and 56% elk in the entire study area (Table 10). The predicted mule deer portion of the wolf diet increased in direct proportion to the distance considered outside the park. Mule deer were predicted to make up 19% of winter wolf diets within the park and the contiguous northern range, 13% in Yellowstone and national forest wilderness areas, and 36% in the entire study area.

Table 10. Numbers of ungulates and likely composition of wolf (*Canis lupus*) diet in three winter scenarios of wolf occupation of lands in the Yellowstone National Park area: park only—high probability of total occupation by wolves; park and contiguous national forest wilderness—moderate probability of total occupation; and park and all nearby adjoining lands—low probability of total occupation.

	Park only			Park and wilderness			Park and all nearby lands		
Species[a]	Number of ungulates	Percent availability	Predicted wolf diet (%)[b]	Number of ungulates	Percent availability	Predicted wolf diet (%)[b]	Number of ungulates	Percent availability	Predicted wolf diet (%)[b]
Elk	21,500	71	70	28,700	64	68	46,000	57	56
Mule deer	4,000	14	19	6,000	13	20	21,000	26	36
Bison	2,800	9	6	2,800	6	5	2,900	3	2
Bighorn	300	1	0.1	3,300	10	2	4,000	5	1
Moose	700	2	1	2,000	4	3	5,500	7	4
Pronghorn	600	2	3	600	1	2	600	0.5	0.5
Mountain goat	200	1	0	250	0.6	0	800	1	0
Total	30,100	100	99.1	43,650	98.6	100	80,800	99.5	99.5

[a] Elk = *Cervus elaphus*; mule deer = *Odocoileus hemionus*; bison = *Bison bison*; bighorn = *Ovis canadensis*; moose = *Alces alces*; pronghorn = *Antilocapra americana*; mountain goat = *Oreamnos americanus*.

[b] Mule deer were predicted to be selected by wolves 1.4 times as often as elk, bison 0.7, moose 0.7, bighorn 0.2, pronghorn 1.4, and mountain goat 0.2 (Cowan 1947; Carbyn 1982; Carbyn et al. 1987).

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Appendix. Distributions, Population Trends, and Harvests for Elk, Mule Deer, Moose, and Bighorn Sheep in the Yellowstone National Park Area.

Information Needs and Data Gaps

We rated essential population survey or information needs for each ungulate as follows: (1) annual aerial counts, (2) annual sex and age classification, (3) accurate sex and age information from the harvest, (4) visibility correction for animals not seen during the counts, (5) a current population harvest model, and (6) research studies or models of populations and their habitats. Elk received the highest information rating, 58%, followed by mule deer, 42%; bison, 29%; bighorn sheep, 28%; and moose, 18%. Mountain goats and white-tailed deer were not rated because they are unimportant to wolf recovery. Population data were adequate for modeling the predicted effects of wolf predation only for the Yellowstone elk populations (Boyce 1993; Vales and Peek 1993). A provisional model was constructed for the northern Yellowstone mule deer population (Mack and Singer 1992), but the moose population models were considered exploratory only (Boyce 1993; Mack and Singer 1993). Obtaining more extensive population data is recommended for mule deer and moose to better evaluate the effects of wolf recovery.

Elk

Seasonal Ranges and Distribution

East of Yellowstone

During spring, elk from the Clarks Fork, North Fork Shoshone, and Carter Mountain herds migrate west from winter ranges into Yellowstone (Fig. 1). Radiotelemetry studies (Yorgason et al. 1981; Rudd 1982; Rudd et al. 1983) show that about 80% of the Clarks Fork and North Fork Shoshone herds migrate into the park.

A small portion of the Carter Mountain herd apparently summers in the Thorofare and upper Yellowstone River area of Yellowstone National Park. Small groups have been tracked through fresh snow twice (from aircraft) from the Thorofare River to South Fork Shoshone winter ranges (in the Carter Mountain herd) after crossing the Absaroka Divide in the Thorofare Buttes area (F. J. Singer, Yellowstone National Park, unpublished data; G. Roby, Wyoming Game and Fish Department, personal communication).

South of Yellowstone

Elk occur in the Jackson and Targhee herds. The Jackson herd primarily winters in the Gros Ventre River Valley and on the National Elk Refuge. These winter ranges are 48 to 64 km south of Yellowstone and are distant from areas wolves would likely inhabit. Based on a sample of 97 radio-collared elk, approximately 40% of the Jackson elk herd summers in Yellowstone (28%) and the adjacent Teton Wilderness (12%).

For 1978–82, spring migration lasted an average of 21 days for elk migrating to Yellowstone. Many cows calved en route to summer ranges, and the mean stay on summer ranges in the park was 160 days (Smith and Robbins, in preparation). October snows precipitated earlier fall migrations but did not necessarily result in earlier arrivals at the National Elk Refuge. Mean fall migration lasted 19 days.

The Targhee herd summers south of Yellowstone in Wyoming. In winter, these elk migrate west onto ranges in Idaho or to southern exposures of several drainages within about 10 km of the Idaho–Wyoming state line (Lockman et al. 1989).

Southwest of Yellowstone

The Sand Creek elk herd occupies the area of Idaho adjacent to Yellowstone. Brown (1985) and Vales (1989) estimated that 76% of the Sand Creek herd occupied areas east of U.S. Highway 20 (including Yellowstone National Park) during summer. Twenty-four percent of the Sand Creek herd migrated into the park each summer (Brown 1985). Spring migrations to summer ranges lasted about 46 days (Brown 1985). Most calving occurred en route to Yellowstone summer ranges except when spring snows were shallow. Therefore, few newborn elk calves from this herd would be available for wolves during typical springs in Yellowstone. Brown (1985) also estimated that Yellowstone elk remained on summer ranges an average of 138 days, and that elk in Harriman State Park stayed on summer ranges 168 days. Naderman (Idaho Fish and Game Department, personal communication) estimated they stay 150 days on summer ranges. Fall migrations to the Sand Creek winter range lasted about 27 days (Brown 1985). The Sand Creek elk herd migrates through sagebrush flats to the Sand Creek winter range located west of the town of Rexburg and north of Idaho Falls. Additional elk from Yellowstone and areas southwest of the park winter on Conant Creek, upper Teton River Canyon, Bitch Creek, Badger Creek, and the Fall River (J. Naderman, Idaho Fish and Game Department, personal communication).

Population Trends

Southwest of Yellowstone

The Sand Creek elk herd increased dramatically during the 1980's following cessation of general either-sex seasons in the mid-1970's (Brown 1985). Elk numbered about 2,300 in 1981 and approximately 2,400 in 1989

(Brown 1985; Vales and Peek 1993). Trend counts averaged 2,435 elk during the 1980's (Parker et al. 1983; Chu et al. 1989). Population models, however, suggest that the herd numbers about 4,900 (Vales and Peek 1993). Management goals call for limiting the elk herd to less than 2,000 on the Sand Creek winter range to reduce potential conflicts with cattle grazing and reduce damage complaints on adjacent private lands (Chu et al. 1989). A number of elk winter in areas near the Sand Creek winter range, and not all elk are observed during the aerial counts (J. Naderman, Idaho Fish and Game Department, Idaho Falls, personal communication). Population models suggest that the 1988 prehunt size of the greater Sand Creek elk herd, including peripheral areas, was about 6,200 (Vales and Peek 1993).

North of Yellowstone

The northern Yellowstone elk herd was reduced to less than 5,000 by 1968 due to population management reductions by trapping and shooting (Houston 1982). After discontinuing artificial reductions (Cole 1971), the northern Yellowstone elk herd nearly tripled through 1988, when the population was estimated at approximately 21,000 (Garton and Singer 1991; Mack and Singer 1993). The Gallatin herd was estimated through population modeling to be about 2,500 elk (Vales and Peek 1993). Recent aerial counts of the Madison–Firehole herd were about 800 elk, although Singer (1991b) estimated the actual herd had at least 1,200 elk due to heavy forest cover and low elk visibility.

East of Yellowstone

The three elk herds on Yellowstone's eastern boundary—North Fork Shoshone, Clarks Fork, and Carter Mountain—increased an average of 62% during the 1980's (Table 3). Each herd was estimated at approximately 2,800 to 3,000 elk in 1988 or 9,000 elk (total) in the 3 herds.

South of Yellowstone

Counts for the Jackson elk herd declined from 1981 to 1983 and averaged 9,573 elk. From 1984 to 1988, the animals counted increased dramatically and averaged 11,346. The higher counts reported in 1987 and 1988 may be because a helicopter was used for these counts. Population estimates reported in the yearly progress reports were much lower than estimates projected from a new population model developed in February 1989 (Lockman et al. 1989). The decline in population and subsequent steady increase from 1983 to 1988 was probably a result of three consecutive mild winters (Lockman et al. 1989) and more restrictive hunting regulations between 1984 and 1987.

Elk in the Jackson herd wintering in Buffalo Valley increased from approximately 30 in 1981 to 604 in 1988. This increase may have been due to mild winters, local public opposition to increased hunting, and feeding by private individuals (Lockman et al. 1989). Preliminary analysis of 12 radio-collared elk revealed that 67% of the individuals wintering in Buffalo Valley spent summer and fall in Yellowstone. The increase of elk wintering in Buffalo Valley caused the public to favor establishing another feeding ground in this area. The Wyoming Game and Fish Department prefers not to establish another artificial feeding ground. Counts and classification data were not collected for the Targhee herd, and only rough population estimates are available from 1980 to 1986. Classification data from 1987 and 1988 indicated relatively high bull/cow and high cow/calf ratios. Buffalo Valley is remote, and we predict that wolf activity will occur there.

Northwest of Yellowstone

The Gallatin elk herd increased approximately 20% during the 1980's, and recent counts yielded 1,500 to 1,800 elk (Taylor 1978–86; Vales and Peek 1993). Goals of the State of Idaho and the Bureau of Land Management are to maintain a high harvest through late-winter hunts and to limit the herd to less than 1,500 (Vales and Peek 1993). Population modeling suggests that the elk population was considerably larger than counts indicated and was about 2,500 in 1988 (Vales and Peek 1993).

Madison Plateau

The nonmigrating Madison–Firehole elk herd was stable or declined slightly during the 1980's (Cole 1983; Singer 1991b). Recent herd counts were less than 800, and the estimated herd size is 1,200 to 1,400 elk (Singer 1991b).

Harvests

East of Yellowstone

Weather influences the timing and magnitude of elk migrations out of Yellowstone for the Clarks Fork and North Fork Shoshone herds. Snow depths have been significantly correlated with fall elk migrations (Rudd 1982; Rudd et al. 1983). As a result of variable snowfalls, harvests for the Clarks Fork and North Fork Shoshone elk herds were also variable (Table 4). Management strategies were implemented in the late 1980's to stabilize elk numbers for both of these herds (Hurley et al. 1988), including hunting seasons, increased antlerless permits, and reduced hunting pressure on mature bulls. Increasing elk hunts on nonmigratory herd segments has complicated the management of the Clarks Fork and North Fork Shoshone elk herds.

Elk harvests from the Clarks Fork and North Fork Shoshone herds increased dramatically from 1980 to 1982 and then remained relatively stable until 1987. Hunter harvest from 1982 to 1986 averaged 713 elk (32% hunter success) and 570 elk (31% hunter success) for the Clarks Fork and North Fork Shoshone herds, respectively (Table 3). The low harvest in 1987 was due to a mild winter. The harvest for both herds again increased in 1988 due to a more normal winter.

South of Yellowstone

Harvests from the Jackson elk herd have varied during the 1980's (Table 4). Average yearly harvests were 3,475 elk between 1980 and 1983 but, with more restrictive regulations beginning in 1984 (that is, no general either-sex or antlerless seasons), harvests were substantially reduced, particularly in the cow and calf groups; the average yearly harvest between 1984 and 1987 was 1,385 elk. In response to rapidly increasing elk numbers projected for 1987, harvests were liberalized, but the harvest was lower than desired due to mild weather conditions. The harvest in 1988 was greater than in 1987 but not enough to bring the population down to the desired level of approximately 11,000 elk (Straley et al. 1986).

Elk harvests on the Targhee herd steadily declined from 1980 to 1986 (Table 4). The average annual harvest from 1980 to 1986 was 50 elk and increased to 70 in 1987 and 1988 (Table 4). The reduced harvest in the mid-1980's was related to more restrictive hunting seasons that lowered the number of resident and nonresident hunters (Lockman et al. 1989). Increased harvests in 1987 and 1988 were probably a result of increased elk numbers and an increase in outfit hunting activity (Moody et al. 1988).

Southwest of Yellowstone

Idaho's Sand Creek elk herd was harvested at high levels (Table 4). Hunter densities were as high as 5.1 hunters/km^2 during the general season. Logging roads and timber cuts make elk more vulnerable to hunters (Parker et al. 1986). Parker et al. (1986) found a correlation between road density and percent yearling bulls in the harvest. They expressed concern that the harvest rates for bull elk may be approaching levels detrimental to herd productivity. They associated high harvests with severe weather.

The general season elk harvest declined from 1980 to 1983 and then increased to a high of 687 elk (Table 3). The legal harvest was composed entirely of antlered bulls during the general season. The number harvested has remained relatively stable since 1985.

Elk harvested during controlled hunts declined from 1981 to 1984. Starting in 1985, controlled-hunt harvests increased to a high of 737 elk in 1988 (Table 4).

Mule Deer

Seasonal Ranges and Distribution

Approximately 20,637 to 21,883 mule deer occupy areas adjacent to the park in eight herds (Table 5). Each herd used the park in summer (Foss 1987; Hurley et al. 1989; Kuck et al. 1989; Lockman et al. 1989; Singer 1991b), but the extent of their migrations into the park is unknown.

North of Yellowstone

Portions of the Gallatin and northern Yellowstone mule deer herds summer within the park (Table 5). The majority of the northern herd winters immediately outside Yellowstone; aerial counts of mule deer wintering within the park on the northern range averaged less than 200 deer (Singer 1991b).

East of Yellowstone

Mule deer populations in the Clarks Fork, North Fork Shoshone, and South Fork Shoshone winter 27 to 48 km from the park. The number of deer summering within the park is unknown (Fig. 2; Table 5).

South of Yellowstone

Mule deer from the Jackson herd winter near the town of Jackson, 64 to 80 km from the park, well away from areas wolves would likely occupy. Summer migrations into Yellowstone are highly probable (Lockman et al. 1989).

Mule deer from the Targhee herd winter in Idaho (84% were seen in Idaho) or in Wyoming, straddling the state line in the Victor, Fox, Kiln, Teton, South Badger, and South Leigh creeks (Fig. 3; Lockman et al. 1989). Some of these deer probably summer in or near the park.

Southwest of Yellowstone

Mule deer from the northeastern area of Idaho adjacent to the park winter primarily in the Junipers–Sand Creek winter range. Deer from the Junipers–Sand Creek herd migrate during summer into the Island Park area, adjacent areas of the Targhee herd in Wyoming, and into Yellowstone.

Population Trends

North of Yellowstone

Since 1980, the mule deer population north of the park has been stable or increased. In response to the increasing populations, the Montana Department of Fish, Wildlife, and Parks increased the available number of antlerless licenses to harvest more of the productive doe segment. As early as 1981, concern developed that unpredictable influxes of elk on a winter range north of the park made managing the deer populations difficult (Foss 1985). Foss indicated that spring fawn/100 adults seemed to be negatively correlated with the number of elk present on the northern winter range. However, Houston (1982) reported that mule deer recruitment showed no significant association with elk numbers. Yearling recruitment on the east and west sides of the Yellowstone River averaged 29 and 33%, respectively, during the 1980's (Mack and Singer 1993).

East of Yellowstone

Mule deer populations in the Clarks Fork, North Fork Shoshone, and South Fork Shoshone herds were stable or increased slightly during the 1980's. Deer numbers were estimated from a computer model, which may have overestimated population numbers (Hurley et al. 1989). Buck/doe ratios in postseason classifications were less than 4, apparently due to the heavy harvest of bucks compared to does from 1980 to 1987. However, buck/doe ratios increased substantially in 1988 because a 4-or-more-points buck restriction was implemented (Hurley et al. 1989).

South of Yellowstone

Mule deer populations increased in the Jackson herd during the 1980's. Fawn/doe ratios for the north Jackson, Wyoming, area were relatively high, especially from 1984 to 1988. Buck/doe ratios increased since 1986 due to low harvest, limited hunter access, and more restrictive seasons (Lockman et al. 1989).

Classification data were collected for the Targhee herd from 1980 to 1986. Populations were stable or increased. Fawn/doe ratios were relatively high in 1987 and 1988 (Lockman et al. 1989).

Southwest of Yellowstone

Mule deer trend counts during December in the Sand Creek area averaged 1,599 during the 1980's. The population objective for this herd is 1,200 (J. Naderman, Idaho Fish and Game Department, personal communication).

December fawn ratios were high for the Sand Creek herd and averaged 95 fawns/100 does. Buck/100 does ratios declined from a high of 65 in 1979–80 to 23 in 1987–88.

Harvests

North of Yellowstone

From 1980 to 1986, an average of 1,762 deer were killed each year. Although the number of bucks killed each year declined, the number of antlerless deer increased, resulting in a relatively stable annual hunt since 1981. From 1980 to 1986, a yearly average of 83% of the total deer harvested from areas adjacent to Yellowstone came from Montana hunting districts 313 and 314. An average of 91% of the annual harvest consisted of mule deer (69% antlered, 22% antlerless). An average of 6% of the annual harvest consisted of antlered white-tailed deer (*Odocoileus virginianus*), and 3% consisted of antlerless white-tailed deer.

East of Yellowstone

From 1980 to 1988, the average annual deer harvests for the Clarks Fork, North Fork Shoshone, and South Fork Shoshone herds were 565 (31% hunter success), 242 (27% hunter success), and 792 (44% hunter success). Total harvests were relatively stable or increased slightly through 1985. Harvests declined from 1986 through 1988 for the Clarks Fork and South Fork Shoshone herds.

Bucks dominated the mule deer harvest from 1980 to 1987 for all three herds. In 1988, 130% more does than bucks were killed in the Clarks Fork and South Fork Shoshone herds. Doe and buck harvests in the North Fork Shoshone herd were nearly equal (81 and 85) for 1988. The change in buck harvest was due to new hunting regulations allowing only the harvest of bucks with at least one antler of four points or more. In 1988, the 4-point rule and a 5-day reduction in the general season length contributed to a low deer harvest. These changes have all been designed to reduce the buck harvest (Yorgason et al. 1986; Hurley et al. 1988).

South of Yellowstone

From 1980 to 1984, the average mule deer harvest from the four hunt areas in the Jackson herd was 608 deer (Lockman et al. 1989). Yearly harvests declined during this period, primarily because of subdivision developments on deer winter range and landowner intolerance of hunting (Straley et al. 1981, 1982).

In 1983, biologists believed large numbers of deer spent summer and fall in hunt areas 148, 155, and 156 but wintered elsewhere (Straley et al. 1984). Poor hunter access, reduced opportunities for rifle hunting, and more restrictive hunting seasons contributed to a declining harvest from 1984 to 1988 (Moody et al. 1988; Lockman et al. 1989).

Harvests for the Targhee mule deer herd were relatively high and stable between 1980 and 1983. The average annual harvest during this period was 106 deer.

Southwest of Yellowstone

Deer harvests declined from 1,239 in 1980 to 238 in 1984. The low harvest in 1984 was due to a combination of high winter-kill in 1983–84 and the elimination of antlerless permits in 1984. Harvest levels increased in 1985 and continued to increase to 2,075 deer in 1988. White-tailed deer made up about 4% of the total deer harvest.

Moose

Seasonal Ranges and Distribution

North of Yellowstone

Portions of three Montana moose populations—the Hebgen Basin, Gallatin, and northern herds—winter and summer within the park (P. Schladweiler, Montana Department of Fish and Game, unpublished report; D. Tyers, Gallatin National Forest, Gardiner, Montana, personal communication). The Hebgen Basin group resides on tributaries of Hebgen Lake, including the lower Madison River, Duck Creek, and Cougar Creek in Yellowstone. Moose occur across the northern elk winter range (Houston 1982) throughout the year. Seasonal movements between summer and winter ranges typically involve elevation shifts and movements of only 5 to 8 km (D. Tyers, Gallatin National Forest, Gardiner, Montana, personal communication).

East of Yellowstone

Moose winter in the Crandall, Sunlight Basin, North Fork Shoshone, and Thorofare areas adjacent to the park. The Thorofare range straddles the park boundary. Moose from the Crandall, Sunlight Basin, and North Fork Shoshone ranges may migrate to the summer range in Yellowstone; however, no radiotelemetry studies investigating seasonal ranges have been conducted.

South of Yellowstone

Two moose herds—the Jackson and the Targhee—occur immediately south of the park. Moose range south of the park in the Jackson herd. Tagging and neckbanding studies conducted in the late 1960's and early 1970's (Houston 1968; Lockman et al. 1989) suggested that moose that winter along the Buffalo River summer in Yellowstone and Grand Teton national parks, the Teton Wilderness, and in upper Spread Creek.

Few moose from the Targhee herd winter in Wyoming. Most winter in Idaho within 10 km of the state line, from Teton Creek south to Bitch and Moose creeks (Lockman et al. 1989). These moose move east and north for the summer. They are joined by moose from the Fall River herd in Idaho, 15% of which summer in Wyoming and 39% of which summer in Yellowstone (Ritchie 1978; Lockman et al. 1989).

Southwest of Yellowstone

Moose from five wintering groups in Idaho migrate in a northeasterly direction in the spring (Ritchie 1978) to summer in areas east of U.S. Highway 20, southwest of Yellowstone and southwest of Montana. The Fall River moose herd summers and winters primarily east of U.S. Highway 20 and occupies Yellowstone lands more than other herds. Studies of tagged moose suggest that equivalent numbers of Fall River moose summered in Idaho and Wyoming (Ritchie 1978). A few moose winter in the Bechler Meadows in Yellowstone.

Population Trends

North of Yellowstone

Due to low visibility of moose remaining in the timber, aerial classification data were not collected for moose populations in Montana hunting districts surrounding the park. Hunter observations from Hellroaring, Buffalo Fork, Slough Creek, and upper Stillwater in the Absaroka high country suggest an increasing moose population since more restrictive hunting regulations were initiated in the mid-1970's. The number of moose seen per hunter significantly increased during 1979–86 compared to 1975–78 (Swenson 1985b; Swenson and Foss 1986). This increase, coupled with a lower reported calf/100 cows ratio (suggesting reduced quality or quantity of forage; P. Schladweiler, Montana Department of Fish and Game, unpublished report), justified issuing more antlerless-only permits in this area.

East of Yellowstone

The Thorofare herd contains the best moose habitat in District 2 and probably has more moose than the Crandall, Sunlight, North Fork Shoshone, and South Fork Shoshone herds combined. The North and South Fork Shoshone River areas support marginal moose habitat (Yorgason et al. 1982, 1983, 1986). Classification and count data are too limited to justify population models for any of these herds.

South of Yellowstone

Moose population estimates for the Jackson herd declined from 1980 to 1984 and increased from 1985 to 1988. Reduced harvests—particularly in the female segment—since 1982 and mild winters have probably increased moose in the Jackson herd (Lockman et al. 1989).

Classification data from hunter and aircraft surveys indicate relatively stable calf/cow ratios between 1980 and 1985. Bull/cow ratios from hunter surveys were lower than aircraft surveys. The relatively high bull ratios, in spite of the high bull harvest, may be because aerial surveys were conducted near Grand Teton National Park where moose are not subjected to hunting pressure (Straley et al. 1985, 1986, 1987; Moody et al. 1988).

High hunter success, even with increasing harvests, suggests that the population is increasing in the Targhee moose herd (Moody et al. 1988). Classification data were collected from hunter surveys between 1980 and 1985. Calf/cow ratios were variable but seemed to be increasing through 1985.

Southwest of Yellowstone

Moose populations in Idaho, adjacent to the park, are relatively productive, and bull/100 cow ratios are high. Twinning rates between 1969 and 1975 were relatively high and averaged 12% (Ritchie 1978).

Moose counts declined in the 1970's, and the hunting season was closed from 1977 to 1982. By 1982, the counts were increasing, and a controlled hunt was reinstituted in 1983.

Harvests

North of Yellowstone

The moose harvest remained relatively constant between 1980 and 1986, averaging 114 animals/year for seven areas. Hunter success was high and stable at about 84% per year. The majority of the harvest was bulls at 75% per year, with cows at 17% per year and calves at 8% per year.

East of Yellowstone

Since 1980, moose harvests along the park's eastern border were relatively stable and consisted of bulls. Hunters in the Crandall area have enjoyed about 96% success, although the number of permits increased from 5 to 10 animals starting in 1981. Annual harvests for the Sunlight area have remained at five bulls, and success rates have remained at 100%.

Despite this high success and because of lack of population data, illegal kills, and habitat changes on private land (Yorgason et al. 1984, 1985), biologists are taking a conservative approach to harvests based on counts. The harvests and success rates in the North Fork Shoshone and South Fork Shoshone herds have been irregular due to the large amount of effort required to kill a moose and the dispersed nature of moose in these areas (Fig. 3). Moose in the Thorofare area have received the most attention and management changes. Concerns that this herd was declining were expressed as early as 1981 (Yorgason et al. 1981). These concerns have led to reducing the number of permits issued, from 35 in 1980 to 24 in 1988. Total harvest of bulls, however, has not declined appreciably.

South of Yellowstone

The moose harvest in the Jackson herd in Wyoming decreased between 1980 and 1987 because fewer permits were offered. The Wyoming Game and Fish Department decreased permits to reverse a decline of moose population (Straley et al. 1985; Moody et al. 1988). Average annual harvest for 1980 and 1981 was 463 moose. Average harvest between 1982 and 1984 was 339 moose. The lowest number of permits and most restrictive regulations occurred between 1985 and 1987. During this period, the average moose harvest was 222 (Table 10). Bulls dominated the harvest from 1980 to 1988 and made up an average of 56% of the total harvest in 1980 and 1981. The proportion of bulls harvested increased between 1982 and 1988, and bulls made up 86% of the total harvest.

Harvests for the Targhee herd in Wyoming have steadily increased from 1980 to 1988 (Table 10). Increased harvests resulted from an increasing population and an increase in total permits offered (Lockman et al. 1989). The average annual harvest from 1980 to 1988 was 31 moose. Bulls dominated the harvest from 1980 to 1987 and made up 87% of the total harvest. The large increase in the cow harvest in 1988 reflects the substantial increase in antlerless moose permits offered to slow population growth of the herd (Moody et al. 1988).

Southwest of Yellowstone

From 1980 to 1982, a bulls-only moose harvest was allowed in only one of five moose hunt units southwest of the park in Idaho. This bull harvest averaged six per year. Moose aerial counts increased, and moose harvests were permitted beginning in 1983. From 1983 to 1988, an average of 58 moose was harvested per year (Trent et al. 1984; Chu et al. 1988).

Bighorn Sheep

Seasonal Ranges and Distribution

North of Yellowstone

In Montana, bighorns inhabit three winter ranges in and adjacent to northern Yellowstone. These winter ranges include the Mount Everts–Specimen Ridge, Cinnabar Mountain, and Tom Miner Basin ranges

(Keating 1982, 1985; Irby et al. 1986; M. Meagher, National Park Service, personal communication). The majority of bighorns in the Mount Everts and Specimen Ridge population reside within the park year-round. Bighorn sheep in the Cinnabar Mountain population winter outside Yellowstone but summer inside the park on Sepulcher Mountain, Electric Peak, Bannock Peak, and Quadrant Mountain (Keating 1982). Bighorns from the Tom Miner Basin population winter outside the park. Summer ranges for this population straddle the park boundary on Sheep Mountain, Ramshorn Peak, and Fortress Mountain (Keating 1982). The Spanish Peaks and Taylor–Hilgards bighorn sheep herds of the Madison Range occupy winter ranges 10–30 km from the Yellowstone boundary. Bighorns from the Stillwater and Rosebud populations winter 30–50 km from the park, but radio-collared individuals travel into the northeast boundary of the park each summer (S. Stewart, Montana Fish, Wildlife and Parks, Red Lodge, personal communication).

East of Yellowstone

Bighorns in the Clarks Fork, Trout Peak, and Yount's Peak areas (Fig. 4) primarily reside year-round outside the park (Hurley 1985; Hurley et al. 1989). However, all three sheep ranges lie between 8 and 24 km from the park, which may be reoccupied by wolves. The Wapiti Ridge population occupies summer and winter ranges in the southeastern corner of Yellowstone (Hurley 1985; Hurley et al. 1989).

South of Yellowstone

Sheep in the Jackson herd winter in the Gros Ventre and Hoback Valley winter ranges located 48 km south of the park. These wintering areas are unlikely to be inhabited by wolves.

One bighorn winter range in the Targhee herd is within 24 km of the park, but a second is 56 km south of the park (Fig. 4). A few sheep seen periodically on Mount Sheridan in Yellowstone may be from the Targhee bighorn herd.

Population Trends

North of Yellowstone

The Mount Everts–Specimen Ridge population is larger than the Cinnabar Mountain or Tom Miner populations. Bighorns on Mount Everts (excluding the Specimen Ridge area) increased from 63 in 1965 to 222 in 1978. The rate of increase from 1965 to 1978 was estimated to be 12% per year (Keating 1982).

The Mount Everts–Specimen Ridge bighorn sheep population was relatively stable from 1974 to 1981 at about 200 (Keating 1982). Meagher (of the National Park Service) estimated this population to be about 400 animals, but an infectious keratoconjunctivitis epidemic in 1982 reduced the population by 75–85% (Meagher 1982 and personal communication).

The population recovered to 136 to 180 individuals by 1988 (M. Meagher, National Park Service, personal communication).

Bighorns were extirpated from the Cinnabar Mountain population (Montana hunting district 300) in the late 1800's. Following colonization from Mount Everts in 1965, the herd rapidly grew from 11 in 1967 to 103 in 1980 (an 18% per year increase; Keating 1982). This population has continued to grow. Irby et al. (1986) estimated that 80–150 bighorns occupy the Cinnabar Mountain in winter. Lamb/ewe ratios have been negatively correlated to the number of ewes present in a population the previous year and may indicate that there are too many bighorns for the forage conditions (Swenson 1985b).

The Taylor–Hilgards area contains three small bands of bighorns. The most numerous band in the Hilgards area experienced a drastic decline (Swenson 1985a), which possibly resulted from competition with increasing numbers of elk on winter range or possibly from an increase in the mountain goat population in this area (Swenson 1985a).

The Stillwater bighorn population has declined since the mid-1980's. Low lamb/100 ewes ratios may be due to increased mining near their preferred winter range (Simmons et al. 1987).

The Rosebud population apparently increased slowly from 1980 to 1987. Poor survey conditions resulted in the unusually low number of observed individuals, except for 1983 and 1986, when adequate counts were obtained.

East of Yellowstone

Bighorn sheep populations for the Clarks Fork, Trout Creek, Wapiti Ridge, and Yount's Peak herds have been increasing slightly from 1980 to 1987. No population model exists for the Clarks Fork herd, but numbers are believed stable at approximately 500.

Population numbers for the Trout Peak herd have been increasing slightly since 1981 and were believed to be near 497 animals in 1988 (Hurley et al. 1989). Lamb/100 ewes ratios have been fairly stable and averaged 38 lambs/100 ewes between 1983 and 1988.

Before 1987, the Wapiti Ridge population was believed to be stable at approximately 875 sheep. After correcting the model, the population was believed to be increasing and near 1,000 animals by 1988. Classification data were more complete for the Wapiti Ridge herd. Except for 1981 and 1988, lamb production was relatively constant and averaged 37 lambs/100 ewes. Low lamb survival in 1988 was attributed to the harsh winter (Hurley et al. 1989).

The Yount's Peak herd was believed stable at approximately 900 animals from 1981 to 1987 (Irwin et al. 1988). This herd declined 13% in 1988 from 1987, primarily because of low lamb survival, poor forage conditions on the winter range (Hurley et al. 1989), and possibly a severe winter. Before 1988, lamb/100 ewes ratios averaged 42 lambs/100 ewes.

South of Yellowstone

Postseason classification data showed that lamb/ewe ratios steadily declined from 1980 to 1984 and averaged 46 lambs/100 ewes in the Jackson bighorn herd. The ratio increased dramatically in 1985, dropped in 1986, and remained relatively constant at 44 lambs/100 ewes between 1986 and 1988. The reasons for these declining ratios may be related to competition with other ungulates (Straley et al. 1982; Moody et al. 1988) and adverse weather conditions such as those in spring 1982 (Straley et al. 1982). Ram/100 ewes ratios steadily declined between 1980 and 1986 but stabilized between 1986 and 1988. This decline may be due to a slightly increased ram harvest and low lamb production, particularly between 1982 and 1984. Population estimates for the Jackson bighorn herd declined between 1980 and 1982 and slowly increased to approximately 550 sheep in 1988.

Between 38 and 58 sheep were counted in the Targhee herd from 1980 to 1987. The most complete helicopter count in 1988 yielded 89 sheep. No population model was developed for this herd, but population estimates averaged 100 sheep from 1980 to 1987, and the population was estimated at 105 in 1988 (Lockman et al. 1989). Preseason hunter survey data suggest ram/ewe ratios declined from 88 in 1980 to 18 in 1984.

Harvests

North of Yellowstone

The unlimited license harvest from six Montana areas bordering the park averaged 16 bighorns/year between 1980 and 1986. Hunter success from unlimited license holders averaged 5% per year. Hunters who obtained a license through a drawing averaged nearly 4 bighorns/year, and success for these individuals was higher, averaging 87% per year.

East of Yellowstone

Bighorn sheep harvests east of the park have been relatively stable or have increased slightly. The unusually low harvest and hunter success for the Clarks Fork herd in 1988 was probably due to forest fires in that area. The average annual harvest of rams (1980–88) was relatively high compared to other areas surrounding Yellowstone. Average ages of rams killed ranged between 5 and 8 years (Hurley et al. 1989).

Average annual hunter success (1980–88) for the four herds was Wapiti Ridge, 79%; Trout Peak, 60%; Clarks Fork, 55%; and Yount's Peak, 53%. Hunter success on Wapiti Ridge is the highest of any area east of Yellowstone and may be related to its easy access. Since 1986, some of the high success rates are partially due to some bighorn sheep hunters holding complimentary licenses.

South of Yellowstone

The annual harvest for the Jackson bighorn sheep herd was relatively stable and averaged 15 legal rams between 1981 and 1988. Average hunter success (45%) was lower between 1986 and 1988 compared to 1981–85 (61%) and is probably related to an increase in available permits (Lockman et al. 1989).

The annual harvest for Targhee bighorn sheep was variable and ranged from zero to two rams. Harvest success has also been variable, despite a decrease from eight permits between 1980 and 1984 to four permits between 1985 and 1988 (Lockman et al. 1989).

Estimating the Relations Between Hunter Harvest and Gray Wolf Predation on the Gallatin, Montana, and Sand Creek, Idaho, Elk Populations

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Abstract. We evaluated the effects of different levels of gray wolf (*Canis lupus*) predation on the Gallatin, Montana, and Sand Creek, Idaho, elk (*Cervus elaphus*) herds using two models. The Gallatin population was estimated to be between 1,800 and 2,400 elk in winter. Up to 10 adult wolves were supported at that elk population level when hunter harvest was reduced from the 1983–85 mean of 436 to between 300 and 400 elk and when the harvest was restricted to bulls. A stable elk population with five wolves—with a cow harvest of half of the 1983–85 mean—yielded a total hunter harvest of 350 to 450 elk. These model estimates assumed no changes in survival or fecundity of elk, but a 5% increase in survival of all sex and age classes did not alter the results. The Sand Creek winter population was estimated to be 4,300 elk. With predation by 10 adult wolves and confined to elk that used Yellowstone National Park for 150 days, hunter harvest ranged from 170 to 270 elk, similar to the 1980–88 average of 219 but with reduced cow harvest and increased bull harvest. With predation by 10 wolves on elk also occurring a short distance outside southwestern Yellowstone National Park during summer and fall, hunter harvest ranged from 640 to 770 elk, similar to the 1980–88 average of 738 elk. Our investigations suggested that these heavily hunted elk populations supported wolves and maintained reasonably high hunter harvest only when hunting was primarily directed at bulls. Intensive monitoring of both predator and prey populations will be needed if wolves are restored to Yellowstone National Park and prey on elk that migrate outside of the park. Potential compensatory responses by elk to the predation will be a major area for study if wolves reoccupy this region.

The potential for reoccupation of Yellowstone National Park by gray wolves (*Canis lupus*; U.S. Fish and Wildlife Service 1987) raises the question of what effect this species may have on the prey base, particularly elk (*Cervus elaphus*) populations. Two elk populations, the Gallatin herd in the northwestern portion of the park and the Sand Creek herd in the southwestern portion of the park, are hunted when they migrate beyond park boundaries. Our purpose was to provide a preliminary assessment of the potential effects of wolves on these two elk populations, estimate the size of wolf populations that could be supported by the prey base, and estimate the number of elk available to hunters if wolves are restored to the area.

Study Areas

The Gallatin River area modeled (Fig. 1) is outside the northwestern corner of Yellowstone National Park and contains elk, bighorn sheep (*Ovis canadensis*), mule deer (*Odocoileus hemionus*), moose (*Alces alces*), mountain goats (*Oreamnos americanus*), and beaver (*Castor canadensis*). The big game species are hunted when they occupy habitats in Montana along the Gallatin River. The winter range used by the Gallatin elk herd is approximately 650 km^2. Distribution of elk on the winter range varies among areas (Peek and Lovaas 1968). Elk primarily winter along the northern boundary of the park and at lower elevations along the Gallatin River and its tributaries north to the West Fork (Fig. 1). The upper Gallatin elk population in Montana hunting district 310 has nonmigratory and migratory segments. A segment migrates northwest into the Madison River drainage to winter on the Bear Creek Game Range and adjacent lands, including the Beaverhead National Forest. Nonmigratory elk are distributed within the Gallatin River drainage outside the park, summering at higher elevations above the winter ranges. Migratory elk summer south of the winter range, at higher elevations both inside and adjacent to Yellowstone National Park. The estimated area used by the Gallatin herd during summer was unavailable, but the area used is probably at least twice the size of the winter range.

Winter range for the Sand Creek elk herd is west of U.S. 20, mostly north of state Highway 33 between Rexburg and Sage Junction, east of Interstate 15 and south of a line drawn between Dubois and Island Park, Idaho, in Idaho management units 60, 60A, and 63A (Fig. 2; Brown 1985). Total area used by the Sand Creek herd in winter was 940 km^2, though 93% of the use occurred on an area of 572 km^2 (Brown 1985). In summer, elk are distributed throughout management units 60, 60A, 61, 62, 62A, 63A, southwestern Yellowstone National Park, Harriman State Park (Fig. 2), Montana, and probably in Wyoming hunt area 73. The eastern edges of management units 61 and 62A and the northeastern corner of management unit 62 border Yellowstone National Park. Brown (1985) documented the distribution of elk on summer ranges and assigned each a subpopulation name (Fig. 2). Brown (1985) calculated an approximate range size used by each subpopulation and estimated summer elk densities for each subpopulation (Table 1). Interchange occurs among elk at Sand Creek and those wintering on the Jackson, Wyoming, and Wall Creek Game Range, Montana (J. Naderman, Idaho Department of Fish and Game,

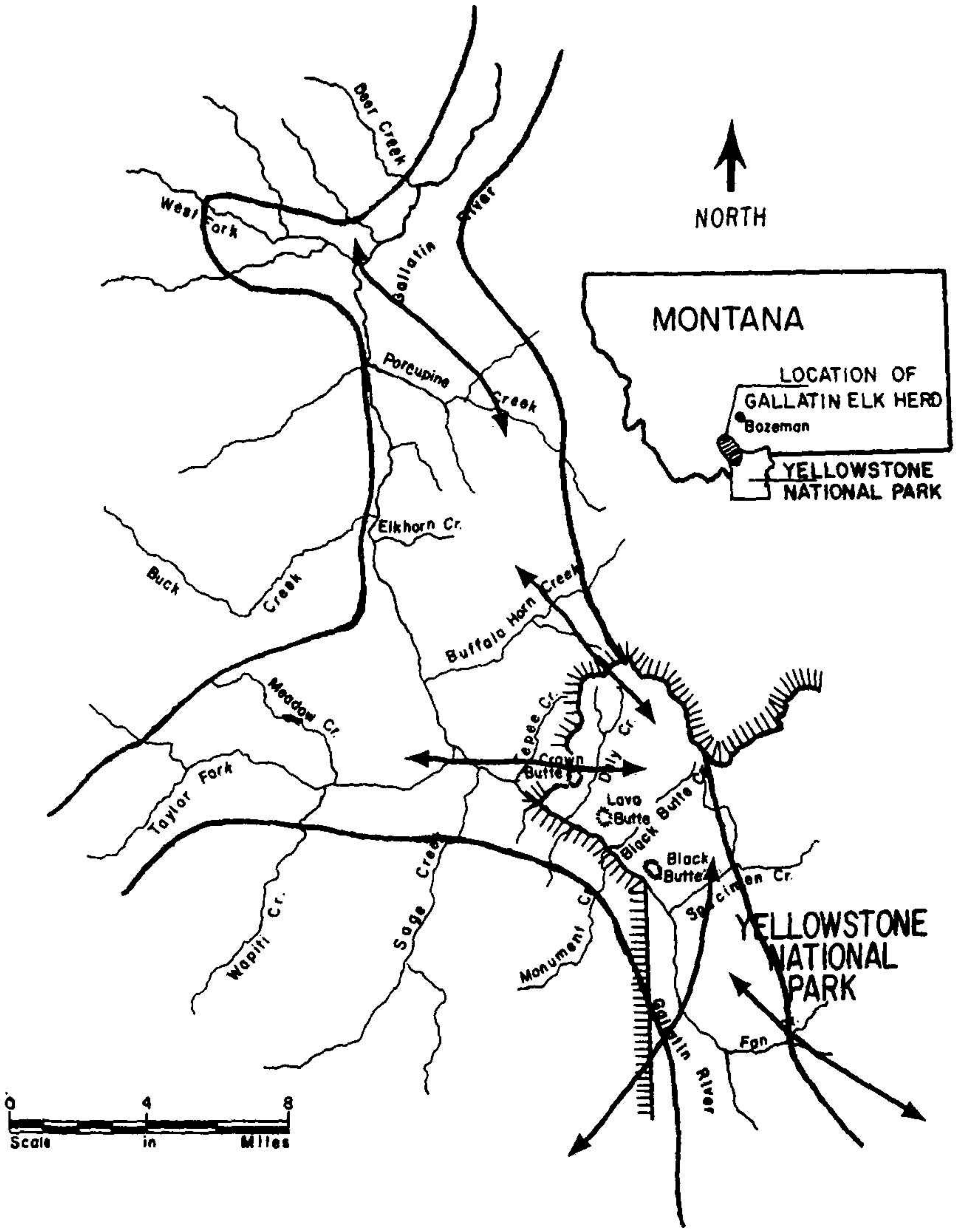


Fig. 1. Map of the Gallatin elk herd winter range with boundary roughly outlined and general migration patterns indicated (adapted from Lovaas 1970).

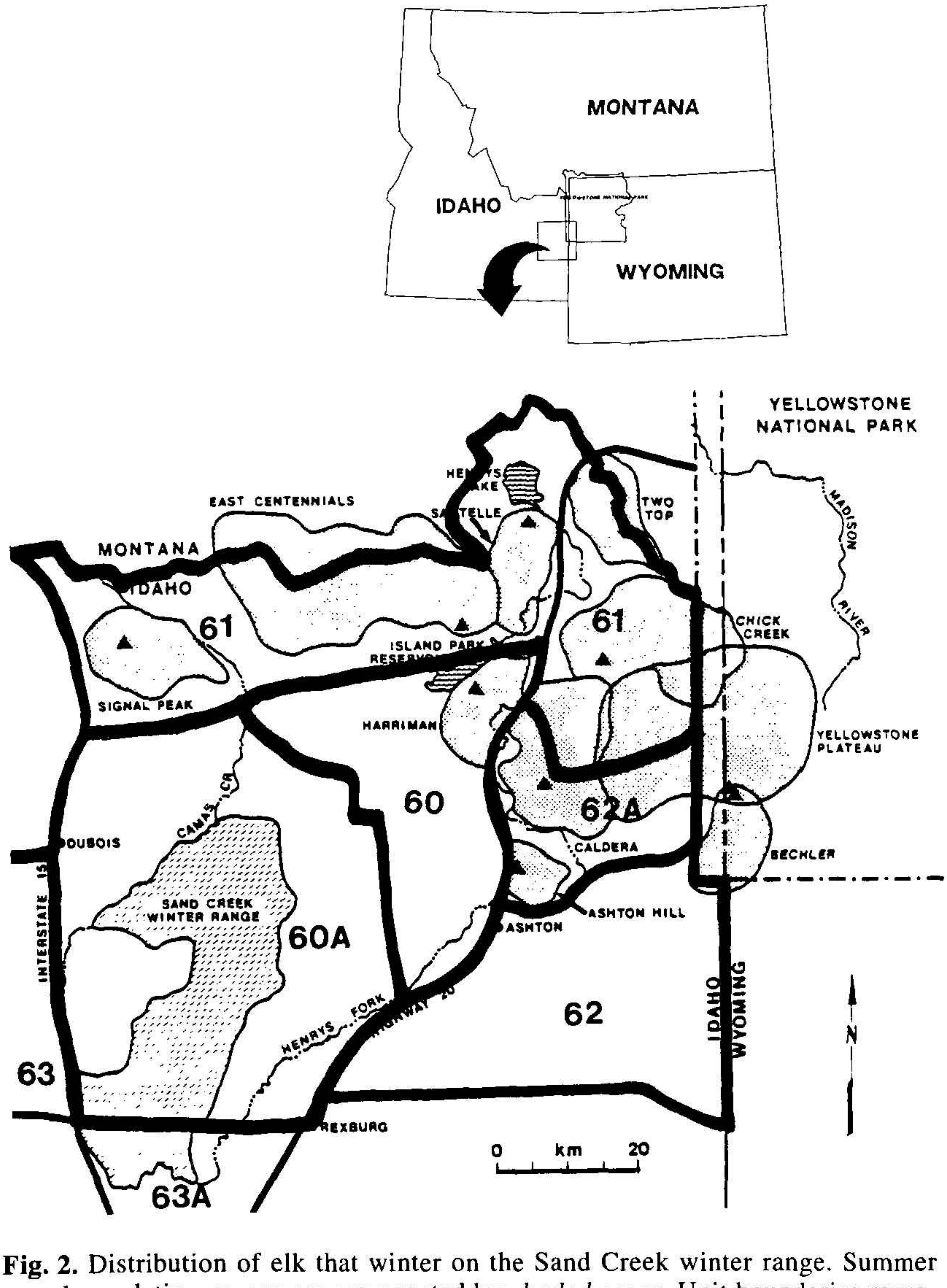


Fig. 2. Distribution of elk that winter on the Sand Creek winter range. Summer subpopulation ranges are represented by *shaded areas*. Unit boundaries represented by *bold lines* (from Brown 1985).

Table 1. Range size, density, and distribution of radio-collared Sand Creek, Idaho, cow elk (*Cervus elaphus*) during summer (Brown 1985).

Management unit	Subpopulation	Range size (km^2)[a]	Elk density (per km^2)[b]	Radio-collared		Percentage of elk observed	Days on summer range
				Number	%		
61	Signal Peak	132	1.95	3	5.8	4.8	170–191
61	East Centennials	423	2.94	6	11.5	18.8	108–206
61	Sawtell	68	2.35	2	3.9	2.7	113–159
61	Two Top	>40	<3	1	1.9	3.1	124
61, YNP[c]	Chick Creek	252	1.45	6	11.5	3.4	128–154
61, 62A	Caldera	188	2.19	5	9.6	7.2	111–152
61, 62A, YNP	Yellowstone Plateau	507	0.70	4	7.7	6.8	136–185
62, 62A, YNP	Bechler	100	7.01	6	11.5	17.1	104–162
62A	Ashton Hill	16	8.44	2	3.9	1.7	153–168
60	Harriman	71	21.25	15	28.8	32.8	125–210

[a] Brown (1985; Table 14) estimated summer range size using the 75% use contour from harmonic mean analyses of collared elk home ranges. Actual area used by all elk may be larger.
[b] From Brown (1985; Table 14).
[c] YNP = Yellowstone National Park.

Idaho Falls, personal communication). Brown (1985) also documented fall migration routes (Fig. 3). Mule deer, some white-tailed deer (*Odocoileus virginianus*), moose, and beaver occur throughout the Sand Creek elk herd summer range. Bison (*Bison bison*) may occupy the southwestern portion of Yellowstone National Park during summer and winter.

Methods

Models Used

We used a Leslie matrix model (Leslie 1945) and a discrete balance equation model (e.g., Starfield and Bleloch 1986; Walters 1986; Eberhardt 1987) for our population analyses and for evaluating effects of wolf predation in combination with hunting. Balance model summaries were provided at the end of the biological year before calving (referred to as spring population). Balance models used three age classes: young-of-the-year, yearling, and 2-year-old and older. Truncating the age structure may affect the dynamics of the model by making it more sensitive to small changes in survival and harvest rates of adult age classes, especially fe-

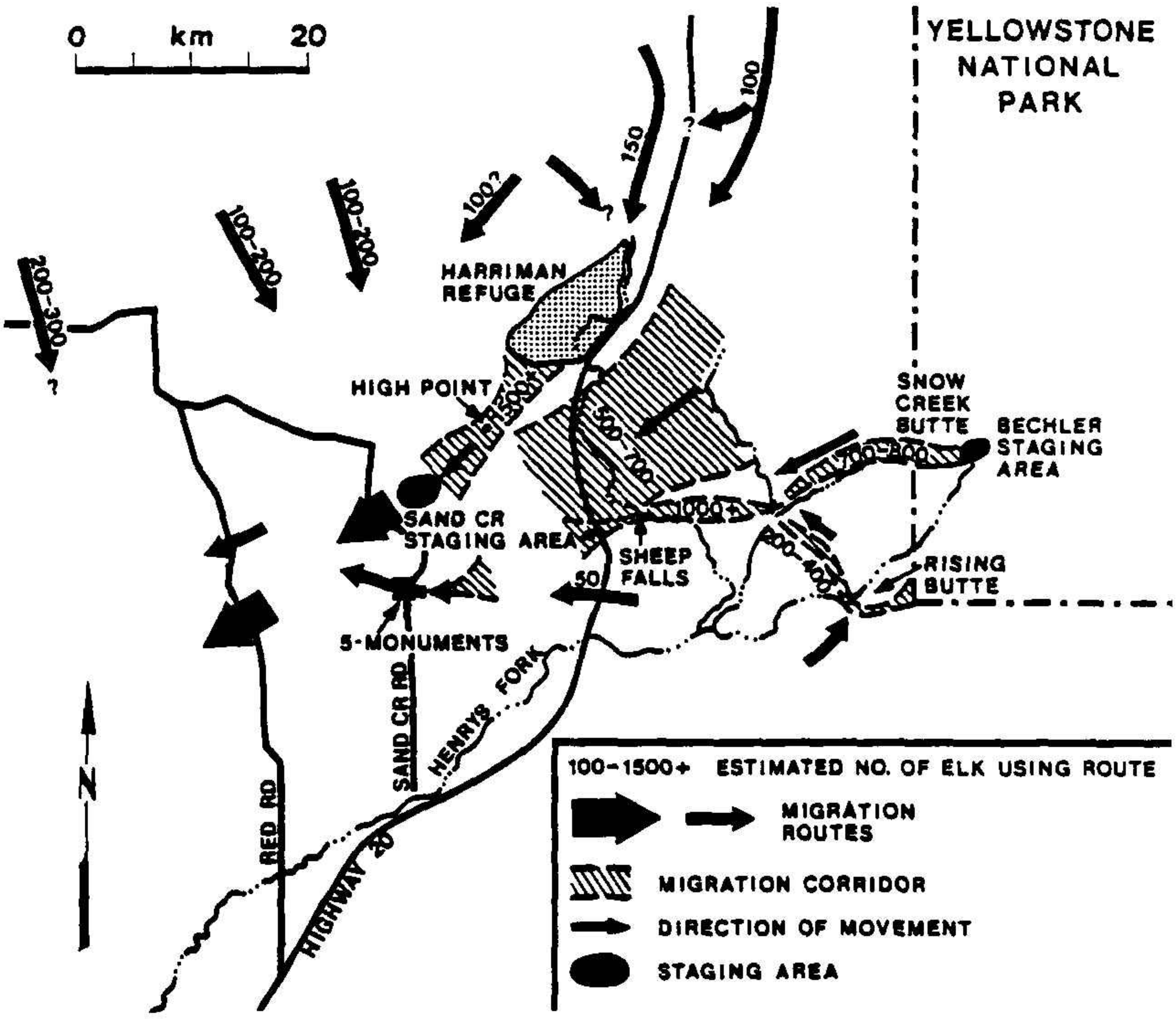


Fig. 3. Fall migration routes and staging areas of the Sand Creek elk herd, 1981–83 (from Brown 1985).

males. Survival rates for the Leslie matrix models were annual rates; those used in the balance models were partitioned to summer and winter seasons and excluded hunting mortality. The sequence of calculations in the balance models allowed elk mortality due to wolf predation to partially compensate for hunting and winter mortality.

Population Analyses

Data on the Gallatin elk herd were obtained from Taylor (1982, 1983, 1984, 1985, 1986). Data on the Sand Creek herd were obtained from DeShon (1982), Parker et al. (1982, 1983, 1986), Trent et al. (1984, 1986), Brown (1985), and Chu et al. (1987, 1988, 1989).

We initially tested for trends over time of the elk population size, composition, and harvest with linear regression. We then separately used the Leslie matrix and balance models to estimate population size, composition, survival, and fecundity from the available data, assuming that the harvest data represented the most accurately measured population parameter. Estimates of population parameters were needed before wolf predation was applied. The models were run iteratively to obtain survival and fecundity rates that resulted in model populations having characteristics similar to real populations, though population size and composition varied from that reported in state progress reports.

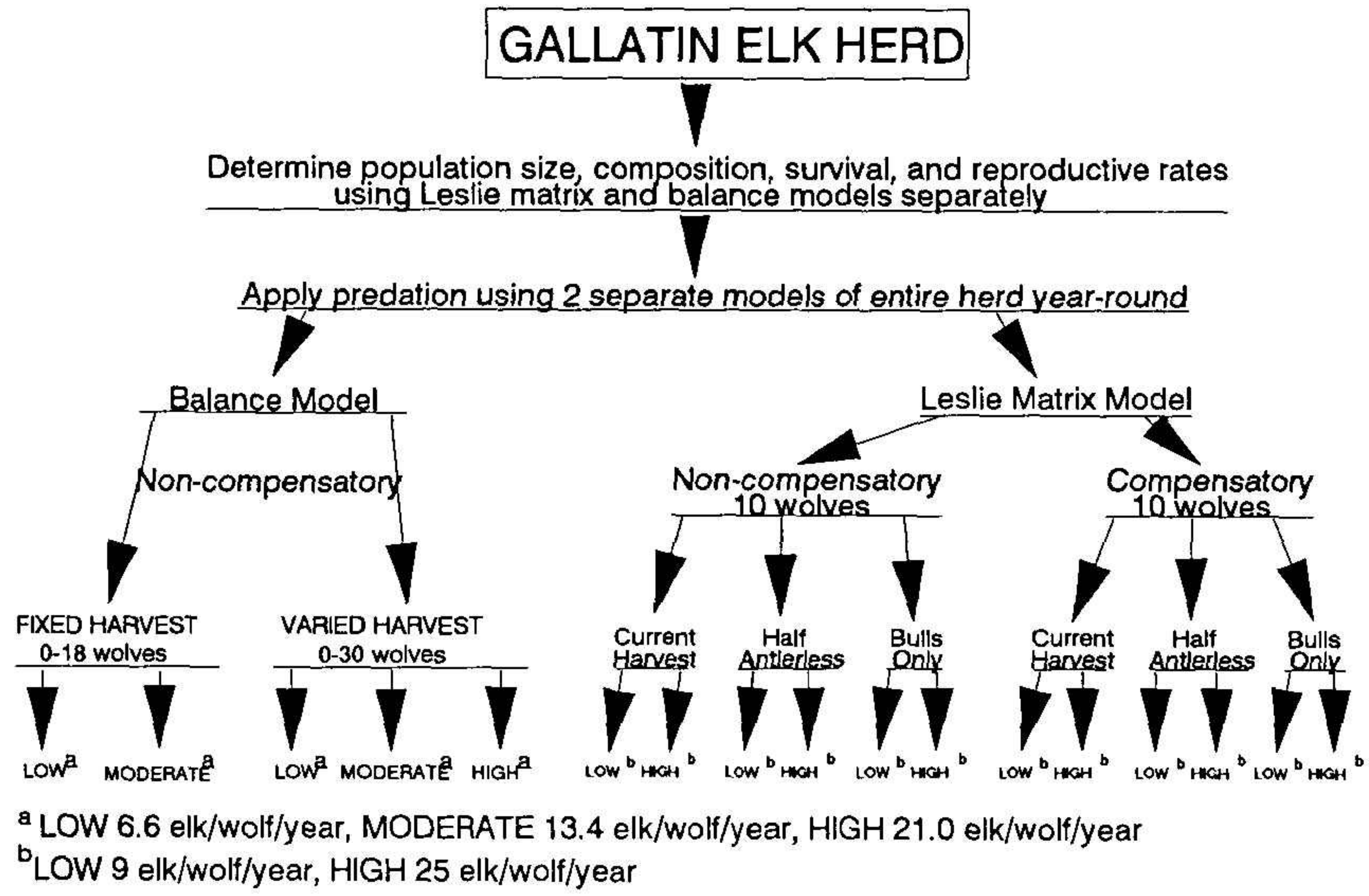
For cases where the observed harvest could not be supported by the population estimated by state agencies, we used a larger population size. In these cases, our model population was the minimum size that could support the average observed harvest and remain stable. Survival rates were high for these models. We speculate that the actual population size was larger and survival rates lower than those used in our models.

For the Leslie matrix projections, we smoothed the harvest age structure of elk aged 1 year or older (Caughley 1977:96). The proportion of animals in each age class was multiplied by the estimated prehunt population size to obtain the number of animals in each age class. Age classes were calves, yearlings, 2-year-olds, 3-year-olds, adults ages 4–7, and old ages 8–12. We then applied this population—plus the total harvest of bulls, cows, and calves—to the Leslie matrix model and adjusted survival and fecundity rates and population size until a stable population representing the wintering herd was obtained.

Wolf Predation

Scenarios Evaluated

We assumed that predation occurred equally across the entire area for the models. Few geographical barriers exist that would restrict movements of wolves. Both Leslie matrix and balance models of wolf predation on the Gallatin herd were evaluated for the entire herd year-round (Fig. 4). Noncompensatory and compensatory (5% increases in survival of all sex and age classes) Leslie matrix models and noncompensatory balance models were evaluated for the Gallatin herd (Fig. 4). The Leslie matrix models included scenarios at high and low predation rates with 10 wolves,



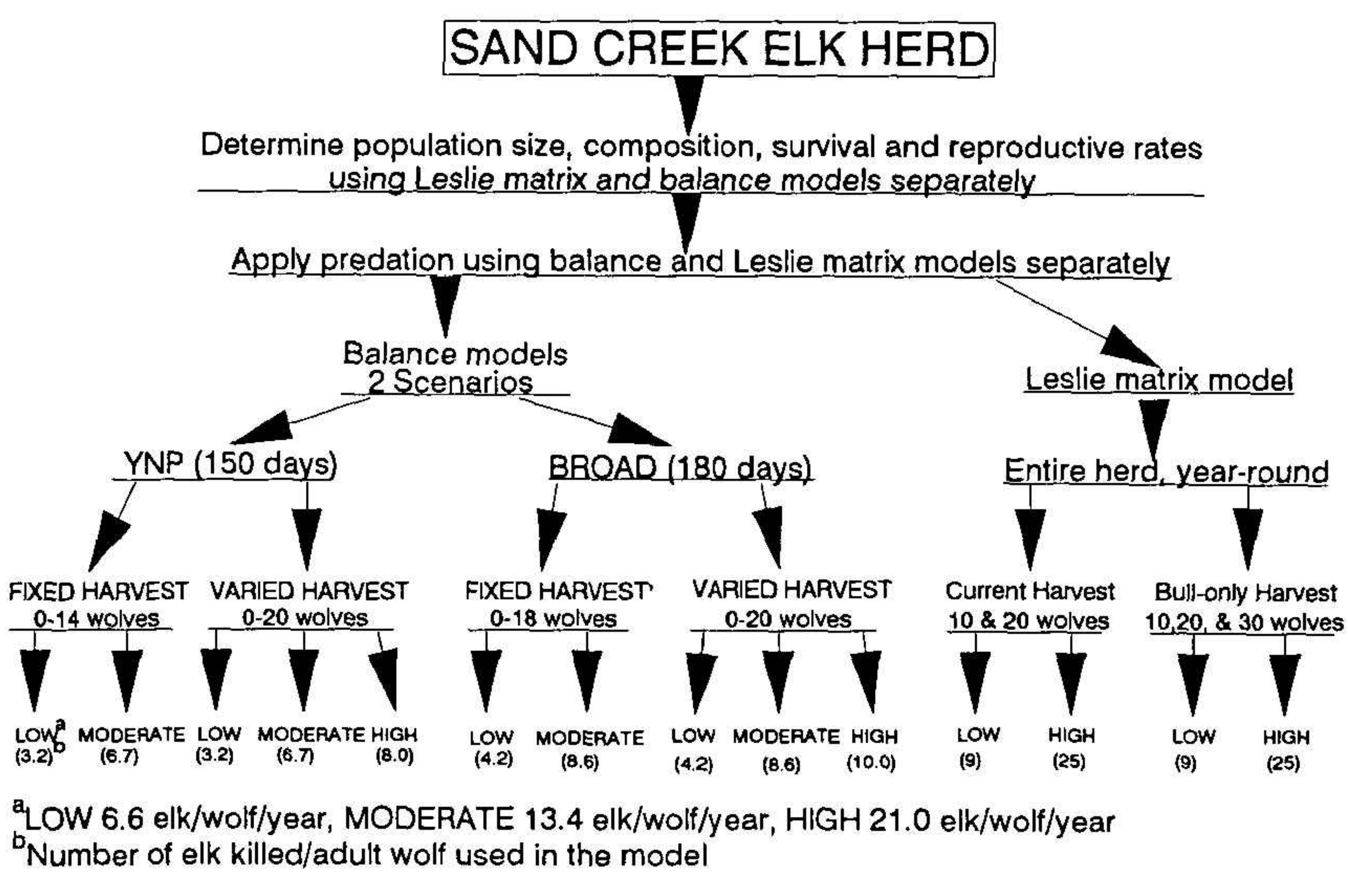


Fig. 4. Outline of the various model scenarios applied to the Gallatin and Sand Creek elk herds.

after preliminary investigations with more wolves suggested that no adjustments in either compensation in survival or reductions in hunter harvest were realistic. Three harvest strategies were explored with the Leslie matrix Gallatin models: hunter harvest of elk at current estimated levels, antlerless harvest at half the current level, and bull-only harvest (Fig. 4).

For each balance model, two methods of simulating predation were used (Fig. 4). One method (FIXED HARVEST) used constant and fixed harvest, survival, fecundity, and predation rates for the Gallatin elk population with 0–18 wolves. Over time, this is unrealistic because populations, harvest, and predation will not be stable. For the FIXED HARVEST models, LOW and MODERATE wolf kill rates were simulated (Fig. 4). The FIXED HARVEST models showed the potential short-term effects of constant wolf predation in the absence of management changes or wolf response. Hunter harvest rates were varied in the second method (VARIED HARVEST) to explore a range of harvest strategies that managers could control. The VARIED HARVEST models explored harvest strategies by examining a range of combinations of calf, cow, and bull harvest rates. For the Gallatin VARIED HARVEST models, calf harvest ranged 1–12%, cow harvest 1–12%, and bull harvest 35–60% of the prehunt population. LOW, MODERATE, and HIGH wolf kill rates were simulated in the VARIED HARVEST models using a range of wolves from 0 to 30 (Fig. 4).

Compensatory responses in elk reproduction or survival were not modeled for the Sand Creek herd because the herd was heavily hunted and was probably near maximum productivity. Two balance model scenarios were used to assess the effects of wolf predation on Sand Creek elk (Fig. 4). One scenario focused only on elk within southwestern Yellowstone National Park during summer and assumed that wolves would not be tolerated outside the park (YNP scenario). The second approach modeled a broader area including southwestern Yellowstone National Park and areas immediately adjacent to it; generally east of U.S. Highway 20 but also including Harriman State Park and the Big Bend Ridge area (BROAD scenario). Predation on elk for the BROAD scenario would occur through summer until fall migration. The BROAD scenario would permit wolves to roam in additional area outside Yellowstone National Park.

The number of wolves ranged from 0 to 14 for the YNP FIXED HARVEST model and from 0 to 18 in the BROAD model. The number of wolves ranged from 0 to 20 in the VARIED HARVEST models (Fig. 4). For the YNP scenario VARIED HARVEST models, calf harvest rates ranged 1–10%, cow harvest was 10–25%, and bull harvest was 10–40% of the prehunt population. For the BROAD scenario models, calf harvest rates ranged from 1 to 10%, cow harvest from 5 to 20%, and bull harvest from 25 to 60% of the prehunt population.

For the Leslie matrix Sand Creek projections, the entire herd was modeled year-round. Leslie matrix scenarios evaluated low and high predation rates for current harvest at 10 and 20 wolves and low and high predation rates for bull-only harvest at 10, 20, and 30 wolves (Fig. 4).

Sex and Age Composition of Wolf Kills

We reviewed the literature and found from studies that included elk or deer or only caribou that kill rates during winter ranged from 11.4 to 27.2 ungulates killed per wolf (Table 2). For our projections, we assumed that observed kill rates would be maintained throughout the year. The likelihood of reductions in kill rates in summer (use of alternate prey) would be offset by the increase in calves in the kill, but our elk kill rates may prove to be high if alternative sources of prey become more important.

In Riding Mountain National Park, Manitoba, Canada, Carbyn (1980) reported that calves constituted 34% of the elk killed by wolves, and animals over 7 years old constituted 40%. Bjorge and Gunson (1989), how-

Table 2. Wolf (*Canis lupus*) kill rate summary, updated from Keith (1983).

Location	Source[a]	Ungulate prey[b]	Mean kill rate in winter (days/kill): Per pack	Mean kill rate in winter (days/kill): Per wolf
Isle Royale	1	moose	3.1	47
Isle Royale	2	moose	3.3	36
NE Alberta	3	moose	4.7	45
Alaska (Tanana)	4	moose	3.4	53
Alaska (Nelchina) summer	5	moose, caribou	7.3–15.7	22–118
Alaska (Nelchina) winter	5	moose, caribou	4.9–10.8	44–62
Alaska (Kenai)	6	moose, caribou	3.1–21.4	42–58
Alaska	4	caribou	1.9–4.6	13–32
Yukon	7	Dall sheep, moose, caribou	7.7–9.0	31–54
SW Quebec	8	moose	19–90	91–250
SE Alaska	4	black-tailed deer	—	24
Ontario	9	white-tailed deer	2.2	18
Manitoba (Riding Mountain National Park)	10	elk, white-tailed deer	3.6–6.9	14–21
W Minnesota	11	white-tailed deer	7.0	32
NE Minnesota	12	white-tailed deer	7.8	25
Alberta	13	elk, mule deer, moose, bighorn sheep	2.5	25

[a] Sources: (1) Mech 1966; (2) Peterson 1977; (3) Fuller and Keith 1980; (4) Holleman and Stephenson 1981; (5) Ballard et al. 1987; (6) Peterson et al. 1984; (7) Sumanik 1987 (estimates provided for Dall sheep only); (8) Messier and Crete 1985; (9) Kolenosky 1972; (10) Carbyn 1983; (11) Fritts and Mech 1981; (12) Mech 1977; (13) Gunson 1986.

[b] Moose (*Alces alces*); caribou (*Rangifer tarandus*); Dall sheep (*Ovis dalli*); black-tailed deer (*Odocoileus hemionus columbianus*); white-tailed deer (*Odocoileus virginianus*); elk (*Cervus elaphus*); mule deer (*Odocoileus hemionus*); bighorn sheep (*Ovis canadensis*).

ever, reported higher kill rates on calves: 65% of the elk killed were calves, while only 35% of the population were calves. Elk calves were killed most frequently in early midwinter, but adult cows were more frequently taken in late winter (Carbyn 1980). All animals examined had high femur marrow fat levels and lacked skeletal or hoof abnormalities. Carbyn (1980) reported that 39 of 57 adult elk killed by wolves were cows, a sex ratio of 46 bulls/100 cows. No sex ratios in the harvest or the population were given, but that ratio seems high and suggests that more bulls were being taken than expected, based on their occurrence in the population. Carbyn (1975, 1983) considered bull elk more vulnerable to predation than cows. Cows are often found in large groups that may facilitate detection of predators. Carbyn (1983) believed that cows were either more alert than bulls or had evolved better escape mechanisms than bulls. Bulls occur in smaller groups, are often injured in fights, and enter the winter in poorer condition, making them more vulnerable to predation than cows.

The relative proportions of calves, adults, and older elk taken in Jasper (Carbyn 1975) and Riding Mountain national parks (Carbyn 1980) by wolves was similar. Averages for the two parks were 37.5% calves, 29% adults, and 33.5% older animals (Carbyn 1975, 1980). In Riding Mountain National Park, calves were taken 1.79 times more than their estimated occurrence in the population, while adults were taken 0.63 times as much, and old animals were taken in proportion to their occurrence. Carbyn (1980) concluded that more elk calves and fewer adult elk (1–11.5 years old) were killed by wolves than by hunters. Hunters harvested an estimated 5% of the elk population in the vicinity of Riding Mountain National Park (Carbyn 1980). In contrast to Riding Mountain, hunters harvest about 10–20% of the Gallatin and Sand Creek elk herds. Of the wolf studies listed in Table 2, Riding Mountain was most similar to Yellowstone in the mix of available prey species and in being a relatively closed system.

Alternative Prey

Populations of bighorn sheep and mountain goats in the areas modeled are relatively low and likely will not be important in the wolf diet. Mule deer, moose, bison, and beaver may provide part of the wolf diet and may buffer wolf effects on elk by providing alternate prey. We concentrated on the effects of wolf predation on elk because they are expected to be the primary prey (Koth et al. 1990), and not enough information on distribution and abundance of other prey is available to project the effects on them. Bjorge and Gunson (1989) reported that elk were preferentially killed over moose: 1 elk was killed per every 3 moose while 1 elk was available in the population per every 10 moose. Carbyn (1983) reported that 2.4 elk were available per moose, but 15 elk were preyed on per each moose preyed on. We recognize that wolves will eat food other than elk and thus reduced our estimated wolf predation rates on elk by the estimated proportion of the diet that might be composed of alternative prey.

Predation Rates

Leslie Matrix Models, Gallatin and Sand Creek

In the Leslie matrix models we assumed that elk will constitute between 75 and 90% of the ungulates killed by wolves. Two predation rates that encompassed the potential range of kill rates were used: low predation at 75% of 12 ungulates killed per wolf per year equalled 9 elk killed per adult wolf per year; and a high rate of 90% of 28 equalled 25 elk killed per adult wolf per year (Table 3). For the Leslie matrix models, we used a ratio of 0.46 bulls (aged 1 or older) to 1 cow killed and used the averages of 38% calves, 29% adults, and 33% old animals in the wolf kill (Table 3). We assumed that an equal proportion of male and female calves were killed. Wolf predation was incorporated into the Leslie matrix models by adjusting annual elk survival rates downward by the amount specified in Table 3. Proportions by sex and age of the population taken per wolf per year were multiplied by the number of wolves and then subtracted from the annual survival rate. This method of applying predation in the Leslie matrix models resulted in wolf mortality being additive to other sources of mortality.

Balance Models, Gallatin

We used LOW, MODERATE, and HIGH kill rates in the balance models. Reported daily biomass consumption by wolves ranged from 2.0 kg/wolf (Fuller 1989) to 7.2 kg/wolf (Peterson 1977) with an average of 4.4 kg/wolf for 14 studies reported by Fuller. Mech (1977) estimated that the maintenance requirement for wolves was 1.7 kg per wolf per day, and that wolves can eat as much as 3 times their maintenance requirement (5.1 kg/wolf/day). We estimated the number of elk killed by sex and age to meet a 2.5- and 5.1-kg/wolf/day consumption rate and converted these estimates to kill rates for use in the balance models.

The following illustrates how partitioning the kill was derived. Summer was estimated as 150 days and winter as 215 days. We assumed that 85% of biomass needs would be obtained from elk. Summer consumption was 2.5 kg/wolf/day × 150 days × 0.85 (proportion of diet that is elk) = 319 kg elk/wolf or 2.1 kg of elk/wolf/day. Winter consumption was estimated at 2.5 kg/wolf/day × 215 days × 0.85 = 457 kg elk/wolf. At 5.1 kg/wolf/day consumption, elk during summer was 650 kg/wolf and in winter was 932 kg elk/wolf (4.3 kg elk/wolf/day). At the 2.5 kg/wolf/day consumption rate, the annual kill rate modeled was 6.6 elk/wolf/year (Table 4) or 45% of the lowest reported kill rate in an ungulate system containing elk (Table 2; Gunson 1986). At 5.1 kg/wolf/day the kill rate was 13.4 elk/wolf (Table 4), 92% of the lowest reported kill rate in an ungulate system containing elk (Gunson 1986) and 51% of the highest reported kill rate on elk (Carbyn 1983; Table 2). The third estimate used the upper value of 26 ungulates killed/year (Table 2; Carbyn 1983); 80% of those killed were elk, resulting in an annual kill of 21 elk (Table 4). At this kill

Table 3. Ages and sexes of elk (*Cervus elaphus*) killed by wolves (*Canis lupus*) each year for the Gallatin, Montana, and Sand Creek, Idaho, elk herds used in the Leslie matrix models.

Number of ungulates taken/wolf/year = 12–28
if elk are 75% of diet = 9–21
if elk are 90% of diet = 11–25

Assuming adult sex ratio of 46 bulls/100 cows, age ratio of 37.5 calves/29.0 adults/33.5 old in the wolf take, then of those 9–25 elk taken/wolf/year,
3.6–9.4 elk will be calves, sex ratio equal;
3.0–7.2 elk will be aged 1–7, with 0.6–2.3 males, 2.4–4.9 females;
3.0–8.4 elk will be aged 8 or older, with 1.0–2.0 males, 2.0–6.4 females.

Herd	Males in population	Proportion of males taken/wolf/year	Females in population	Proportion of females taken/wolf/year
Gallatin[a]				
Calves	468	0.004–0.010	468	0.004–0.10
Adults	300	0.002–0.008	948	0.002–0.005
Old	1	1.000	129	0.015–0.049
Total	769	—	1,545	—
Sand Creek[b]				
Calves	856	0.0035–0.004	849	0.0035–0.004
Yearlings	743	0.0005–0.001	737	0.0003–0.0004
Adults	665	0.0009–0.001	1,522	0.0005–0.0007
Total	2,264	—	3,108	—

[a] Total Gallatin herd fall population is 2,314.
[b] Total Sand Creek herd fall population is 5,372.

rate, summer biomass consumption was estimated at 4.9 kg elk/wolf/day, and during winter was 7.7 kg elk/wolf/day for an annual average intake of 6.6 kg elk/wolf/day. Because the reported kill rates in systems containing elk ranged 14.6–26.1 ungulates/wolf/year (Table 2), the first estimate of 6.6 elk killed/wolf/year provided a low kill rate (LOW), the second of 13.4 elk killed/wolf/year a moderate kill rate (MODERATE), and the third of 21 elk killed/wolf/year provided a high (HIGH) kill rate.

Balance Models, Sand Creek

For the YNP scenario, we assumed that wolves would prey on elk during summer and fall and then migrate to either the upper Snake River or Madison–Firehole areas of Yellowstone National Park. Wolves might also eat bison, if available, during winter in the Bechler Meadows area of the park. Since wolves have their pups in April, they would not be able to migrate with the elk herds until late June, after the pups had grown. Late migration would reduce the amount of time that wolves preyed on migratory elk and newborn calves during early summer. Brown (1985) determined length of stay by radio-collared elk on the summer range (Table 1). Amount of time varied with animal, subpopulation, and weather. Brown

Table 4. Distribution of estimated predation by wolves (*Canis lupus*) on elk (*Cervus elaphus*) and approximate biomass consumption, by age and sex, used in the Gallatin elk balance models. LOW, MODERATE, and HIGH kill rates are presented.

	Number of elk killed/wolf				Mass of prey	Consumption (kg/wolf)		
Sex and age	LOW	MODERATE	HIGH	Utilization[a]	(kg)	LOW	MODERATE	HIGH
Summer (150 days)								
Female								
Calves	1.10	2.20	3.50	0.80	30	26	53	84
Yearling	0.13	0.27	0.30	0.75	240	23	49	54
2+ cows	0.57	1.23	1.20	0.75	240	103	221	216
Male								
Calves	1.10	2.20	3.50	0.80	30	26	53	84
Yearling	0.35	0.75	0.75	0.75	260	63	146	146
2+ bulls	0.35	0.75	0.75	0.75	260	63	146	146
Subtotal	3.60	7.40	10.00	—	—	304	668	730
Winter (215 days)								
Female								
Calves	0.50	0.95	2.00	0.75	114	46	87	171
Yearling	0.16	0.36	0.60	0.75	240	29	65	108
2+ cows	0.74	1.64	2.40	0.75	240	133	295	432
Male								
Calves	0.50	0.95	2.00	0.75	114	46	87	171
Yearling	0.55	1.10	2.00	0.75	260	107	215	390
2+ bulls	0.55	1.10	2.00	0.75	260	107	215	390
Subtotal	3.00	6.10	11.00	—	—	468	964	1,662
Total	6.60	13.50	21.00	—	—	772	1,632	2,392

[a] Proportion of carcass mass consumed.

estimated that the median time spent on the summer range was 138 days for elk not using Harriman State Park and 168 days for those using Harriman. For the YNP scenario, we assumed that elk were vulnerable to predation by wolves for 150 days. For the BROAD scenario, we assumed that wolves would prey on elk during summer and early fall and then either migrate to the upper Snake River or Madison–Firehole areas of Yellowstone or spend winter on Big Bend Ridge preying on moose and the few elk that winter there. For the BROAD model, we used 180 days (mid-May through mid-November) as days spent by elk on summer range and as days vulnerable to predation by wolves.

LOW, MODERATE, and HIGH kill rates by wolves on elk were again used (Table 5). Predation rates on Sand Creek elk for the YNP scenario were derived by assuming summer was 150 days, 90% of the diet by biomass were elk, and 85% of the elk were Sand Creek elk. The LOW scenario estimated that consumption was 290 kg of Sand Creeek elk per wolf (1.9 kg elk/wolf/day) with 3.2 Sand Creek elk killed per wolf during summer

Table 5. Distribution of estimated predation by wolves (*Canis lupus*) on Sand Creek elk (*Cervus elaphus*) and approximate biomass consumption, by age and sex, used in the YNP and BROAD scenario models. LOW, MODERATE, and HIGH kill rates are presented.

Scenario	Number of elk[a] killed/wolf				Mass of prey	Consumption[a] (kg/wolf)		
Sex and age	LOW	MODERATE	HIGH	Utilization	(kg)	LOW	MODERATE	HIGH
				YNP scenario (150 days)				
Female								
Calves	0.95	2.00	3.00	0.80	30	23	48	72
Yearling	0.13	0.27	0.20	0.75	240	23	49	36
2+ cows	0.52	1.08	0.80	0.75	240	94	194	144
Male								
Calves	0.95	2.00	3.00	0.80	30	23	48	72
Yearling	0.28	0.58	0.40	0.75	260	55	113	78
2+ bulls	0.37	0.77	0.60	0.75	260	72	150	117
Total	3.20	6.70	8.00	—	—	290	602	519
				BROAD scenario (180 days)				
Female								
Calves	1.25	2.60	3.50	0.80	30	30	62	84
Yearling	0.16	0.32	0.30	0.75	240	29	58	54
2+ cows	0.64	1.28	1.20	0.75	240	115	230	216
Male								
Calves	1.25	2.60	3.50	0.75	30	30	62	84
Yearling	0.46	0.92	0.75[a]	0.75	260	90	179	146
2+ bulls	0.44	0.88	0.75[a]	0.75	260	86	172	146
Total	4.20	8.60	10.00	—	—	380	763	730

[a] Includes 0.5 killed prehunt and 0.25 killed posthunt by wolves.

(Table 5). The MODERATE scenario consumption was estimated as 602 kg of Sand Creek elk per wolf (4.0 kg/wolf/day) with 6.7 Sand Creek elk killed per wolf. For the HIGH scenario, we estimated that eight Sand Creek elk may be killed per wolf (150 days vulnerable to predation/365 × 28 ungulates/wolf/year = 12 ungulates × 0.8 [proportion of ungulates killed are elk] = 10 elk × 0.85 [proportion of elk in southwest YNP that are Sand Creek elk] = 8 Sand Creek elk/wolf preyed on during summer). Consumption rate for the HIGH scenario was estimated at 4.8 kg/wolf/day of all prey types, or 3.5 kg of Sand Creek elk per wolf per day (Table 5). Biomass consumption in the HIGH scenario was lower than with the MODERATE scenario, although the number of elk killed was greater, because calf predation was proportionately greater and adult predation lower than in the MODERATE scenario.

The estimated consumption for the BROAD scenario at low predation was 180 days × 2.5 kg/wolf/day × 0.85 (diet consisting of elk) × 0.95 elk are Sand Creek elk = 363 kg elk, or 2.0 kg/wolf/day of Sand Creek elk. The kill rate for the LOW scenario was 4.2 elk/wolf (Table 5). MODERATE consumption was 763 kg, or 4.2 kg/wolf/day of Sand Creek elk (Table 5). The estimated kill rate for the MODERATE scenario was 8.6 elk/wolf. An estimated 10 elk killed/wolf was used for the HIGH model (180 days vulnerable to predation/365 × 28 ungulates/wolf/year = 14 ungulates × 0.7 [proportion of ungulates are elk (because more deer and moose occur outside of YNP)] = 10 elk/wolf). Consumption rate for the HIGH model was estimated at 5.6 kg/wolf/day of all prey types, or 4.1 kg/wolf/day of Sand Creek elk (Table 5).

Results

Gallatin Elk Populations

Details of the Gallatin elk herd population and harvest characteristics are in Appendix A. Average harvest from 1983 to 1985 was 436 elk. The Leslie matrix models indicated that a summer prehunt elk population of 2,500 was needed to sustain the observed average harvest. In the balance models, a winter population of 2,400 elk, or 3,100 elk prehunt, was necessary for a sustained harvest of 436 elk with no change in population size. Population estimates derived from both models were above those reported by Taylor (1982, 1983, 1984, 1985, 1986). Elk density during winter likely ranged from 3 to 4 elk/km^2.

Effects of Predation on the Gallatin Elk Herd, Leslie Matrix Projections

When no compensatory responses in survival were used and the harvest was not changed, the elk population declined with both high (90% of 28 = 25 elk/adult wolf/year) or low (75% of 12 = 9 elk/adult wolf/year) predation rates by 10 wolves (Table 6). When the antlerless elk harvest was reduced to half the current level (5% harvest rate of cows and calves available before the hunt), the elk population increased at low predation rates but declined at the higher level of predation. The population increased at either level of predation if only bulls were taken. When survival of all sex and age classes was increased 5%, the model population increased at low predation rates but declined at the higher rates (Table 6).

Effects of Predation on the Gallatin Elk Herd, Balance Model Projections

During 5 years with 10 wolves, the FIXED HARVEST models projected a decline in winter population size from 2,400 elk to 2,200 under LOW predation and from 2,400 to 2,000 elk at MODERATE predation. With 10 wolves, harvests declined from 436 to 390 at LOW predation and to 340 with MODERATE predation. Because these models were derived from average harvest and assumed stable populations, any additional mortality due to wolves

Table 6. Rates of increase of the Gallatin elk (*Cervus elaphus*) model population with different levels of wolf (*Canis lupus*) predation, harvest strategies, and survival rates.

Hunter harvest	Level of wolf predation[a]	Survival	Finite rate of increase of elk population
1983–86 level[b]	none	[c]	1.0001
	low	no change	0.9683
	high	no change	0.9086
50% of bulls	low	no change	1.0689
	high	no change	1.0055
Cows and calves 5%	low	no change	1.0193
	high	no change	0.9389
1983–86 level	low	up 5%	0.9936
	high	up 5%	0.9405
50% of bulls	low	up 5%	1.1080
	high	up 5%	1.0378
Cows and calves 5%	low	up 5%	1.0493
	high	up 5%	0.9897

[a] Wolf predation is specified to be exerted by 10 wolves. Low level of wolf predation specifies 9 elk killed; high level specifies 25 elk killed.
[b] Antlerless harvest = 10.5%; bull harvest = 50%.
[c] Survival rates: calves = 0.55; bulls = 0.90; and cows = 0.95.

caused population and harvest declines in the absence of management changes. The FIXED HARVEST models assumed no change in harvest rates, something managers can control as shown in the VARIABLE HARVEST models. The models also assumed predation rates would not decrease as elk population numbers declined because elk density would likely still be high enough to allow wolves to kill near maximum rates. Model output is detailed in Appendix B.

The VARIED HARVEST models for a spring precalving population of 2,400 projected that a narrow range of harvest could be obtained for a set number of wolves (Fig. 5). These models were for stable elk populations with constant wolf predation for 15 years. The range of harvest was due to examining many different harvest rate combinations for different sex and age classes. As wolf predation increased, harvest had to decrease to keep the population stable. Model stability was achieved by reducing cow harvest. Bulls then made up a larger percentage of the total harvest as wolf numbers increased (Fig. 6). Bulls averaged 55% of the total elk harvest between 1983 and 1985. For the Gallatin herd, the opportunity to offset harvest reductions from reduced cow harvest by increasing bull harvest was not presented because bulls were already being harvested near maximum rates without causing significant reductions in the bull/cow ratio.

The reduction needed in the antlerless (calf and cow) harvest rate to maintain a stable population in the presence of wolf predation at the LOW and MODERATE kill rate is shown in Fig. 7. For a given number of wolves,

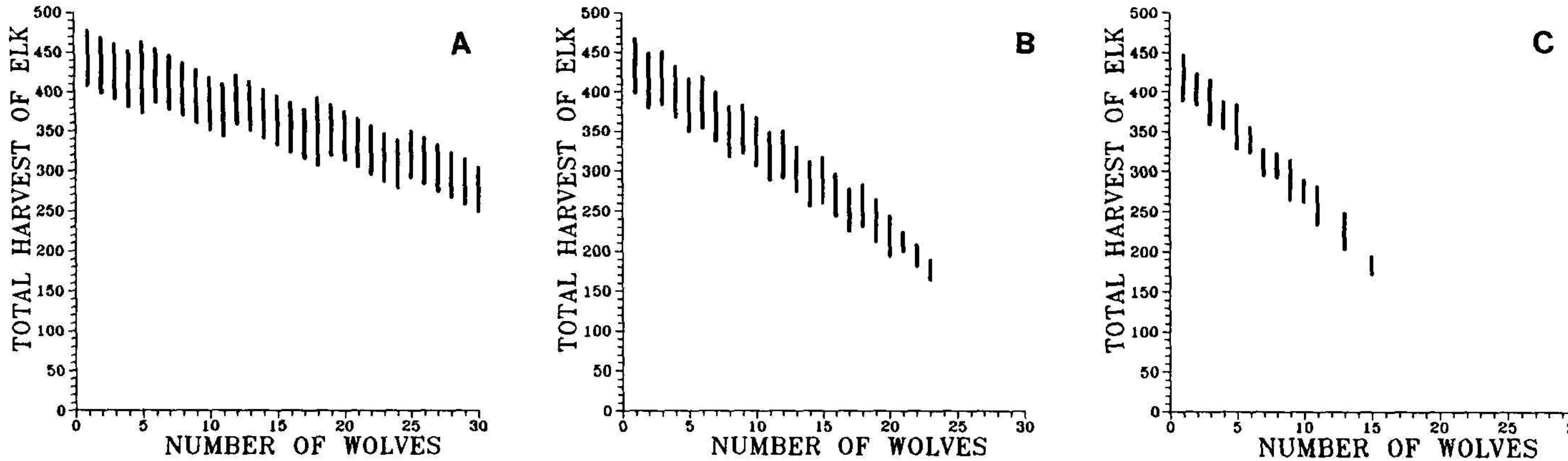


Fig. 5. Range in potential total hunter harvest of elk related to number of wolves for the LOW (*A*), MODERATE (*B*), and HIGH (*C*) kill rates evaluated for the Gallatin elk herd VARIED HARVEST model with a spring precalving population of 2,400 elk. Range in harvest results from evaluating many sex–age combinations of hunter harvest rates. Model results are for stable populations.

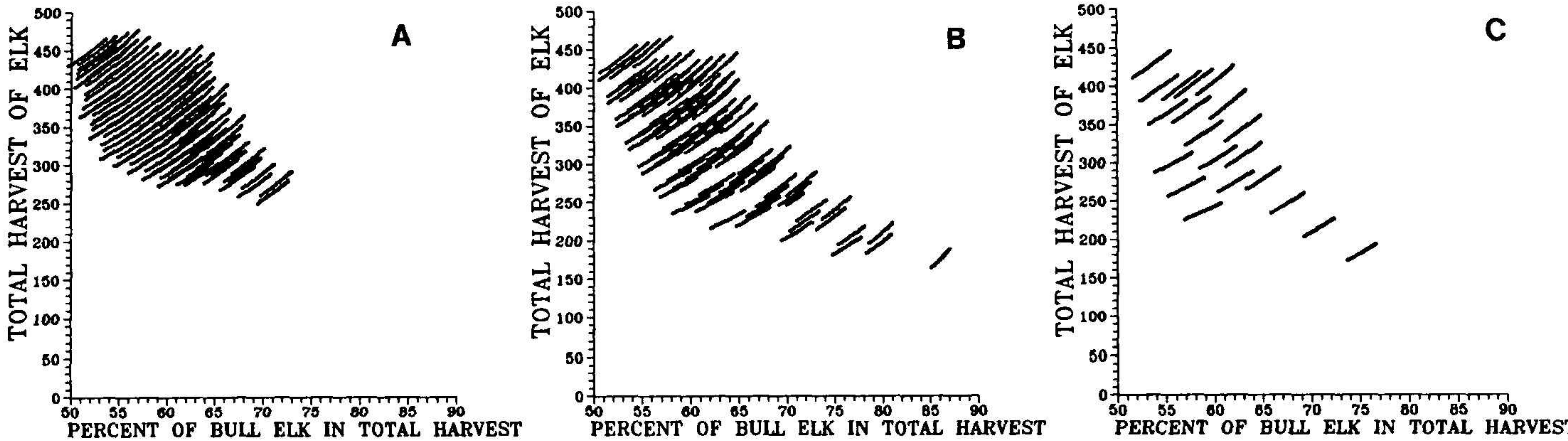


Fig. 6. Range in potential total hunter harvest of elk related to percent of bulls in total harvest for the LOW (*A*), MODERATE (*B*), and HIGH (*C*) kill rate scenarios evaluated for the Gallatin elk herd VARIED HARVEST model with a spring precalving population of 2,400. Ranges in total harvest relate to the range of wolves shown in Fig. 5.

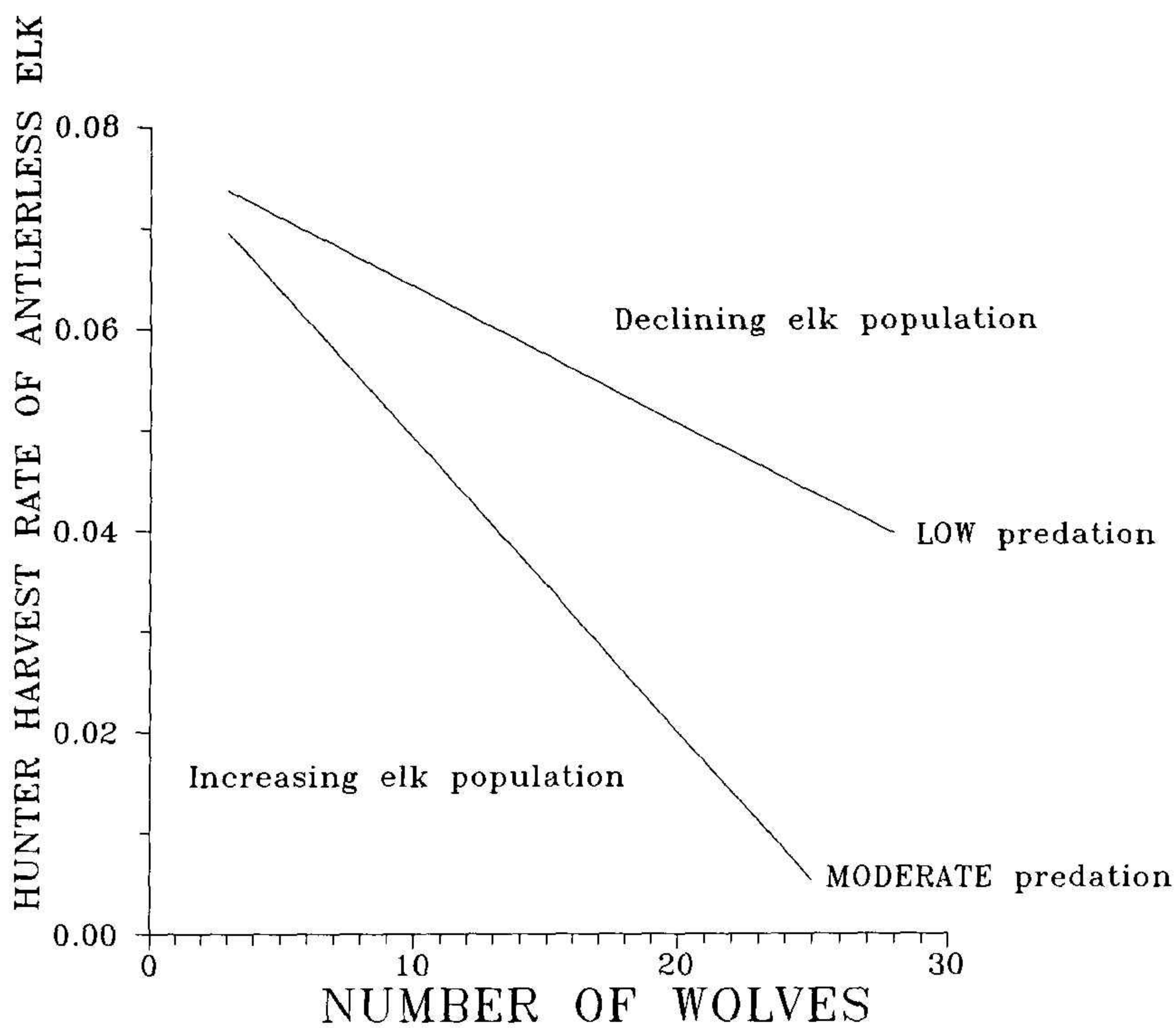


Fig. 7. Change in hunter harvest rate of antlerless elk needed to maintain a stable population at varying number of wolves for the LOW and MODERATE kill rates evaluated in the Gallatin elk herd model with a spring precalving population of 2,400 elk. Harvest rates below the MODERATE predation line result in increasing populations; harvest rates above the LOW predation line result in declining populations. Region of uncertainty exists between the two lines; harvest rate will be dependent on wolf response and predation rate on elk.

antlerless harvest rates below the MODERATE predation equilibrium line may allow elk to increase. Harvest rates above the LOW predation equilibrium line might cause a population decline. The area between the two lines is the range of predation (assuming elk were 85% of the wolf diet) that may occur, and the elk population will either increase or decrease depending on the intensity of predation, use of alternative prey, and antlerless elk harvest rate with survival and fecundity being constant. If cow elk were killed by wolves in proportion to their occurrence in the population rather than the lower estimated proportions used (Table 4), then cow harvest reductions greater than those projected in these models would be required and total harvest would be less than projected.

The VARIED HARVEST balance models with a spring precalving population of 2,400 elk projected that the average annual harvest could be between 350 and 460 elk, depending on the wolf kill rate; support 5 adult wolves (Fig. 5); and remain stable, assuming no change in elk survival or fecundity rates. With five wolves, antlerless elk harvest rates would be reduced to 6–7% of the prehunt cow and calf population (Fig. 7), and the bull harvest rate would be near 50% of the prehunt bull population.

Sand Creek Elk Populations

Details of the Sand Creek elk herd population and harvest characteristics are in Appendix C. No trend was detected in the estimated Sand Creek total harvest between 1980 and 1987 ($P > 0.10$) or in winter population size during 1981–89 ($P > 0.10$). Excluding an unusually high harvest in 1988, total harvest averaged 958 elk. The balance models projected that a winter population of 4,300 elk—or 5,700 prehunt—was necessary for a sustained harvest of 958 elk with no change in population size. For the Leslie matrix models, a summer prehunt population of 5,373 elk was used. Both population estimates were above those reported by DeShon (1982), Parker et al. (1982, 1983, 1986), Trent et al. (1984, 1986), Brown (1985), and Chu et al. (1987, 1988, 1989). Elk density in summer was generally greater than 0.7/km^2 (Table 1). For the YNP scenario, we calculated that an average of 219 elk was harvested from a prehunt subpopulation of 1,555 (1,175 in winter). For the BROAD scenario, harvest averaged 738 elk from a prehunt subpopulation of 4,330 (3,241 in winter).

Projections of the Effects of Predation on the Sand Creek Elk Herd—YNP Scenario Using Balance Models

During 5 years with 10 wolves, the FIXED HARVEST YNP models projected a decline in winter population size from 1,175 elk to 1,060 under LOW predation and 930 elk at MODERATE predation. With 10 wolves, harvest declined from 219 to 200 at LOW predation and 175 with MODERATE predation. The additional mortality due to wolf predation caused population and harvest declines because the models started with stable populations. Detailed model output is in Appendix B.

The VARIED HARVEST models (stable elk populations experiencing constant wolf predation for 15 years using constant survival, fecundity, and predation rates) projected that a range of harvests could be obtained for a set number of wolves (Fig. 8). Elk harvests greater than the estimated average of 219 were obtained in the presence of wolf predation by reducing cow harvest and increasing the percent of total harvest obtained from bulls (Fig. 9). Our population analysis of the YNP portion of the Sand Creek herd indicated that bull/cow ratios were higher than for the entire herd, and that cow survival rates (excluding hunter harvest) were very high. These analyses suggested that cows migrating from Yellowstone National Park were being intensively harvested, but that bulls migrating from the park were not as heavily harvested as other portions of the Sand Creek population. The reduction in antlerless (cow and calf) harvest required to maintain a stable herd over a range of wolf numbers for LOW and MODERATE kill rates are shown in Fig. 10.

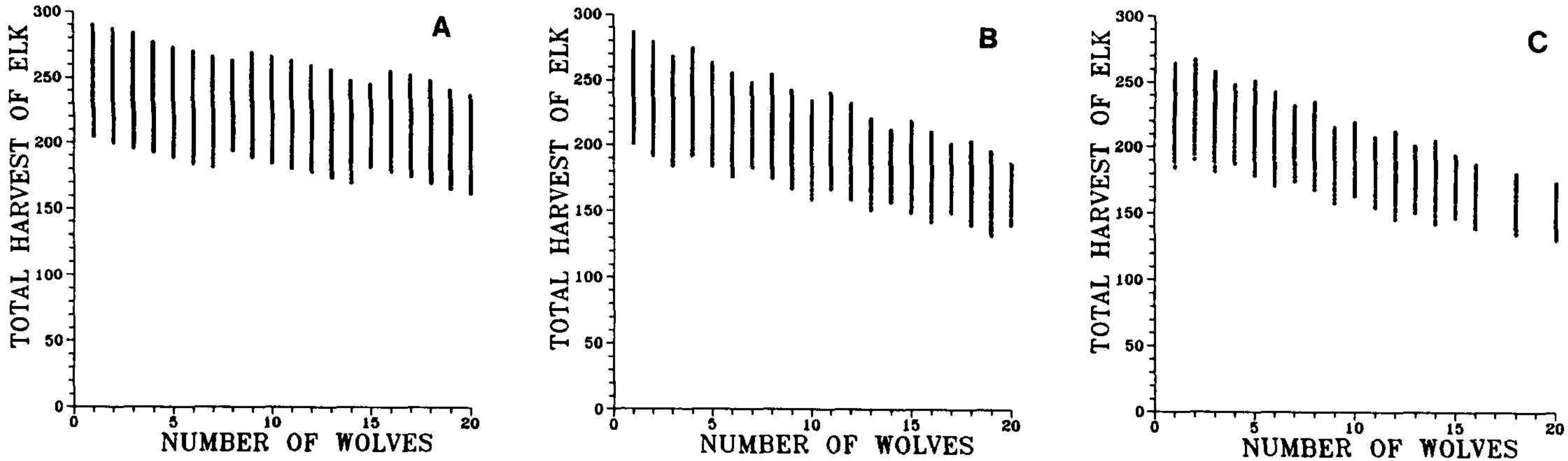


Fig. 8. Range in potential total hunter harvest of elk related to number of wolves for the LOW (*A*), MODERATE (*B*), and HIGH (*C*) kill rates evaluated for the Sand Creek YNP scenario VARIED HARVEST models. Range in total harvest results from evaluating many sex–age combinations of hunter harvest rates. Model results are for stable populations.

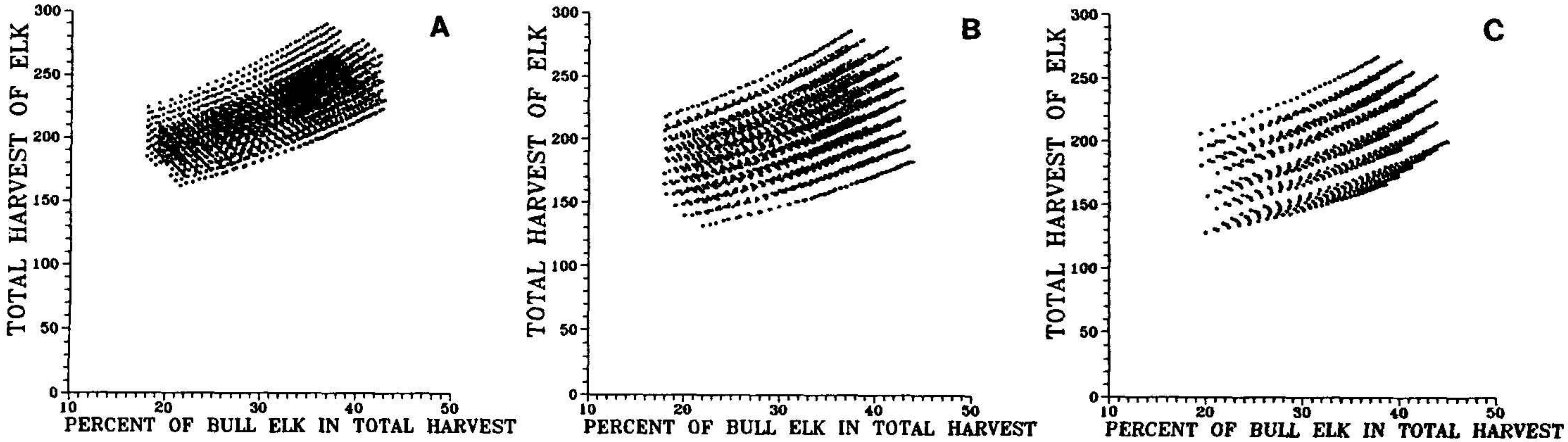


Fig. 9. Range in potential total hunter harvest of elk related to percent of bulls in total harvest for the LOW (*A*), MODERATE (*B*), and HIGH (*C*) kill rate scenarios evaluated for the Sand Creek YNP scenario VARIED HARVEST models. Ranges in total harvest relate to the range of wolves shown in Fig. 8.

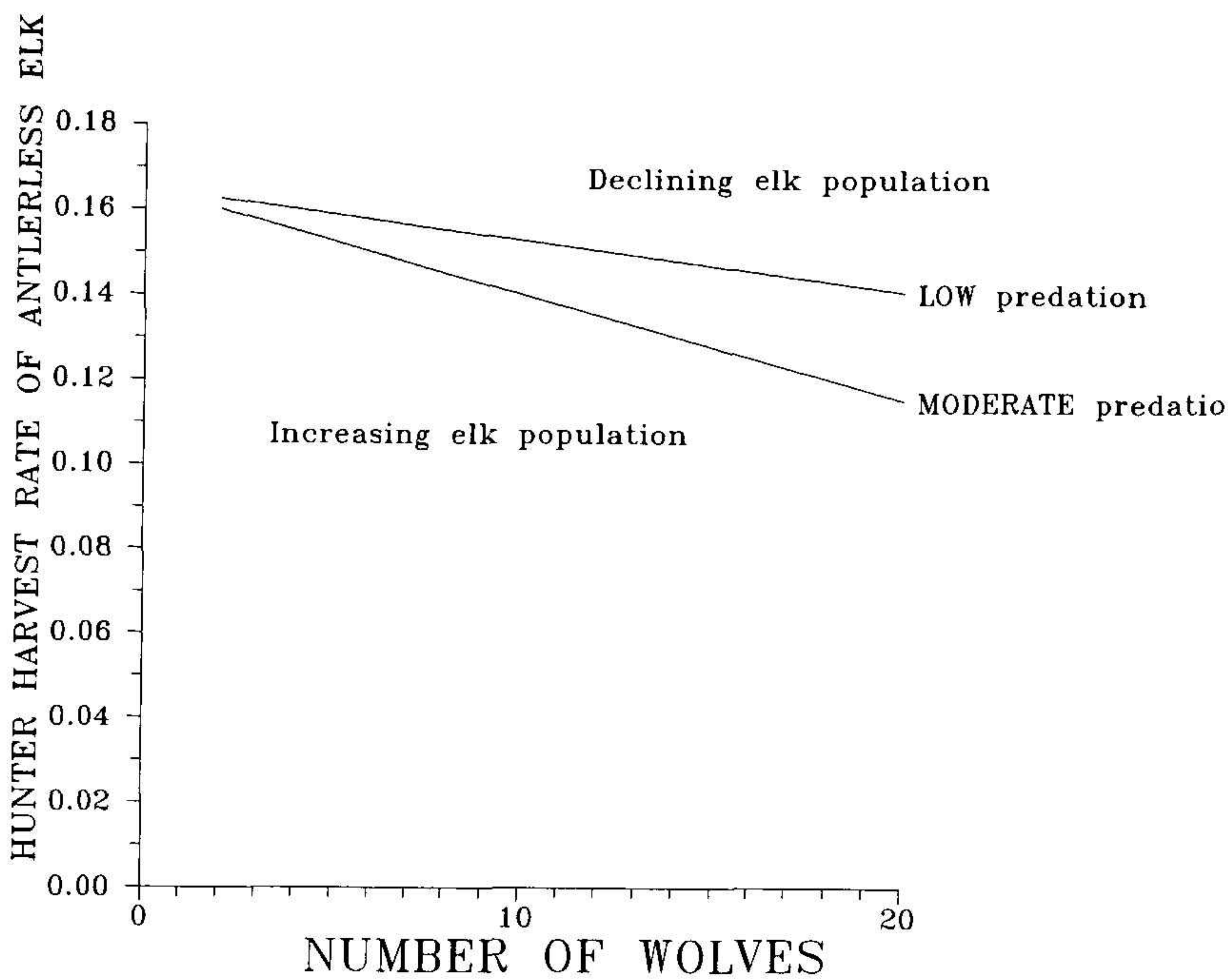


Fig. 10. Change in hunter harvest rate of antlerless elk needed to maintain a stable population at varying number of wolves for the LOW and MODERATE kill rates evaluated in the Sand Creek YNP scenario. Harvest rates below the MODERATE predation line result in increasing populations; harvest rates above the LOW predation line result in declining populations. Region of uncertainty exists between the two lines; harvest rate will be dependent on wolf response and predation rate on elk.

The YNP scenario VARIED HARVEST balance models projected that, with 10 adult wolves preying on elk only during summer, the Yellowstone portion of the Sand Creek herd (1,555 elk in late summer) could be stable and could support an average annual harvest of between 170 and 270 elk (Fig. 8), if fecundity and mortality from sources other than hunting and wolf predation did not change. Harvest of antlerless elk must be between 14 and 16% of the prehunt cow and calf population, while bull harvest could be more than 30% of the prehunt bull population.

Projections of the Effects of Predation on the Sand Creek Elk Herd—BROAD Scenario Using Balance Models

During 5 years with 10 wolves, the FIXED HARVEST BROAD models projected a decline in winter population size from 3,241 elk to 3,120 under LOW predation rates and to 2,975 elk at MODERATE predation. With 10 wolves, harvest would decline from 738 to 700 at LOW predation and to 660 with MODERATE predation. Detailed model output is in Appendix B.

The VARIED HARVEST balance models showed a proportionately narrower range of possible harvest for a given level of wolf predation than the YNP scenario (Fig. 11). The narrower range resulted from the Sand Creek herd already producing maximum bull harvest with little opportunity to increase or maintain harvest by increasing overall bull harvest rate. As the number of wolves increased, the cow harvest rate that was needed to maintain a stable population decreased, and thus total harvest declined. In this scenario, highest harvests were reached by maximizing the cow contribution to the total harvest. As bulls contributed a larger fraction of the total harvest, harvest declined (Fig. 12) because nearly all bulls were harvested. High total harvest was obtained by slightly increasing the cow fraction of the total harvest, but hunting pressure should be on cows other than those migrating from Yellowstone. Management options, such as manipulating hunter harvest, provide few opportunities to support a substantial wolf population at the current level of hunter harvest in the BROAD scenario. The implication is that a modest reduction in the Sand Creek harvest will be necessary if wolves are present.

The BROAD scenario balance models projected that this portion of the Sand Creek herd (4,354 elk in late summer) could be stable; support an average annual hunter harvest between 640 and 770 elk (Fig. 11), depending on intensity of predation; and support 10 adult wolves over 180 days if elk survival and fecundity rates remained constant.

Entire Herd Using Leslie Matrix Models

Leslie matrix projections were run only on the entire Sand Creek herd year-round. When the hunter harvest was set to 975 elk, the population dropped with either high (90% of 28) or low (75% of 12) predation and with either 10 or 20 wolves present (Table 7). However, when hunter harvest was constrained to only bulls, the population increased in the presence of up to 30 wolves (Table 7). These model results project that if wolves were kept below 30, some antlerless harvest on the entire population could be allowed, assuming that predation was distributed throughout the entire Sand Creek herd summer range.

Discussion

We concluded that both elk herds from which the harvest was derived were larger than reported by state agencies. Our population analyses assumed that hunter harvest was more accurately estimated than population size, and we based our population estimates on the number of elk that could support the estimated average harvest. We acknowledge that wintering populations may be accurately estimated by state agencies and may be less than what our models suggested. Prehunt populations may be composed of several herds that winter in different areas, yet contribute to the reported harvest.

The Leslie matrix and balance models were basically similar, although the balance models were used to examine a variety of hunter harvest re-

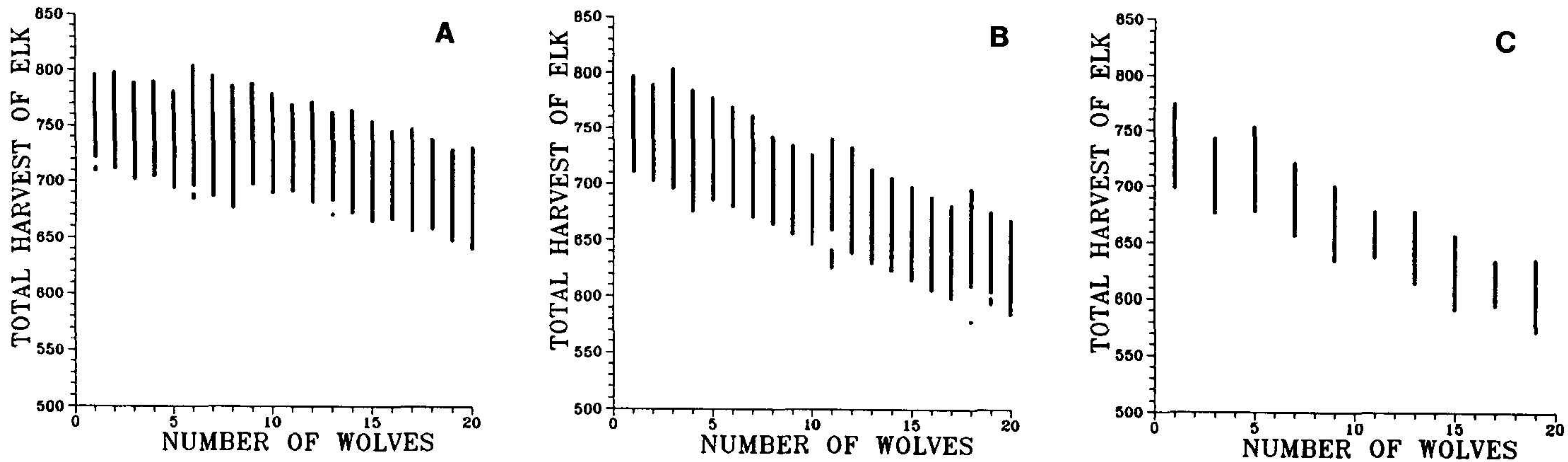


Fig. 11. Range in potential total hunter harvest of elk related to number of wolves for the LOW (*A*), MODERATE (*B*), and HIGH (*C*) kill rates evaluated for the Sand Creek BROAD scenario VARIED HARVEST models. Range in total harvest results from evaluating many sex–age combinations of hunter harvest rates. Model results are for stable populations.

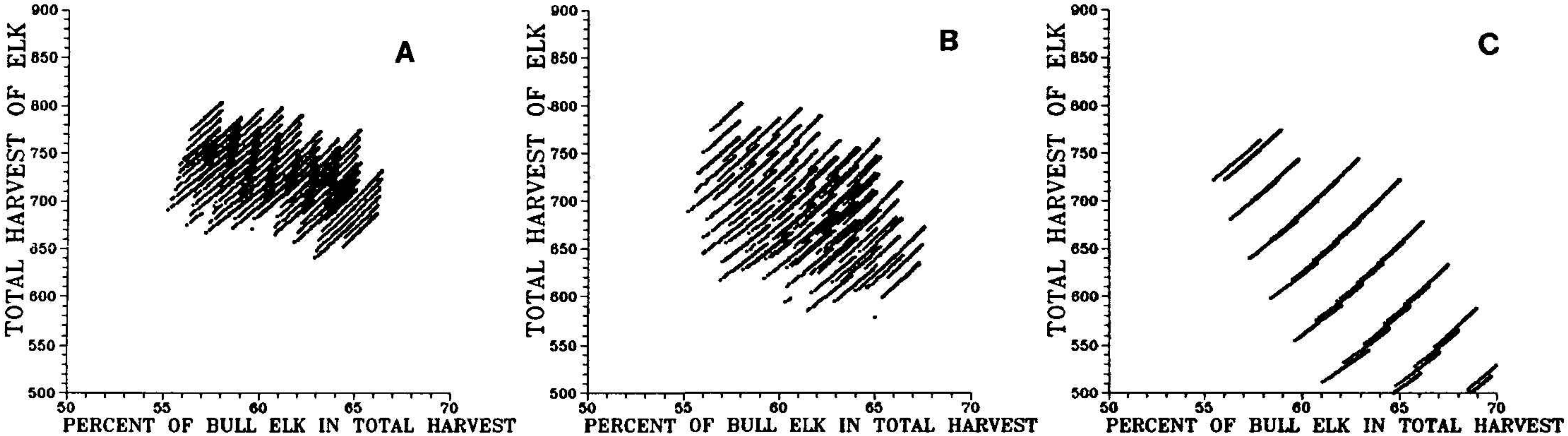


Fig. 12. Range in potential total hunter harvest of elk related to percent of bulls in total harvest for the LOW (*A*), MODERATE (*B*), and HIGH (*C*) kill rate scenarios evaluated for the Sand Creek BROAD scenario VARIED HARVEST models. Ranges in total harvest relate to the range of wolves shown in Fig. 11.

Table 7. Rates of increase of the Sand Creek elk (*Cervus elaphus*) model population with different levels of wolf (*Canis lupus*) predation, with and without antlerless harvest.

Hunter harvest	Number of wolves	Level of wolf predation[a]	Finite rate of increase of elk population
1980–87 level[b]	none	none	1.0005
	10	low	0.9873
	10	high	0.9808
	20	low	0.9641
	20	high	0.9567
No antlerless	20	low	1.0812
	20	high	1.0728
	30	low	1.0611
	30	high	1.0476

[a] Low level of wolf predation specifies 9 elk killed; high level specifies 25 elk killed. Predation is modeled as if occurring on the entire Sand Creek herd year-round.
[b] Average was 975 elk.

gimes. Output differences between the models were due more to differences in elk survival and fecundity used in the models, estimating the number of elk killed by wolves, and partitioning predation among sex–age classes rather than to structural differences of the models.

Our models projected that reduced harvest of both the Gallatin and Sand Creek elk herds would be needed in the presence of wolves if no population increase, compensatory response in diminished mortality from other causes, or increased elk survival was to occur. The reduction in harvest would be less than our estimates if wolf predation rates were lower than what we used in the models. Compensatory (density-dependent) responses—such as increased calf survival or increased yearling elk fecundity—would result in greater production, yielding more elk for harvest or supporting more wolves. However, compensatory responses may not occur in either the Gallatin or Sand Creek herds because they both have been heavily harvested and were probably near maximum productivity. As we suggested for the Rocky Mountain east-front winter ranges east of Glacier National Park, Montana (Peek and Vales 1989), it is especially critical to investigate compensatory responses in the prey populations when wolves begin to exert significant predation.

We acknowledge that predation may be density dependent, but we used constant predation rates for our models in part because functional response equation coefficients are unknown. Our use of a range of predation rates and wolf numbers likely compensates for the unknown functional response asymptote as well as a range of potential density-dependent predation rates. Management objectives for both herds were for stable populations that minimize grazing effects on the winter ranges. Without a change in elk population size, and assuming constant distribution over time, wolves should not exhibit a functional response because prey numbers would not change. A change in herd age or sex structure, however, could alter our predictions of the proportions of each age and sex killed by wolves. Elk density was generally greater than 2/km^2 over much of the summer range, which may be high enough for wolves to be at the asymptote of the functional response curve allowing for maximum density-independent predation rates.

If wolf numbers increase and drive elk densities down to a point where predation rates become density dependent, the change in elk population, or calf/cow ratio, will be obvious, and managers will rapidly respond with wolf control or reduced hunter harvest. With no management changes, wolf numbers might decline naturally if elk decline and alternate prey was not available. If alternate prey supported a large wolf population after an elk decline, then the elk population could be held at a low equilibrium by wolves. But, if wolves left or died out, elk might rebound if harvest was low and weather were favorable. Drought-induced mortality or winterkill may be additive to wolf predation to result in steeper population declines or lower harvests than we projected in our models. Mild weather, good forage conditions, or use of alternate prey by wolves, however, would buffer the effects of wolf predation and reduce our projected effects on elk.

Both the Gallatin and Sand Creek elk herds have special hunts to keep the populations within predetermined limits. The purpose of the special hunts are to manage population sizes, and wolf predation could substitute for some of the removal attributed to special hunts and help keep populations at desired levels. The harvest reductions we project with wolves may be of similar magnitude to those required to keep populations stable once population sizes are reduced to levels desired by the state agencies.

Our investigations indicated that more information on actual population size, survival rates, and sex and age composition of these populations will be needed when wolves are restored to Yellowstone. With wolves present, intensive monitoring of both predator and prey will be needed to quickly respond with management actions to keep hunter harvest and populations at desired levels. Our modeling efforts are considered qualitative rather than strictly quantitative because of the many unknowns involved. In evaluating our models, the assumptions of the models and weaknesses in the data base must be considered. However, the main conclusion is similar to what we reported for the elk populations along the Rocky Mountain east-front east of Glacier National Park (Peek and Vales 1989) and Van Ballenberghe and Dart (1982) reported for moose in central Alaska: For elk populations that are essentially regulated by hunting, hunter harvest will likely be confined to males most of the time when wolves are present.

Acknowledgments

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Appendix A. Characteristics and Population Analyses of the Gallatin Elk Population.

The acceptable carrying capacity of the winter range was 1,400–1,600 elk during 1978–85 (Taylor 1982, 1983, 1984, 1985, 1986). This number was predicted to allow plant conditions on the winter ranges to improve. Population estimates before the hunting season ranged from 1,746 to 2,269 animals (average 2,070) for 1978–85 (Table 8). The population increased slightly from 1979 to 1985, concomitant with a decrease in the cow/calf ratio. The observed percentage of adult bulls in this population changed from 10% in 1978–79 to 20% in 1980–82 to 15% in 1983–86, suggesting that the age and sex distribution of males is fluctuating and the population is not stable.

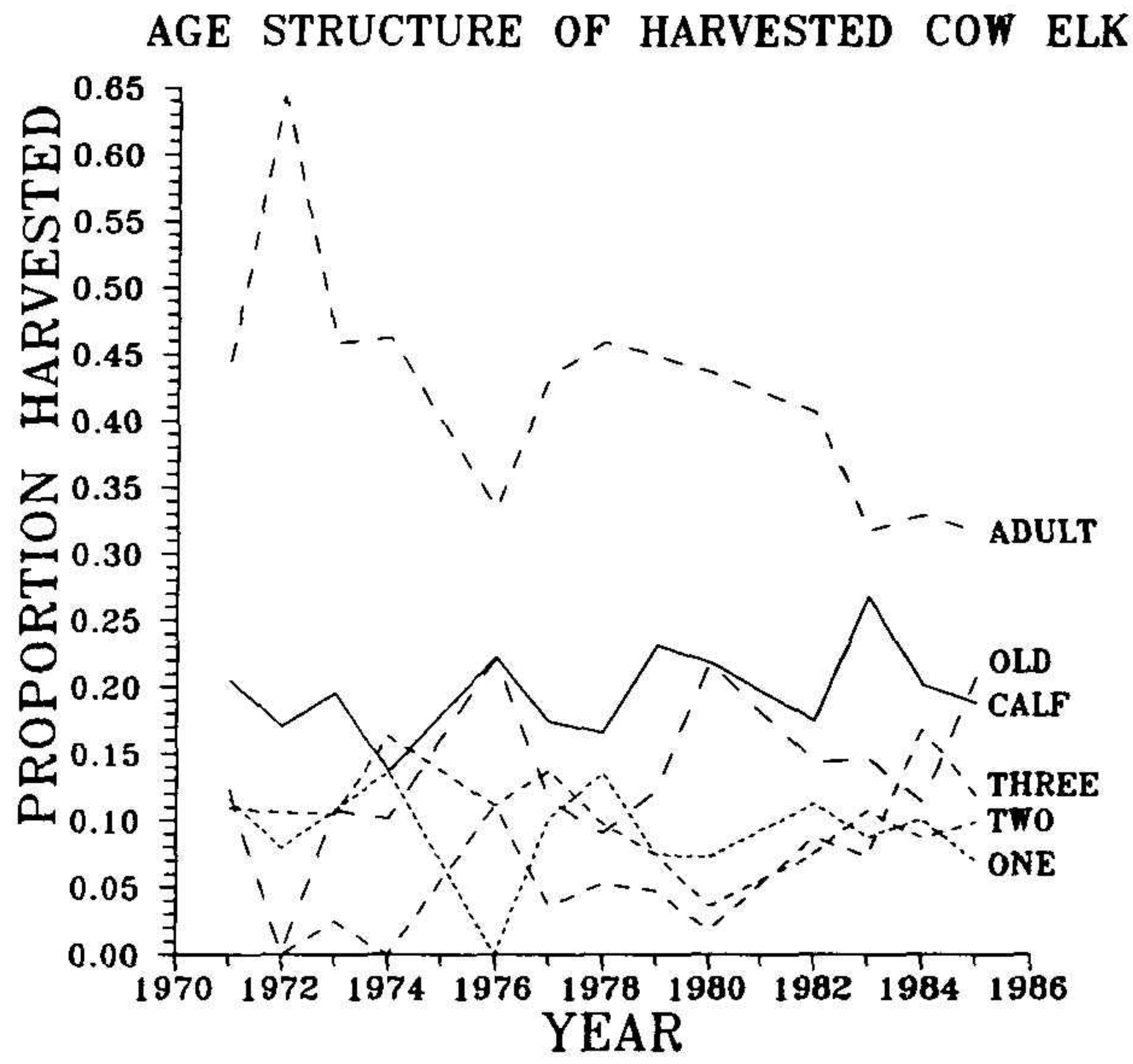
Resident, nonmigratory elk were mostly harvested during the general hunting season. An average of 190 animals (range 77–320) was harvested annually from the nonmigratory population between 1978 and 1985 (Table 8). From 1983 to 1985, the general harvest averaged 214 elk, including an antlerless hunt set by drawing permits. The migratory population is typically not subject to significant hunter harvest until after the general October to November season ends. Special late season hunts based on drawings are used to maintain the population at desired levels. A harvest quota is established each year based on the previous winter survey and estimates of mortality and recruitment (Table 8). Typically, 1,200–1,750 permits for either sex are issued for hunts beginning in mid-December and lasting through late January. Harvests from 1978 to 1985 averaged 246 elk. The 1983–85 average was 221, giving a 1983–85 average combined harvest of 436 elk, which we used in our models. A decline in adult bulls resulted in changing the traditional either-sex permit hunt to one emphasizing antlerless harvest in 1984.

Regression analyses of proportion of age classes in the late season harvests were used to assess possible trends in age structure of the harvest for 1971–84 (Fig. 13). We found no trends in the proportion of old, adult, 3-year-old, 2-year-old, or yearling bulls or cows related to size of the harvest. However, bulls older than 3 years and adult cows have declined in numbers over the 14 years (Fig. 13). Three-year-old bulls, 3-year-old cows, and old cows apparently increased. The decline in the age structure of bulls and the increase in age of cows may explain the observed decline in sex ratio (Table 8). These analyses indicated that the population has been undergoing internal adjustments in age structure of both sexes if the check station information reflects population trends. We used

Table 8. Determination of late season harvest quota for the Gallatin elk (*Cervus elaphus*) herd (Taylor 1982, 1983, 1984, 1985, 1986).

	Year							
	1978	1979	1980	1981	1982	1983	1984	1985
Winter survey								
Gallatin	1,043	808	1,245	1,142	1,450	1,150	1,125	1,200
Madison	672	481	474	540	430	918	400	1,097
Total counted	1,715	1,289	1,719	1,682	1,880	2,068	1,525	2,297
– YNP residents	100	50	150	200	430	500	—	500
– winter road kill	100	53	70	50	25	60	—	60
– bulls[a]	152[b]	237[b]	300[b]	286[b]	285[b]	241	229	260
+ calf crop	750	560	588	585	445	494	583	532
+ bulls	152	237	300	286	286	241	229	260
– carrying capacity of winter range	1,400	1,400	1,400	1,400	1,400	1,400	1,600	1,600
Total	865	346	687	617	471	602	508	669
Quota	850	350	600	600	—	600	500	675
Summer calf/cow ratio	55	59	49	51	39	39	45	36
Prehunting season population estimate	2,265	1,746	2,087	2,017	—	2,002	2,108	2,269
Elk removals								
General hunt	77	107	150	225	320	192	135	315
Late season hunt	248	263	134	361	296	317	211	136
Illegal kill	21	—	10	25	20	20	30	20
Winter kill	3	12	30	250	30	30	50	25
Road kill	19	7	20	40	30	30	25	30
Total removals	368	389	344	901	696	589	451	526

[a] 1978–79 10% bulls; 1980–82 20% bulls; 1983–85 15% bulls.
[b] Calculated, not listed in state progress report.



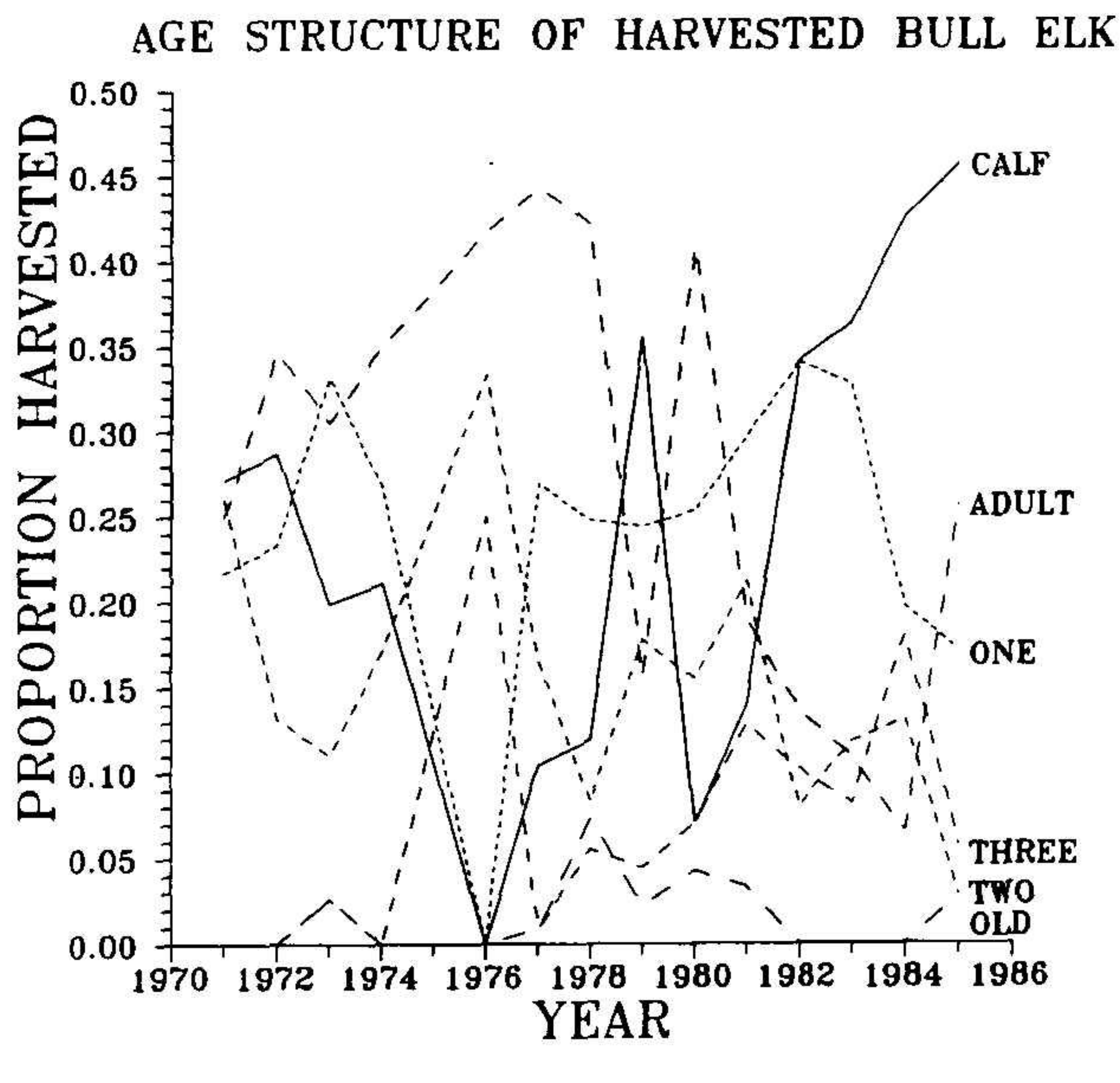


Fig. 13. Trends over time in the age structure of harvested bull and cow elk for the Gallatin herd.

the 1983–84, 1984–85, and 1985–86 age structures from the general and late season hunts (Table 9) to calculate survival rates and population composition. This provided a sample of 1,110 ages from the 3 most recent years of information we had available.

Population Analysis of the Gallatin Herd—Leslie Matrix Projections

The Leslie matrix model indicated that a summer prehunt population size of 2,500 was necessary to maintain the observed harvest and the observed sex and age composition of the herd. Fecundity rates for production of one calf each year were 50% of yearling females, 98% of adults aged 2–5, and 96% of older adults. We considered these rates to be high. A harvest of 439 elk was obtained from the model population, including 212 1-year-old-and-older bulls, 78 calves, and 148 1-year-old-and-older cows. This harvest represented 50% of the bull and 13.5% of the cow and calf summer prehunt population. The actual population was obviously not stable because the estimated population varied (Table 8). Comparison of

Table 9. Estimation of fall age structures from hunter harvests for the Gallatin elk (*Cervus elaphus*) herd with population adjusted to 2,498 (resident and migratory segments included).

	Check station 1983–85[a]		Regression (smoothed)		Adjusted to 2,498[b]	
Age	Male	Female	Male	Female	Male	Female[c]
0.5	84	108	0	0	484	484
1.5	239	46	204	80	234	230
2.5	94	48	127	65	105	187
3.5	58	57	79	53	47	155
4.5	0	0	49	43	21	127
5.5	0	0	30	35	10	103
6.5 (adult)	(132)[d]	(160)	19	28	4	84
7.5	0	0	12	23	2	73
8.5	0	0	7	18	1	63
9.5 (old)	(11)	(73)	5	15	1	46
10.5	0	0	0	12	0	29
11.5	0	0	0	10	0	9
12.5	0	0	0	8	0	0
Total	618	492	532	390	909	1,590

[a] From Taylor (1984, 1985, 1986).
[b] Based on sex ratio of 21 bulls/100 cows and 51 calves/100 cows.
[c] Results of Leslie matrix model using mean harvest, sex, and age structures from 1983, 1984, and 1985.
[d] Check station classified as adult (4–7) or old (7+).

the model and the checked age structure suggested that different proportions of the various sex and age classes became available for harvest for the early and late seasons from this population from year to year. Migration patterns change for the migratory segment and local hunting conditions affect the vulnerability of the nonmigratory segment.

Population Analysis of the Gallatin Herd—Balance Model Projections

Models were developed for 3 stable late-winter (spring precalving) populations of 1,600, 1,800, and 2,400 elk with a stable harvest of 436. Bull survival rates (0.98) and prehunt calf/cow ratios (52/100) were extraordinarily high for the population of 1,600 elk (for estimated winter range carrying capacity, see Table 8), suggesting that the herd from which the harvest was derived was probably larger than 1,600. A larger population would allow cow/calf ratios to drop to near the observed summer ratio of 100/40 (Table 8). The model with a stable precalving population of 1,800 elk (the size estimated from field observations) also had a higher calf/cow ratio (51/100) than estimated from the field. Bull survival rates of 0.93 were more acceptable, though the adult fecundity rate of 0.98 was high (Table 10). The summer prehunt population was 2,413, similar to that obtained for the Leslie matrix model. The model using a spring precalving population of 2,400 elk had what we considered acceptable bull survival rates (0.85) and late-summer calf/cow ratios (Table 10). We used the model population of 2,400 (Table 11) to simulate predation effects with the balance models because it represented what we considered the most realistic estimate of composition and survival.

Table 10. Gallatin elk (*Cervus elaphus*) herd population characteristics for a stable winter population of 18,000.

Characteristic	Spring precalving[a]	Summer postcalving[b]	Summer prehunt[c]	Fall posthunt[d]
Population				
Female calves	253	455	332	298
Yearling cows	211	253	245	229
2+ cows	875	1,086	1,053	939
Male calves	253	455	332	298
Yearling bulls	122	253	248	126
2+ bulls	85	207	203	87
Total	1,799	2,709	2,413	1,977
Composition				
Bulls/100 cows	19	34	35	18
Calves/100 cows	47	68	51	51
Yearling cows/100 2+ cows	24	23	23	27
Yearling bulls/100 2+ bulls	144	122	122	145
Fecundity rates				
Yearling cows	0.25			
2+ cows	0.98			

Survival rates	Summer	Winter	Annual (winter × summer)
Female calves	0.73	0.86	0.63
Yearling cows	0.97	0.92	0.89
2+ cows	0.97	0.93	0.90
Male calves	0.73	0.86	0.63
Yearling bulls	0.98	0.95	0.93
2+ bulls	0.98	0.95	0.93

Harvest[e]	Number	Harvest rate
Female calves	34	34/332 = 0.102
Yearling cows	16	16/245 = 0.065
2+ cows	114	114/1,053 = 0.108
Male calves	34	34/332 = 0.102
Yearling bulls	122	122/248 = 0.492
2+ bulls	116	116/203 = 0.571
Total	436	

[a] Spring precalving is late winter before birthdays and after winter mortality.
[b] Summer postcalving is after birthdays, after births, but before summer mortality.
[c] Summer prehunt is before hunter harvest and after summer mortality.
[d] Fall posthunt is after fall harvest but before winter mortality.
[e] Harvest of 436 is stable and constant from observed 1983–86 average.

Table 11. Gallatin elk (*Cervus elaphus*) herd population characteristics for a stable winter population of 2,400.

Characteristic	Spring precalving[a]	Summer postcalving[b]	Summer prehunt[c]	Fall posthunt[d]
Population				
Female calves	294	608	395	61
Yearling cows	251	294	285	269
2+ cows	1,245	1,496	1,451	1,337
Male calves	294	608	395	361
Yearling bulls	147	294	282	160
2+ bulls	177	324	311	195
Total	2,408	3,624	3,119	2,683
Composition				
Bulls/100 cow	22	35	34	22
Calves/100 cow	39	68	46	45
Yearling cows/100 2+ cow	20	20	20	20
Yearling bulls/100 2+ bull	83	91	91	82
Fecundity rates				
Yearling cow	0.23			
2+ cows	0.93			

Survival rates	Summer	Winter	Annual (winter × summer)
Female calves	0.65	0.83	0.54
Yearling cows	0.97	0.93	0.90
2+ cows	0.97	0.93	0.90
Male calves	0.65	0.83	0.54
Yearling bulls	0.96	0.88	0.85
2+ bulls	0.96	0.88	0.85

Harvest[e]	Number	Harvest rate
Female calves	34	34/395 = 0.086
Yearling cows	16	16/285 = 0.056
2+ cows	114	114/1,451 = 0.079
Male calves	34	34/395 = 0.086
Yearling bulls	122	122/282 = 0.433
2+ bulls	116	116/311 = 0.373
Total	436	No data

[a] Spring precalving is late winter before birthdays and after winter mortality.
[b] Summer postcalving is after birthdays, after births but before summer mortality.
[c] Summer prehunt is before hunter harvest and after summer mortality.
[d] Fall posthunt is after fall harvest but before winter mortality.
[e] Harvest of 436 is stable and constant from observed 1983–86 average.

Appendix B. Details of the FIXED HARVEST Models.

Details of the FIXED HARVEST models are shown for the Gallatin (Fig. 14), YNP (Fig. 15), and BROAD (Fig. 16) scenarios at LOW and MODERATE predation rates.

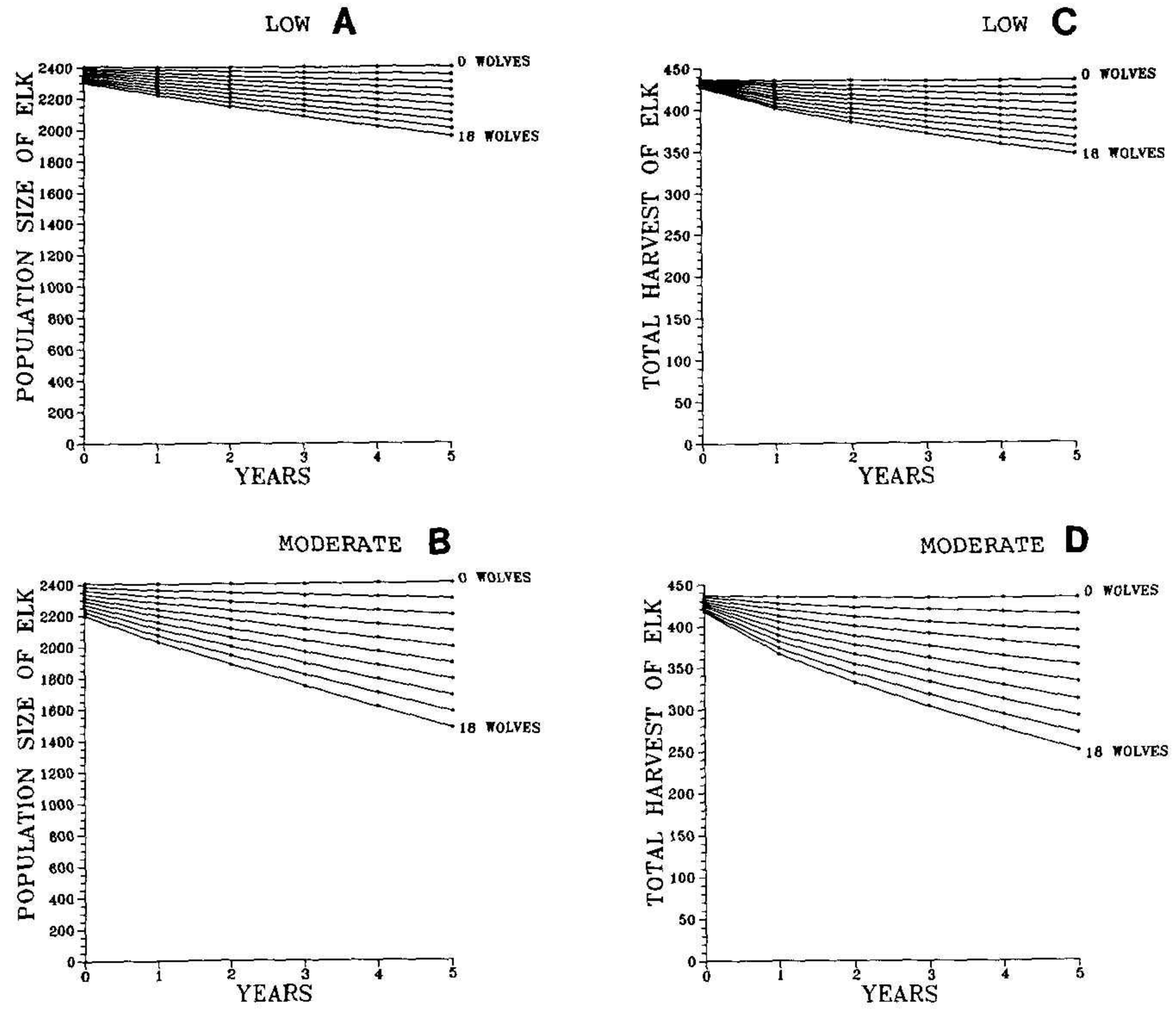


Fig. 14. Potential initial 5-year wolf restoration effects on the Gallatin elk population size (*A*, *B*) and total hunter harvest (*C*, *D*) for the FIXED HARVEST models. Model elk population initially at 2,400 in spring, precalving. Models assume no changes in elk management or in wolf numbers, distribution, or behavior. Low (*A*, *C*) and moderate (*B*, *D*) wolf kill rates are presented.

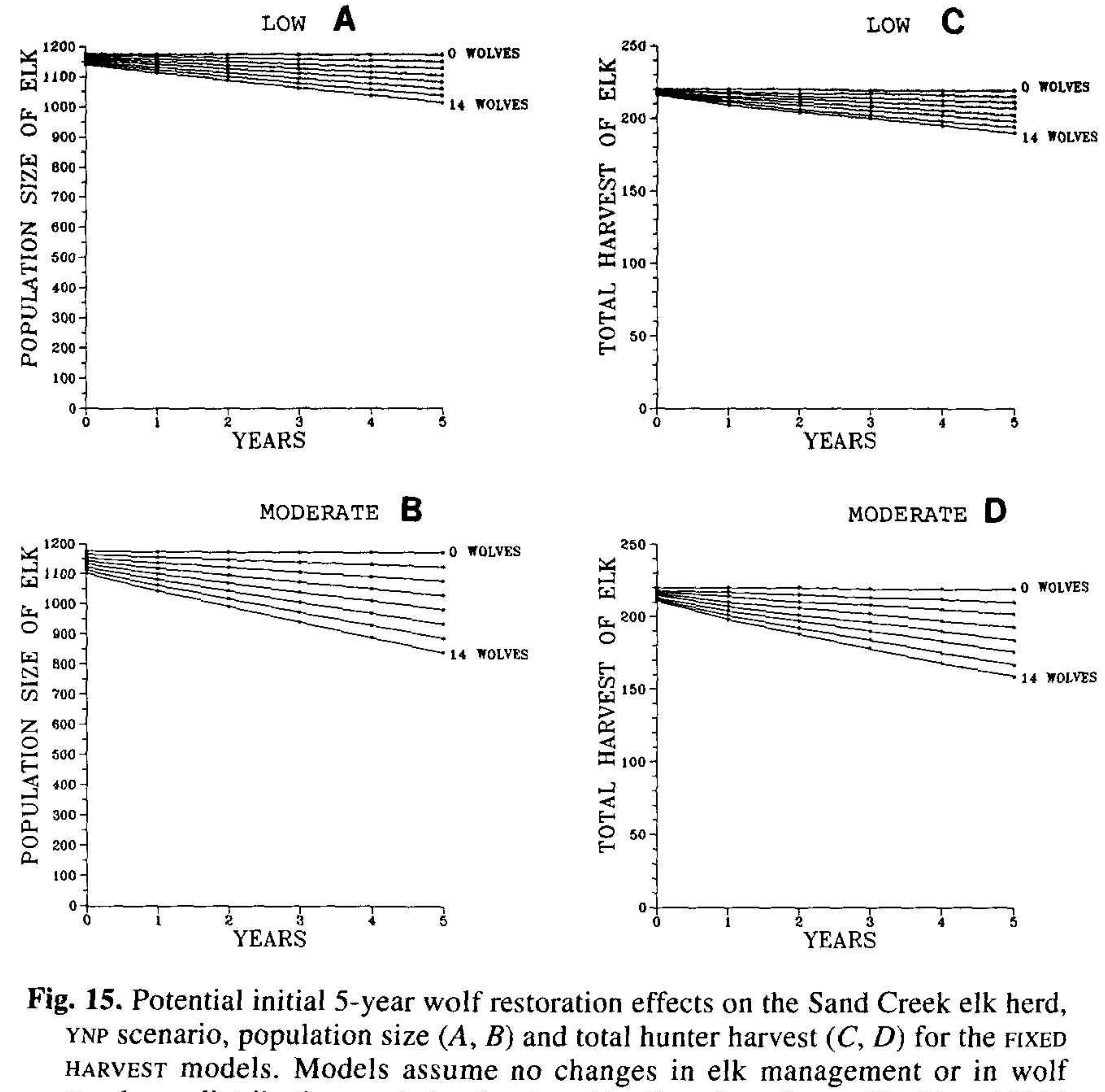


Fig. 15. Potential initial 5-year wolf restoration effects on the Sand Creek elk herd, YNP scenario, population size (*A*, *B*) and total hunter harvest (*C*, *D*) for the FIXED HARVEST models. Models assume no changes in elk management or in wolf numbers, distribution, or behavior. low (*A*, *C*) and moderate (*B*, *D*) wolf kill rates are presented.

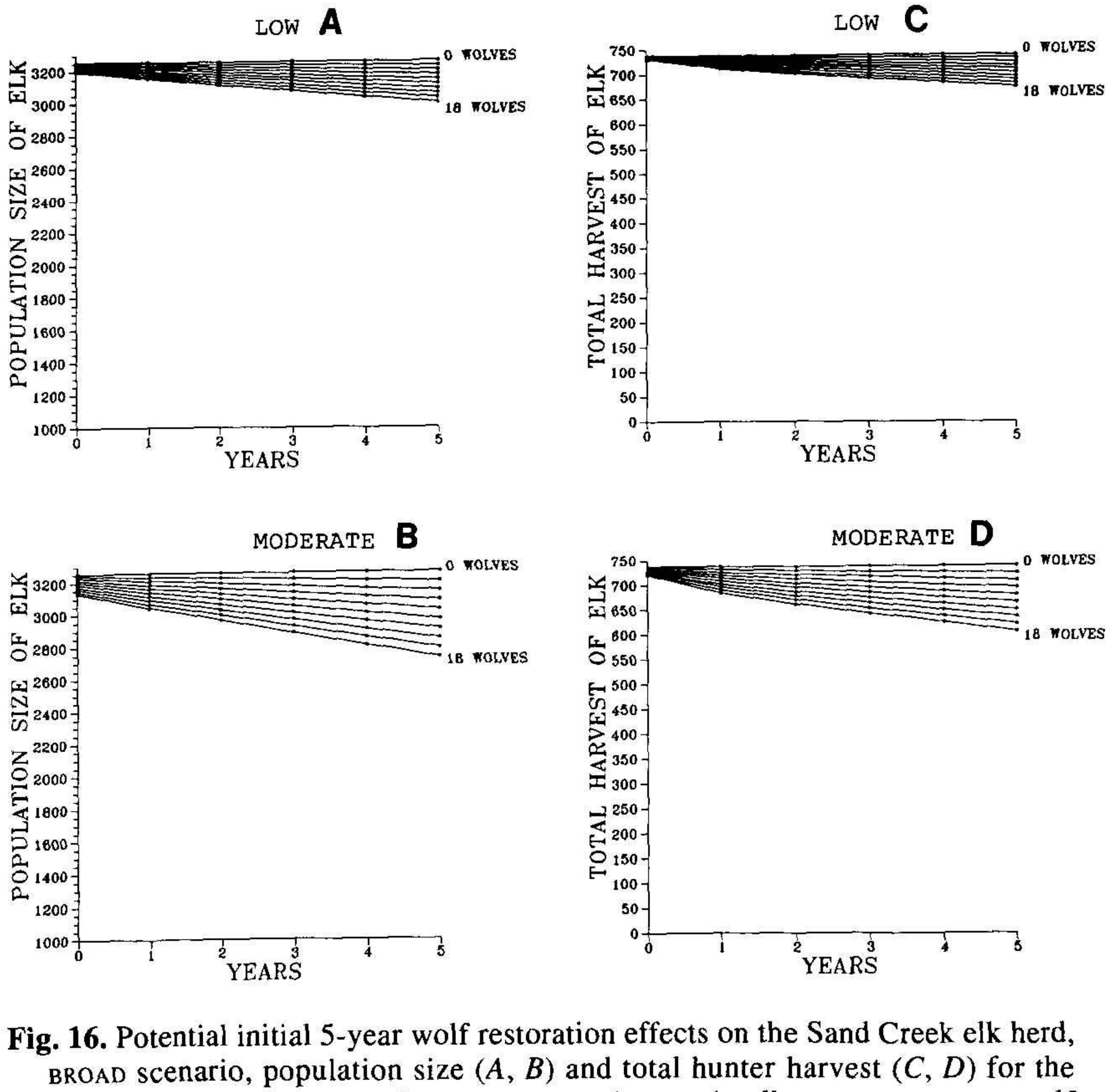


Fig. 16. Potential initial 5-year wolf restoration effects on the Sand Creek elk herd, BROAD scenario, population size (*A*, *B*) and total hunter harvest (*C*, *D*) for the FIXED HARVEST models. Models assume no changes in elk management, or wolf numbers, distribution, or behavior. Low (*A*, *C*) and MODERATE (*B*, *D*) wolf kill rates are presented.

Appendix C. Characteristics of the Sand Creek Elk Population.

Winter population counts for the Sand Creek elk herd increased between 1959 and 1983, with oscillations in numbers counted since 1983 around 2,500 elk (Table 12). There was no significant trend in population size between 1981 and 1989 ($P = 0.27$). Naderman (Idaho Department of Fish and Game, Idaho Falls, personal communication) estimated that the counts reflected about 80% of the entire Sand Creek herd, giving an average of 3,125 elk in the herd during winter. Brown (1985) estimated the summer prehunt population of the Sand Creek herd to be 4,900 animals in 1983, after the 1982–83 winter trend count of 2,959 animals. The 5-

Table 12. Population characteristics of the Sand Creek, Idaho, elk (*Cervus elaphus*) herd in winter.

Year	Winter trend count[a]	Bulls: Yearling	Bulls: Branch antlered	Bulls: **Total**	Anterless	Calves/ 100 cows[b]	Bulls/ 100 cows[c]	Yearlings/ 100 branch-antlered bulls
1988–89	(2,441 minimum estimate)	—	—	—	—	not done	—	—
1987–88	2,815	117	231	348	2,469	54	33	67[d], 51[e]
Big Bend	74	5	3	8	66	—	—	—
1986–87	not done	—	—	—	—	46	20	108[d]
1985–86	2,269	84	119	203	2,066	60	19	100[d], 71[e]
1984–85	2,553	—	—	291	2,262	44	18	181[d]
1983–84	1,803	(April)	—	—	—	53[f]	20	82
(Brown)[g]	2,287	(January)	—	241	2,046	57	19	—
1982–83	2,959	148	157	305	2,654	65	18	96[d], 95[e]
(Brown)[g]	—	—	—	—	—	56	18	—
1981–82	2,327	136	201	337	1,990	50[h]	25[i]	68
1980–81	2,310	135	169	304	2,006	50[h]	23[i]	80
Average	2,502	—	—	—	—	54	22	86

[a] From yearly aerial count on Sand Creek winter range (management units 60 and 60A). Counts usually done in January.
[b] From ground herd composition counts usually done in December.
[c] From ground herd composition count.
[d] Yearling bulls/100 adult bulls from herd composition count.
[e] Yearling bulls/100 adult bulls calculated from trend count.
[f] Calculated from approximate distribution of elk on winter range.
[g] Survey reported in Brown 1985.
[h] Assumed ratio (Parker et al. 1983:274).
[i] Calculated from assumed calf/cow ratios.

year elk management plan (Toweill et al. 1985) specified that a summer population of 4,750 elk be maintained to produce a harvest of 935 animals.

Herd composition counts were done from the ground by the Idaho Department of Fish and Game on the winter range, usually in December. Average bull/cow/calf composition between 1980 and 1987 was 22/100/54 (Table 12). Yearling bull/2.5-year-old-and-older bull ratios averaged 86/100, excluding the 1984–85 classification of 181/100. Specific age data for the population were obtained during the 1980–82 hunting seasons (Table 13), but none since. The present age structure is probably younger than it was in 1980–82 (Naderman, personal communication). Additional age data included herd composition counts (Table 12) and the ages of harvested bulls (Table 14). We initially assumed that the Sand Creek herd in late winter (spring precalving) was composed of 22 bulls/100 cows/54 calves, with 20% of the females being yearlings and 46% of the bulls being yearlings (Table 12).

Table 13. Age structure of Sand Creek, Idaho, male and female elk (*Cervus elaphus*) harvested 1980–1982 from management units 60, 61, 62, and 62A (Parker et al. 1983).

	Percentage in each age class									
	1980–82 Unit 60		1980–82 Unit 61		1981–82 Unit 62		1981–82 Unit 62A		1980–82 Combined	
Age	Male	Female	Male	Female	Male	Female	Male	Female	Male[a]	Female[b]
1.5	63	23	39	21	35	25	41	22	49	22
2.5	24	19	32	26	27	25	32	18	28	21
3.5	7	16	14	13	16	25	7	15	10	16
4.5	3	10	8	8	1	0	8	18	5	9
5.5	1	9	3	12	5	10	5	4	3	10
6.5	1	4	2	2	5	10	1	0	1	3
7.5	1	4	2	3	5	0	1	0	1	3
8.5	0	5	0	7	2	0	1	7	1	5
9.5	1	1	0	3	1	0	3	4	1	2
10.5	1	3	1	1	0	5	0	0	1	2
11.5	0	2	0	1	1	0	0	0	1	2
12.5	0	2	0	1	0	0	0	4	0	2
13.5	0	1	0	1	0	0	0	0	0	1
14.5	0	1	0	0	0	0	0	0	0	1
15.5	0	0	0	0	0	0	0	0	0	1
16.5	0	0	0	0	0	0	0	0	0	0
17.5	0	1	0	0	0	0	0	0	0	1
Sample size	350	210	252	126	87	20	147	27	836	383

[a] Calculated survival rate of males 2.5 and older = 0.523.
[b] Calculated survival rate of females 2.5 and older = 0.733.

Table 14. Yearling bull elk (*Cervus elaphus*) harvest as a percent of total bull harvest for general hunts of the Sand Creek, Idaho, herd.

	Management unit				
Year	60	61	62	62A	**Total**
1988	68	39	33	37	51
1987	64	38	15	41	47
1986	70	42	28	38	59
1985	54	18	22	50	43
1984	60	29	10	33	45
1983	69	45	63	67	61
1982	76	36	32	41	52
1981	50	42	33	39	44
1980	65	39	63	48	51
Average	64	36	33	44	50

Excluding the high elk harvest in 1988, harvest between 1980 and 1987 averaged 958 animals (Table 15). There were no significant trends in general, controlled, or total harvest over time. However, excluding 1983 data, harvest from 1979 to 1988 was linearly related to the count the previous winter (general harvest $r^2 = 0.99$, $P < 0.01$; controlled harvest $r^2 = 0.50$, $P = 0.11$; and total harvest $r^2 = 0.97$, $P < 0.01$). Because no trend in harvest was seen over time, we used the average harvest of 958 elk between 1980 and 1987 in our models and assumed that 50% of the bull harvest was yearlings (Table 14), 25% of the cow harvest was yearlings (Table 13), and 6% of the antlerless harvest was calves in an equal sex ratio. Resident elk were usually harvested during general seasons unless snows forced elk to migrate early. Controlled hunts were designed to regulate elk populations, prevent depredations, and reduce the effect elk have on their winter range.

Population Analysis of the Sand Creek Elk Herd

Balance Model Projections of the Entire Herd

We modeled the Sand Creek elk winter population size (2,502 average count/0.8 proportion of herd counted = 3,125), composition (22 bulls/100 cows/54 calves), and harvest to reflect averages from DeShon (1982), Parker et al. (1982, 1983, 1986), Trent et al. (1984, 1986), and Chu et al. (1987, 1988, 1989) in Tables 12–15. If the average estimated harvest between 1980 and 1987 (to exclude the 1988 high) of 958 animals from all hunts is deducted each year, the bull/cow ratio immediately drops to near zero and the number of adult bulls (bulls 2 years and older are known as branch-antlered bulls) drops below zero after 2 seasons.

Table 15. Sand Creek elk (*Cervus elaphus*) herd harvest characteristics by unit, hunt, and sex derived from telephone survey (DeShon 1982; Parker et al. 1982, 1983, 1986; Trent et al. 1984, 1986; Chu et al. 1987, 1988, 1989).

	Hunt Unit																			
	60				61				62				62A				Total (Includes 63A)			Other documented mortality (archery and muzzleloader hunts included)
	GH[a]	CH			GH	CH			GH	CH			GH	CH						
Year	M	M	F	T	M	M	F	T	M	M	F	T	M	M	F	T	M	F	T	
1988	253	43	288	584	309	0	0	309	80	102	54	236	45	56	181	282	921	537	1,458	—
1987	191	0	137	328	250	0	0	250	42	27	43	112	25	27	150	202	563	331	894	28
1986	262	3	180	445	211	0	0	211	62	40	34	136	32	46	94	172	656	308	964	39
1985	246	24	159	429	239	7	13	259	68	20	10	98	67	32	109	208	707	292	999	56
1984	193	0	38	231	134	0	39	173	77	48	39	164	26	29	62	117	507	178	685	61
1983	174	22	190	386	156	17	86	259	39	24	68	131	0	39	78	117	483	427	910	112
1982	192	17	90	299	259	6	117	382	67	59	65	191	67	31	66	164	699	338	1,037	—
1981	283	44	256	583	157	14	178	349	31	48	37	116	63	58	57	178	698	528	1,226	—
1980	284	18	154	456	185	8	37	230	62	8	16	86	82	51	57	190	698	264	962	—
Average	231	19	166	416	211	6	52	269	59	42	41	141	45	41	95	181	659	356	1,015	59

[a] GH = general hunt; CH = controlled hunt; M = males; F = antlerless and may include calves; T = total.

The harvest and population estimates do not relate well, so the following suggestions are offered:

1. Population estimates were too low.
2. Herd composition counts (bull/cow or calf/cow ratios) were inaccurate due to underestimates of bulls. Models with a population of 3,100 animals and various spring precalving ratios as high as 50 bulls/100 cows/ 70 calves still did not support the estimated average harvest.
3. Estimate of harvest is incorrect. Estimated harvest confidence intervals for 1987 and 1988 were broad (±325 in 1987 and ±387 in 1988; Nelson 1988, 1989).
4. Elk harvested in Idaho may have come from Montana because there have been elk tagged in Montana and killed in Idaho. The Wall Creek game range in Montana winters approximately 2,000 elk (in 1987), some of which may summer in Idaho. We do not know what proportion of the Sand Creek elk harvest came from animals that wintered in Montana. Some Idaho elk moved to Montana (Brown 1985) or were killed in Montana (Naderman, personal communication), and we thus assumed that immigration equaled emigration for our models.
5. Not all elk that contribute to the harvest spend winters on the Sand Creek winter range. Elk may winter in other areas (e.g., Jackson, Teton River, Fall River, Big Bend Ridge) and make the entire population that is hunted larger than that counted on the Sand Creek winter range. An estimated additional 800–1,000 elk summer in the area of the Sand Creek herd but do not winter on the Sand Creek winter range (Naderman, personal communication).

Because our initial model population of 3,125 elk did not support a harvest of 958, we then iteratively ran balance models until a population size was found that supported a continuous harvest of 958 elk and had a composition similar to field estimates. The resulting model population had to be at least 4,300 animals in spring before calving (using the survival and fecundity rates in Table 16) to approximate the observed winter herd composition. Spring precalving herd composition was 27 bulls/100 cows/ 57 calves. Of the summer prehunt population (Table 16), the harvest rate of calves was 1%, yearling cows 12%, adult cows 10%, yearling bulls 48%, and adult bulls 50%. Although our model population was larger than that estimated on the Sand Creek winter range, the entire population that contributed to the harvest may be closer to our estimates.

Leslie Matrix Projections of the Entire Herd

The Leslie matrix model was run until we obtained the minimum population that would sustain a hunter harvest of 975 elk of approximate composition represented in the harvest. The summer prehunt model population was stable at 5,373 elk, with 39 bulls/100 cows and 77 calves/100 cows. Approximately 46% of the bulls and 14% of the cows and calves were harvested from this model population (20 calves, 297 yearling bulls, 352 adult bulls, and 307 adult cows). Approximately 46% of the modeled bull harvest was yearlings.

Table 16. Sand Creek elk (*Cervus elaphus*) herd model population characteristics. Entire herd modeled for stability.

Characteristic	Spring precalving[a]	Summer postcalving[b]	Summer prehunt[c]	Fall posthunt[d]
Population				
Female calves	661	959	767	757
Yearling cows	507	661	641	563
2+ cows	1,824	2,331	2,261	2,026
Male calves	661	959	767	757
Yearling bulls	328	661	654	342
2+ bulls	308	636	630	317
Total	4,289	6,207	5,720	4,762
Composition				
Bulls/100 cows	27	43	44	26
Calves/100 cows	57	64	53	59
Yearling cow/100 2+ cow	28	28	28	28
Yearling bull/100 2+ bull	106	104	104	108
Fecundity rates				
Yearling cows	0.33			
2+ cows	0.96			

Survival rates	Summer	Winter	Annual (winter × summer)
Female calves	0.80	0.88	0.70
Yearling cows	0.97	0.89	0.86
2+ cows	0.97	0.90	0.87
Male calves	0.80	0.88	0.70
Yearling bulls	0.99	0.96	0.95
2+ bulls	0.99	0.97	0.96

Harvest	Number	Harvest rate
Female calves	10	10/767 = 0.013
Yearling cows	78	78/641 = 0.122
2+ cows	235	235/2,261 = 0.104
Male calves	10	10/767 = 0.013
Yearling bulls	312	312/654 = 0.477
2+ bulls	313	313/630 = 0.497
Total	958	

[a] Spring precalving is late winter before birthdays and after winter mortality.
[b] Summer postcalving is after birthdays and births but before summer mortality.
[c] Summer prehunt is before hunter harvest and after summer mortality.
[d] Fall posthunt is after fall harvest but before winter mortality.

Balance Model Projections of the YNP *Scenario*

The proportion of elk summering in Yellowstone National Park was estimated from collared animal studies of Brown (1985) and Chu et al. (1987, 1988, 1989). Percentages of collared cow elk in the Yellowstone Plateau and Bechler summer subpopulations were 7.7 and 11.5%, respectively (Table 1), or 19.2% total (Brown 1985:95). Brown (1985) produced a variety of estimates of cow elk summering in and adjacent to Yellowstone ranging from 16 to 29% of the entire Sand Creek herd. Between 26 and 40% of radio-collared bull elk summered in Yellowstone, with another 5% in management units adjacent to the park (Trent et al. 1986; Chu et al. 1987, 1988). About 50% of the collared bulls older than 2 years summered in Yellowstone (Chu et al. 1987, 1988, 1989). We assumed that 27% of the Sand Creek herd (1,555 elk) summered within Yellowstone Park for the YNP scenario models.

We assumed that the harvest from the Idaho Department of Fish and Game controlled hunt in management unit 62A (hunt 262A) was entirely composed of Yellowstone National Park elk, and we added 40% of the average harvest from controlled hunts in management units 60 and 62 (hunts 260 and 262). Early migration out of Yellowstone or late-rut movements would result in some bull harvest in the general hunt, but this is less predictable than with the controlled hunts. Total harvest from animals that summer in Yellowstone was estimated at 219 elk (from Table 15: 1980–87 average controlled hunt harvest management unit 62A = 123 + 40% of 167 management unit 60 = 67 + 40% of 73 from management unit 62 = 29 = 219), of which 16 were calves (equal sex ratio), 24 were yearling bulls, 35 were 2-year-old-and-older bulls, 36 were yearling cows, and 108 were 2-year-old-and-older cows. We assumed that 10% of the antlerless harvest were calves. A 25% yearling cow (Table 13) and a 40% yearling bull (Table 14) composition of the cow and bull harvest was used.

We attempted to model the YNP scenario population using composition, survival, and fecundity rates derived for the entire Sand Creek herd. Our models could not support the intense cow harvest on the migrants from Yellowstone National Park, so different survival and fecundity rates were needed. Calf and cow survival rates used for the YNP scenario were higher (0.73 and 0.96), and bull survival rate lower (0.71) than for the entire herd (Table 17). Higher bull/cow and calf/cow ratios were used than for the entire herd, but the yearling bull/adult bull ratio was lower (Table 17). The proportion of older bulls is probably greater in Yellowstone than for the herd average (Chu et al. 1987, 1988). Our estimated low bull survival probably includes some harvest of bulls during the general season outside Yellowstone that we did not explicitly model. The harvest of calves was possibly higher than our estimated 10% composition of total antlerless harvest, but no supporting data were available. If it was higher, cow survival rates could be lower than those we used in the model. Additionally, if more than 27% of the entire herd summers in Yellowstone National Park or if the herd is larger than 4,300 elk in winter, cow survival rates could be lower. Our estimated population size was the minimum number of elk that could support both the average controlled hunt harvest from management unit 62A and 40% of the average controlled hunt harvest from management units 60 and 62 and remain stable.

Table 17. Sand Creek elk (*Cervus elaphus*) herd population characteristics: YNP scenario with 27% of entire herd modeled for stability.

Characteristic	Spring precalving[a]	Summer postcalving[b]	Summer prehunt[c]	Fall posthunt[d]
Population				
Female calves	169	246	206	198
Yearling cows	129	169	167	131
2+ cows	482	611	605	497
Male calves	169	246	206	198
Yearling bulls	98	169	159	135
2+ bulls	128	226	212	177
Total	1,175	1,667	1,555	1,336
Composition				
Bulls/100 cows	37	51	48	50
Calves/100 cows	55	63	53	63
Yearling cow/100 2+ cow	27	28	28	26
Yearling bull/100 2+ bull	77	75	75	76
Fecundity rates				
Yearling cows	0.26			
2+ cows	0.95			

Survival rates	Summer	Winter	Annual (winter × summer)
Female calves	0.84	0.86	0.72
Yearling cows	0.99	0.97	0.96
2+ cows	0.99	0.97	0.96
Male calves	0.84	0.86	0.72
Yearling bulls	0.94	0.72	0.68
2+ bulls	0.94	0.72	0.68

Harvest	Number	Harvest rate
Female calves	8	8/206 = 0.039
Yearling cows	36	36/167 = 0.217
2+ cows	108	108/605 = 0.179
Male calves	8	8/206 = 0.039
Yearling bulls	24	24/159 = 0.151
2+ bulls	35	35/212 = 0.165
Total	219	

[a] Spring precalving is late winter before birthdays and after winter mortality.
[b] Summer postcalving is after birthdays, after births, but before summer mortality.
[c] Summer prehunt is before hunter harvest and after summer mortality.
[d] Fall posthunt is after fall harvest but before winter mortality.

Our summer prehunt population estimate for the Sand Creek herd in southwestern Yellowstone National Park was 1,555. Using Brown's (1985) data, Singer (1988) estimated that 1,056 Sand Creek, 300 northern range, and 70 Madison–Firehole elk were in the Bechler area of the park during summer. To avoid overestimating the potential effects of wolves on Sand Creek elk, we assumed that wolves would kill elk proportionately, and we used Singer's (1988) estimates of northern and Madison herds that summer in southwestern Yellowstone to partition the wolf kill [1,555/(1,555 Sand Creek + 300 northern + 70 Madison–Firehole) = 0.81 portion of elk killed by wolves are Sand Creek elk]. For the YNP scenario models, we estimated that 80% of the elk killed by wolves would be Sand Creek elk (20% northern range and Madison–Firehole).

Balance Model Projections of the BROAD Scenario

The BROAD population model assumed wolves may occupy a broader area, including areas used by the Bechler, Yellowstone Plateau, Caldera, Two Top, Chick Creek, Ashton Hill, and Harriman summer elk subpopulations (Fig. 2). About 75% of the Sand Creek herd (Table 1), or roughly 4,290 elk (0.75 × 5,720), summer in these areas. We estimated that the harvest for the BROAD scenario came from (1) entire harvests from the general and controlled hunts in management units 62 and 62A; (2) 39% of the elk in management unit 61 (because that proportion summered east of Highway 20; Brown 1985); and (3) an estimated 90% of the general hunt and 80% of the controlled hunt from the management unit 60 harvest. This resulted in a total average harvest of 738 elk, of which 14 were calves (equal sex ratio), 63 yearling cows, 189 adult cows, 236 yearling bulls, and 236 adult bulls. Our model population (Table 18) had composition and survival rates similar to the entire Sand Creek herd (Table 16).

Table 18. Sand Creek elk (*Cervus elaphus*) herd population characteristics: BROAD scenario with 76% of entire herd modeled for stability.

Characteristic	Spring precalving[a]	Summer postcalving[b]	Summer prehunt[c]	Fall posthunt[d]
Population				
Female calves	497	740	592	579
Yearling cows	372	497	482	427
2+ cows	1,398	1,771	1,700	1,515
Male calves	497	740	592	579
Yearling bulls	248	497	492	256
2+ bulls	229	477	472	236
Total	3,241	4,722	4,330	3,592
Composition				
Bulls/100 cows	27	43	44	25
Calves/100 cows	56	65	54	60
Yearling cow/100 2+ cow	27	28	28	28
Yearling bull/100 2+ bull	108	104	104	108
Fecundity rates				
Yearling cows	0.33			
2+ cows	0.97			

Survival rates	Summer	Winter	Annual (winter × summer)
Female calves	0.80	0.86	0.69
Yearling cows	0.97	0.89	0.86
2+ cows	0.96	0.92	0.88
Male calves	0.80	0.86	0.69
Yearling bulls	0.99	0.97	0.96
2+ bulls	0.99	0.96	0.95

Harvest	Number	Harvest rate
Female calves	13	13/592 = 0.022
Yearling cows	55	55/482 = 0.114
2+ cows	185	185/1700 = 0.109
Male calves	13	13/592 = 0.022
Yearling bulls	236	236/492 = 0.480
2+ bulls	236	236/472 = 0.500
Total	738	

[a] Spring precalving is late winter before birthdays and after winter mortality.
[b] Summer postcalving is after birthdays, after births, but before summer mortality.
[c] Summer prehunt is before hunter harvest and after summer mortality.
[d] Fall posthunt is after fall harvest but before winter mortality.

Controlling Wolves in the Greater Yellowstone Area

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Abstract. Wolf (*Canis lupus*) control in the Greater Yellowstone area will be highly visible to the American public and controversial. Nonetheless, the ability to assure the local public that conflicts between wolves and humans can be managed is fundamental to wolf reintroduction. While the need to control wolves inside Yellowstone National Park is expected to be negligible, some wolf management outside the park would be needed to reduce depredations of livestock and possibly effects on ungulates. Management options for wolves outside the park depend on the manner in which wolves reach the area. Natural recolonization would require management under all protections of the Endangered Species Act of 1973, as amended, and control would be the same as that implemented in Montana because wolves naturally returned there. Reintroduction as an experimental population under Section 10(j) of the Endanged Species Act offers more management flexibility and would allow the states a major role in wolf management. A congressionally mandated and structured reintroduction would likely specify the exact type of management to be implemented. If relocation of wolves as a management action is planned, the involved agencies would need to identify and prioritize potential release sites and obtain advance authority from land-management agencies to release wolves captured in control actions. Such operations require good coordination. More intensive control means less potential for conflicts, greater mortality risk to the wolf population, more time required to reach recovery and remove the wolf from the endangered species list (delisting), and risk of not achieving recovery. Conversely, with less control, the potential for conflicts increases, but the risk to the wolf population decreases. Time to recovery and delisting decreases, and the likelihood of reaching recovery increases. Different management strategies in different areas of the Greater Yellowstone area (zones) provide reasonable means of balancing biological needs of the wolf with socioeconomic concerns in the area and offer trade-offs in conflict reduction and recovery potential. Without adequate control, more illegal killing may occur, as those with the greatest opportunity to kill wolves may have the least favorable attitudes about them.

Gray wolf (*Canis lupus*) control is the least appealing and most controversial aspect of wolf recovery. Nonetheless, every successful wolf recovery program eventually requires wolf management (Mech 1979). Furthermore, wherever wolf reintroduction is planned or proposed, major debate may be expected over the control issue. Wolf management essentially means wolf control.

In this paper I broadly define control as any nonlethal or lethal intentional taking of wolves, directed at specific individuals or populations, and conducted by government agents, their designees, or private citizens. Wolves that are controlled could be killed, relocated, or placed in captivity. Control could be directed at specific problem individuals who prey on domestic animals or have become nuisances. Control could be used to reduce population levels either locally or over a large area. Nuisance behavior is defined here as behavior that causes concern for the safety of humans or pets by repeated appearance, unusual behavior, and aggression toward humans, or loss of fear of them.

Attempting to protect wolves that leave the area designated for them is unrealistic. Their presence should not be promoted in areas where the potential for conflicts with human interests is high (U.S. Fish and Wildlife Service 1987), especially after recovery goals have been met. The ability of wolves to disperse long distances is well documented (Van Camp and Gluckie 1979; Ballard et al. 1983; Fritts 1983; Pletscher et al. 1991). If wolves are established in Yellowstone, an estimated 14 to 25 wolves/year could disperse from the park (Boyce 1990). After population establishment, those individuals will not be essential to the welfare of the population and can be taken. Wolves that prey on livestock and pets will have to be controlled (Fritts 1982; Fritts and Paul 1989; Fritts et al. 1992; Gunson 1983; Tompa 1983).

If practiced broadly and intensively, control of wolves could slow or seriously jeopardize recovery. The issue of taking of wolves in the Greater Yellowstone area—including the circumstances that warrant taking, the extent of taking needed, and the methods of control—are examples of issues that will have to be faced before wolves are reintroduced. Some individuals and wolf advocate groups seem inherently opposed to most control of wolves, especially at the hands of the public, even when the effects on wolf populations are negligible. On the other hand, those who feel their economic interests will be threatened oppose reintroduction (M. Axsom 1986, personal communication to A. J. Bath, cited in Bath 1987b:4; Miniclier 1987) and believe that intensive wolf control will be necessary to minimize the effect of wolves on livestock and big game (Bath 1987c).

Wolf control seems to be unpopular with the national public, except in the case of control directed at specific wolves that have preyed on livestock (Kellert 1985a). Public opinion surveys conducted in the Yellowstone area suggest that conservation groups and livestock organizations have widely differing expectations about the effects of wolves on livestock and game species (Bath 1987a; 1987b; 1987c), so they will have differing views on how much wolf control will be needed.

The following discussion anticipates the need for, and the type of, wolf control that would be likely inside and outside of Yellowstone National Park if wolves reoccupy the Greater Yellowstone area. Five important control-related questions about the restoration of wolves into Yellowstone National Park and the surrounding area follow: (1) would control be needed and how much would be advisable; (2) does the legal authority exist, or can it be obtained, to sanction control; (3) under what conditions or criteria would control occur; (4) specifically who would be authorized to take wolves under those conditions, and would state or federal authorities conduct or oversee the taking; and (5) what means of control would be used? A high degree of interest centers on these questions, and the answers are pivotal in determining the level of public support that a restoration program in the Greater Yellowstone area may expect locally and nationally. The control issue will have to be resolved creatively if wolf recovery in the Greater Yellowstone area is to be accepted by the diverse public interested in this issue. Therefore, prudence dictates that we try now to envision what may lie ahead in confronting this issue.

Methods

I reviewed a variety of documents and information sources in preparing this report. The Northern Rocky Mountain Wolf Recovery Plan (U.S. Fish and Wildlife Service 1987) was especially helpful, as was the Interim Wolf Control Plan for the Northern Rocky Mountains of Montana and Wyoming (U.S. Fish and Wildlife Service 1988). I also examined federal and state laws, regulations, and agency policies and management guidelines, court cases, and solicitors' opinions that relate to wolf control within the Greater Yellowstone area. *An Aggregation of National Park and National Forest Management Plans* produced by the Greater Yellowstone Coordinating Committee in 1987 (hereafter referenced as Greater Yellowstone Coordinating Committee 1987) provided much information. The Greater Yellowstone Ecosystem Report, prepared in 1986 by the Congressional Research Service for the Committee on Interior and Insular Affairs, U.S. House of Representatives, was also helpful. I reviewed public opinion surveys on wolves from Montana, Wyoming, Idaho, Yellowstone National Park, Minnesota, and Michigan, as well as national attitude surveys. I also examined pertinent technical literature on wolves and their prey.

Greater Yellowstone Area as Wolf Recovery Area

Because of its size, wildness, and abundance of prey (Yellowstone National Park et al. 1990), the Greater Yellowstone area seems to meet the biological requirements of wolves. Yellowstone National Park lies at the heart of federal lands within a relatively undeveloped area that includes

4.7 million ha. This area is called the Greater Yellowstone area, or Greater Yellowstone ecosystem. The contiguous portions of two national parks and six national forests encompass an area approximately 270 km north–south by 225 km east–west and include parts of Idaho, Montana, and Wyoming. Some state (3%) and privately owned (24%) lands are dispersed among the federal lands, mainly along the area's perimeter, major roads, or drainage areas.

Approximately 32% of the national forest and national park lands in the Greater Yellowstone area are designated wilderness (1,532,400 ha), with an additional 991,110 ha recommended to Congress for wilderness designation (Greater Yellowstone Coordinating Committee 1987:5–17). Currently, almost all of the designated wilderness in the Greater Yellowstone area is within national forests, and most adjoins Yellowstone National Park. Road construction, timber harvest, and motorized use are generally prohibited in designated wilderness. Camping, hiking, hunting, horseback riding, fishing, and livestock grazing are allowed in national forest wilderness, but hunting and grazing are not allowed in national park wilderness, except in Grand Teton National Park (for a limited area and season only, to help manage the large Jackson elk herd).

Big game animals are hunted in each of the national forests, including designated wilderness areas within these forests. State wildlife management agencies established regulations that attempt to keep population levels commensurate with habitat carrying capacity. Elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) are the most commonly hunted species; bighorn sheep (*Ovis canadensis*), moose (*Alces alces*), and mountain goats (*Oreamnos americanus*) are the most highly prized ungulates hunted (Mack et al. 1990).

Potential prey for wolves abounds in the Greater Yellowstone area, with eight ungulate species present: elk, mule deer, white-tailed deer (*Odocoileus virginianus*), pronghorn (*Antilocapra americana*), moose, bighorn sheep, bison (*Bison bison*), and mountain goats (Mack et al. 1990). Elk and mule deer probably would provide most of the diet of wolves, both in terms of numbers and biomass (Koth et al. 1990). Although wolves eat mainly ungulates, they also consume a variety of small mammals, birds, and other small animals, primarily in summer (Mech 1970).

Roughly 31,000 elk from 7 or 8 herds summered in Yellowstone National Park before the 1988 fires (Singer 1991). A decrease in elk numbers by 8,000 to 10,000 occurred in the park in 1989 (Singer and Schullery 1989). However, the 1988 fires are expected to be beneficial for the range in the long run, resulting in an increase in the elk herd (Singer et al. 1989). About 22,500 elk from 4 herds winter in the park in some years, including 20,800 from the northern herd. In severe winters, nearly half of the northern herd may leave the park. Other ungulates include 2,000–3,000 mule deer on the northern range, in and north of the park, that mostly leave the park in winter due to deep snow (Singer 1991). Mule deer use some of the same winter range as elk, and migration patterns are similar. Approximately 300 bighorn sheep winter on the northern range. Moose are found throughout the park in summer and winter, but their numbers are poorly documented. Over 2,000 bison in 3 herds inhabit the park.

On federal portions of Greater Yellowstone area lands, the number of elk, mule deer, white-tailed deer, mountain goats, bighorn sheep, pronghorn, moose, and bison totaled roughly 205,600 individuals in 1987 (Greater Yellowstone Coordinating Committee 1987:5-41 through 5-48). Substantial fluctuation in numbers of these ungulates occurs in the Greater Yellowstone area, due mainly to variation in winter severity (Singer and Schullery 1989). Of all the ungulate species in the area, elk are the most abundant and most significant biologically and economically (Houston 1982). Mule deer are also widely distributed across the area, totaling around 88,000 on federal lands. Bighorn sheep and moose number approximately 7,700 and 6,000, respectively, on Greater Yellowstone area federal lands. Both are more abundant outside Yellowstone. Most bison within the Greater Yellowstone area live within the park (Greater Yellowstone Coordinating Committee 1987).

Yellowstone National Park is not a biologically self-contained area. Although the level of prey biomass in the park in summer is enormous, a substantial portion of the prey (especially the southern portion) migrate out of the park to winter range at a lower elevation, leaving most park ungulates concentrated in the north-central and west-central areas (Mack et al. 1990; Singer 1991).

Some wolf territories could include areas outside the park. Wolves could either be truly migratory—as in some northern areas where they follow caribou migrations—or they could maintain year-round territories that extend across portions of both the summer and winter ranges of elk herds (Koth et al. 1990). Opinions of biologists differ on whether or not Yellowstone's wolf packs would be migratory (Koth et al. 1990). No analogous ecosystems exist for comparison. In the most similar wolf–prey systems in Canada, some seasonal altitudinal movement of wolves does occur (Cowan 1947; J. L. Weaver, personal communication). Unfortunately, little information was obtained on this subject when wolves occupied the area. Some evidence that the original Yellowstone wolves did follow their prey in at least altitudinal migrations was cited by Weaver (1978:18–19).

Migration of wolves with certain elk herds would require wolf movement well outside the wildernesslike habitat. For example, wolves could follow members of the Jackson elk herd from the park to their winter range on the National Elk Refuge. They could also follow the Sand Creek herd from the southwestern part of the park to their wintering grounds, approximately 56 km away in Idaho (Mack et al. 1990; Vales and Peek 1990). Any wolves that follow elk to their wintering grounds outside the park would have a higher probability of becoming involved in conflicts and could be vulnerable to being killed by the public, whether legal or illegal.

The Greater Yellowstone area economy is dominated by tourism and other recreational land uses, including skiing, sight-seeing from motorized vehicles, hunting, fishing, wildlife viewing, camping, picnicking, hiking, and climbing. Commercial outfitters and guides rely on the public lands and water for a large portion of their operations. Big game hunting, with or without the assistance of guides, plays a major role in creating jobs in several areas, particularly in the Bridger–Teton National Forest and the northern part of the Shoshone National Forest. Recreation supports 14,300 jobs (80% of total) and produces $217 million in annual income. Nine million visitor-days of recreation occur in developed Greater Yellowstone area sites each year (Greater Yellowstone Coordinating Committee 1987). Wildlife viewing is an important reason for visiting the area (A. J. Bath, unpublished data). Nearly one-half million hunter-days are spent annually in pursuit of ungulate species on Greater Yellowstone area federal lands (Fritts 1990), and about 70% of that time is for elk hunting (Congressional Research Service 1986).

Livestock producers in the area rely on public lands for grazing cattle, sheep, and horses in summer. In 1989, some 75,000 cattle, 121,000 sheep, and 1,200 horses were on grazing allotments on the six national forests in the Greater Yellowstone area (Table 1). Grazing produces 1,300 jobs and $30 million in income to the local economy (Greater Yellowstone Coordinating Committee 1987).

Wolf recovery could result in lower ungulate populations and, thereby, reduced hunting opportunity. Wolf recovery could also lead to depredation on livestock with some reduction in agricultural productivity. However, based on a recent estimate, wolf recovery would have a net positive annual economic effect of $25–30 million on the regional economy (Duffield 1992). This estimate is, in part, based on a Yellowstone visitor survey that showed that wolf presence would increase visits to the park. Increased nonresident tourism expenditure would outweigh a possible reduction in hunting expenditure and the market value of livestock exports (Duffield 1991).

Public Attitudes and Wolf Control

In an issue as controversial as wolf reintroduction to Yellowstone, the human dimension must be considered (Bath and Buchanan 1989). Experience in managing wolves in North America has shown that wolves and wolf control are controversial and that local human tolerance is critical to the survival and successful management of this species. Even when wolves are protected by the amended Endangered Species Act of 1973, humans are a major cause of mortality (Mech 1977; Fritts and Mech 1981; Fuller 1989). The only reintroduction of gray wolves into the United States to date (Michigan) failed because all four wolves were killed by humans

Table 1. Livestock grazing in national forests in the Greater Yellowstone area (U.S. Forest Service at Beaverhead, Custer, Bridger–Teton, Shoshone, Gallatin, and Targhee national forests.)

National forest	Acres in allotments	Livestock			Permits[a]		
		Cattle	Sheep	Horses	Cattle	Sheep	Horses
Beaverhead	336,352	8,825	5,350	65	61	4	17
Custer	64,000	2,030	0	0	23	0	0
Bridger–Teton	596,372	14,191	3,700	257	52	3	32
Shoshone	1,076,816	18,684	12,489	256	94	11	8
Gallatin	618,659	7,403	5,941	462	93	9	14
Targhee	1,182,130	23,735	93,129	191	165	89	33
Total	3,874,329	74,868	120,609	1,231	488	116	104

[a] Table shows total number of permits, not permitees. One individual may hold more than one permit.

within 8 months of release (Weise et al. 1975). The level of local opposition to wolf reintroduction in the Greater Yellowstone area may generally suggest the extent of illegal killing that may be expected. Also, the degree of satisfaction with wolf management may influence local attitudes. Members of the public that live, work, and play in wolf habitat can make the difference in whether or not a wolf population becomes established, at least outside of Yellowstone National Park. Therefore, wolf control in the Greater Yellowstone area should recognize local, as well as national, attitudes about wolves and about expectations on the need for control. Residents of the area have frequently expressed the opinion that no wolf control would occur there, despite the intent of government wildlife agencies to exercise control, because of litigation from conservation groups. That skepticism, shared to some extent by state wildlife agencies, has helped fuel opposition to wolf reintroduction.

Studies of public attitudes toward wolves and aspects of wolf reintroduction to the park and the Greater Yellowstone area have been conducted within the past few years (Bath 1987a, 1987b, 1987c, 1991; McNaught 1987; Bath and Buchanan 1989; Tucker and Pletscher 1989; Bath and Phillips 1990; Thompson and Gasson 1991; M. L. Lenihan, Bureau of Business and Economic Research, University of Montana, unpublished report). These studies, in conjunction with similar ones in other areas of the United States, are interesting when considering wolf control in the Greater Yellowstone area. Their pertinent findings are summarized here.

Nationwide data suggest that the public likes the wolf and, within the Rocky Mountain Region, 50% like the wolf while 30% dislike the animal (Kellert 1985b). Local attitudes on wolf reintroduction are mixed but generally favorable (Bath 1987b; Bath and Phillips 1990; M. L. Lenihan, Bureau of Business and Economic Research, University of Montana, unpublished report).

Public opinion surveys in Montana, Idaho, and Wyoming have revealed favorable views toward wolves in each state (Bath 1987a, 1991; Bath and Buchanan 1989; Tucker and Pletscher 1989; Bath and Phillips 1990; Thompson and Gasson 1991; M. L. Lenihan, Bureau of Business and Economic Research, unpublished report). In a 1987 survey, the majority of Montanans surveyed (n = 408) indicated approval (52 vs. 38% who disapproved) of wolf reintroduction into areas in Montana, Idaho, and Yellowstone National Park where wolves are now extinct. However, 56% of those from rural areas did not approve, versus 39% who did (M. L. Lenihan, Bureau of Business and Economic Research, University of Montana, unpublished report). Bath and Phillips (1990) reported that 43.7% of Montana residents (n = 672) were in favor of reintroduction to Yellowstone National Park, with 40.3% not in favor and 16.0% expressing no opinion. Most survey respondents from the Wyoming general public (n = 371) were in favor of wolf reintroduction (48.5 vs. 34.5%; Bath 1987a; Bath and Buchanan 1989), but support diminished with increasing proximity to the park (Bath 1987b; Bath and Buchanan 1989). Members of the Wyoming Stock Growers Association were adamantly opposed (Bath 1987c). A more recent survey of Wyoming residents (n = 804) indicated that 44% support reintroduction to Yellowstone, while 34.5% are opposed and 21.5% are undecided or have no opinion (Thompson and Gasson 1991). Bath and Phillips (1990) surveyed Idaho residents (n = 618) and found 56.0% in favor, 27.0% opposed, and 17.0% expressing no opinion.

The surveys have indicated that most of those opposed to reintroduction were adamant in their opposition and were unwilling to change their minds. Primary reasons for opposition included cost of a reintroduction program, expected livestock losses, and expected big game declines (Bath 1987a; 1987b, 1987c; Bath and Phillips 1990; Thompson and Gasson 1991). Bath (1987c) mentioned that in responding to his survey several Wyoming Stock Growers wrote supplementary comments asking where they could obtain compound 1080 (a wolf poison) if wolves were reintroduced. Overall, survey respondents who were most likely to favor reintroduction were more likely to have a positive attitude toward the wolf. The unwillingness of ranchers to change their opinion about wolf reintroduction, even if livestock losses and other expected concerns could be kept low (Bath 1987b; Bath and Phillips 1990; Thompson and Gasson 1991), suggests that the underlying reason for their opposition has not been identified by public-opinion surveys. I believe that underlying reasons for objection relate to concern that wolves will ultimately mean loss of grazing allotments on public lands, increased government regulation, and reduced opportunity to remove timber and minerals from public land.

About 82% of overnight visitors to Yellowstone (n = 1,061) supported the concept of wolf reintroduction to the park (McNaught 1987). Correspondence to the U.S. Fish and Wildlife Service (528 letters reviewed as of spring 1991) was running over 97% in favor of wolf reintroduction to the park (Fritts, unpublished data). Over 90% of that correspondence is from outside Montana, Idaho, and Wyoming. Approximately 51% of individuals writing from within the three-state region favored wolf recovery and 49% were opposed. Letters from outside the region were 99.6% in favor.

Different attitudes toward wolves among different interest groups have been revealed by some of the surveys in the Greater Yellowstone area and elsewhere. Kellert (1985a, 1986) reported a favorable attitude toward the wolf among all sample groups except farmers in a Minnesota survey; nonetheless, a high rate of illegal killing was occurring. Although killing of wolves by the public is illegal, about 12% of farmers and 17% of trappers in Minnesota said they had personally killed or captured a wolf. More than 25% of Minnesota hunters and residents within the Minnesota wolf range indicated they might shoot a wolf if they encountered one while hunting (Kellert 1985a). More than 40% of farmers, hunters, and trappers, and northern county residents reported knowing someone who had captured or killed a wolf. They did not indicate whether this was before or after wolves were protected by the Endangered Species Act, yet biological data indicate that (with wolves protected) humans are the major cause of wolf mortality in northwestern and north-central Minnesota, where the human-caused annual mortality rate is reported as 0.17 and 0.29%, respectively (Fritts and Mech 1981; Fuller 1989). Chances of being apprehended are low, and prosecutions are uncommon. Persecution from humans may be why the wolf has not recovered in Michigan, even though biological conditions are favorable (Hook and Robinson 1982). Illegal killing could be similarly high in accessible areas of the Greater Yellowstone area, including private land. Most killing of wolves in the accessible areas of Minnesota occurs during the deer and moose hunting seasons (Van Ballenberghe et al. 1975; Mech 1977; Fritts and Mech 1981; Fuller 1989) simply because that is when more people carrying rifles encounter wolves. The same would likely be true in portions of the Greater Yellowstone area where hunter density is high. Wolves could be more vulnerable to shooting in some portions of the Greater Yellowstone area than in Minnesota and many areas of southern and western Canada because mountainous or rolling terrain, less forest cover, and less understory could increase their visibility. Although Yellowstone National Park is about 79% forested, the degree of forest cover in the six national forests around the park ranges from 89% in the Targhee to 21% in the Shoshone and averages only 57% for the forests combined. By comparison, the primary range of the wolf in Minnesota is 77% forested (G. L. Radde, personal communication). Wolf populations apparently can withstand a sustained harvest of up to 30% of fall populations (Keith 1983).

Montanans surveyed did not believe that wolves would be a serious threat to big game populations; they were evenly divided on whether wolf reintroduction would cause high livestock losses (M. L. Lenihan, Bureau of Business and Economic Research, University of Montana, unpublished report). When asked whether wolves would be a serious predator on the livestock around Yellowstone National Park, 39.1% of Wyoming residents, 44.7% of Montanans, and 32.9% of Idahoans agreed, and 42.0, 39.9, and 45.9% disagreed, respectively (Bath 1987a; Bath and Phillips 1990). Most Wyoming residents did not believe that wolves would reduce big game hunting opportunities near the park, but residents closer to the park were less decisive in that view, and members of the Wyoming Stock Growers Association expressed the opposite opinion (Bath 1987a, 1987b, 1987c). A similar response pattern emerged on whether wolves reintroduced into Yellowstone National Park would cause more livestock damage than in Minnesota. Most Wyoming residents, including residents from counties surrounding the park, thought wolves would not cause more damage than in Minnesota, but members of the Wyoming Stock Growers Association held the opposite view (Bath 1987a, 1987b, 1987c).

National surveys may suggest how the public views wolf control in the Greater Yellowstone area. Kellert (1979, 1985b) found that attitudes of the general public on control of coyotes (*Canis latrans*) differed substantially from attitudes of sheep producers and cattlemen. The general public disapproved of nonspecific shooting or trapping, strongly disapproved of the use of poisons, approved of hunting only individual coyotes known to have killed livestock (whenever possible), approved of capture and relocation of coyotes away from sheep even though this was an expensive solution, and disapproved of paying ranchers for sheep losses out of general tax revenues (while avoiding killing of coyotes). Sheep producers and cattlemen disagreed with the general public on all of these points except on paying compensation from general tax revenues.

Most survey respondents from Montana (60.0%) and Idaho (48.9%) agreed with the statement that "if reintroduced wolves killed livestock, the problem wolf should be killed" (Bath and Phillips 1990). However, almost 30% of Montana respondents and 37% of Idaho respondents disagreed with that statement. Approximately 58% of the Wyoming general public thought that if a wolf killed livestock the problem wolf should be killed, whereas about 25% disagreed (Bath 1987b:80). Most members (87.5%) of the Wyoming Stock Growers Association surveyed agreed that reintroduced wolves should be killed if they killed livestock. (Interestingly, 7.5% strongly disagreed with that statement.) By contrast, about 46% of Wyoming Wildlife Federation respondents and only about 28% of Wyoming members of the Defenders of Wildlife believed that the problem wolf should be killed (Bath 1987c). The more recent survey in Wyoming indicated that 56.8% of the general population thought a problem wolf should be killed, with 28.6% believing it should not, and 14.6% expressing no opinion (Thompson and Gasson 1991). Over three-fourths of Montanans polled said that ranchers should be able to shoot wolves that attack livestock on their property, with more rural Montanans agreeing than the general population (84 vs. 75%; M. L. Lenihan, Bureau of Business and Economic Research, University of Montana, unpublished report). National surveys have shown that the public favors control that is site-specific and animal-specific and relatively humane (Arthur et al. 1977; Kellert 1979; Stuby et al. 1979).

Most Minnesotans surveyed supported the concept of controlling wolf depredations on livestock (Kellert 1985a). Wolves were never eliminated in Minnesota, so the public there has a long history of living with the species and is more accustomed to wolf control (Van Ballenberghe 1974; Fritts 1982). The majority of Minnesotans (except farmers) strongly favored the use of humane control methods focusing on individual problem animals. Most respondents disapproved of using poisons, destroying wolves without proof of guilt, reducing indiscriminately the overall populations of wolves in areas where they are abundant, or killing pups. The most preferred wolf control procedures were eliminating individuals that had preyed on livestock, capturing and relocating wolves, compensating those who had lost livestock, and using guard dogs. Farmers and hunters expressed the greatest support for eliminating wolf pups, paying farmers for losses to wolves, reducing wolf numbers, and shooting and trapping individual wolves known to have preyed on livestock (Kellert 1985a:39). The most favored methods (except among farmers) for increasing the deer population were reducing the number of hunters or doing nothing, whereas the least preferred option was reducing the wolf population (Kellert 1985a:11). Acceptability of various control measures to Wyoming residents were capturing and relocating (73.2%), hunting (47.4%), kill trapping (29.2%), and poisoning (12.2%; Thompson and Gasson 1991).

During recent years, the public has objected to efforts by state and provincial agencies to implement or liberalize wolf control programs in Alaska, Minnesota, and Canada, and some programs have been the subject of litigation. Recent U.S. Fish and Wildlife Service wolf control efforts in northwestern Montana (in response to livestock depredations) have been spotlighted by local and state press, and anticontrol sentiment has been strong. Because of the national prominence of Yellowstone and with broad interest in the wolf, control efforts in the Greater Yellowstone area likely would be covered by the national press and come under immediate scrutiny by the public.

Only 21% of Wyoming residents surveyed and less than 25% of Montana and Idaho residents surveyed indicated that the wolf reintroduction issue was not important to them (Bath 1987b; Bath and Phillips 1990). Therefore, public involvement with the process of deciding on and planning for a reintroduction may be important to future public acceptance of the program.

The American public has received little exposure to wolf control issues in recent decades, so conceivably the public may not be prepared for the realities of wolf control in the Greater Yellowstone area. Wolves are symbolic, with perceptions of the animal varying considerably among diverse demographic groups in American society (Kellert 1985a, 1985b; Bath 1987c; McNaught 1987; Bath and Buchanan 1989; Bath and Phillips 1990; M. L. Lenihan, Bureau of Business and Economic Research, University of Montana, unpublished report). Killing wolves is an emotional subject, and the lack of agreement among Wyoming, Montana, and Idaho residents on killing wolves for controlling livestock depredations might foretell conflict on this issue.

The comments received in response to the deaths of three of four wolves that were relocated in a control action in northwestern Montana in September and October 1989 led me to question whether the public is willing to acknowledge the need for control or to accept the biological realities and risks involved in relocating animals. In fact, major misconceptions may exist about the difficulties and uncertainties in (1) verifying wolf depredations on livestock; (2) capturing wolves, especially specific problem wolves; and (3) ensuring survival chances for relocated wolves. Any deliberate killing of wolves or death by handling (i.e., relocating) wolves in the Greater Yellowstone area may contribute to the creation of still another battleground where advocates and opponents of wolf control do combat. However, in this case, the conflict would be on center stage for the entire nation. Education on the realities of wolf control must be a part of wolf recovery, whether occurring naturally or by reintroduction.

Legal Basis for Wolf Control

Current Wolf Control Programs in the United States

The extent of wolf control is determined by the degree of legal protection afforded the species. Under the Endangered Species Act, the wolf is classified as an endangered species in all the conterminous United States except Minnesota. Wolves have been protected by state law in Montana since 1973 and in Idaho since 1977. Wyoming currently lists the wolf among predatory animals, although protection under the Endangered Species Act supersedes less protective state law. At present, the most active wolf control program under the Endangered Species Act is in Minnesota. The program's sole purpose is to address depredations of domestic animals. Extensive and controversial wolf control programs for ungulate management were initiated in Alaska where the wolf is not listed as an endangered or threatened species (Harbo and Dean 1983).

In Minnesota, the wolf currently is classified as threatened (43 Federal Register (FR) 9612, 9 March 1978). Litigation has played a major role in the history of wolf management in Minnesota (Van Ballenberghe 1974) and in the evolution of the current depredation control program (Brzoznowski v. Andrus 1978; Fund for Animals v. Andrus 1978; Coggins and Russell 1982; Fritts 1982; Goldman-Carter 1983; Kellert 1985a; Sierra Club v. Clark 1985; O'Neill 1988). The Minnesota depredation control program is shaped by federal standards and conducted by federal personnel. The state is allowed to implement the program, but so far has declined to do so under the federal guidelines. Trapping is essentially the only method of control used in Minnesota (Fritts 1982; Fritts et al. 1992). Wolf control to increase ungulate populations does not occur.

Current U.S. Fish and Wildlife Service regulations applicable to Minnesota wolves allow problem wolves to be taken in management zones 2, 3, 4, and 5 only "in response to depredations on lawfully present domestic animals; provided that such taking must occur within 0.8 km (0.5 mi) of the place where such depredation occurred and must be performed in a humane manner; and provided further, that any young of the year taken on or before 1 August of that year must be released" (50 Code of Federal Regulation (CFR) 17.40 (d)(2)). A compensation program, funded by the state and administered by the Minnesota Department of Agriculture, has been in place since 1977 and has paid out an average of $23,715/year through 1989 (Fritts et al. 1992). Until the status of wolves in Minnesota was changed from endangered to threatened in 1978 (i.e., between 1974 and 1978), translocation was the sole method of control (Fritts 1982; Fritts et al. 1984, 1985). The success of that program was questioned because some wolves returned to their capture locations or other farms where they were implicated in further depredations. Since 1978 the U.S. Fish and Wildlife Service has killed problem wolves (except for pre-August pups because of a court order). For 1975–89, 641 wolves were captured and 445 destroyed or otherwise removed from the population; the remainder were translocated in the earlier years or released as pups (Fritts et al. 1992). The U.S. Fish and Wildlife Service conducted the program until March 1986 when control responsibility was transferred to the U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Animal Damage Control. This control program in Minnesota has generally received the approval of both wolf conservationists and the agricultural community (O'Neill 1988), although a recent increase in depredations (Fritts et al. 1992) corresponding with an increase in the wolf population (Fuller et al. 1992) has resulted in calls for more liberal taking of wolves.

Wolf control is an issue in Montana where the wolf is classified as endangered. The Northern Rocky Mountain Wolf Recovery Plan, signed in 1987, recommended developing a wolf control contingency plan, in part to reduce opposition to wolf recovery in designated recovery areas (U.S. Fish and Wildlife Service 1987). In 1988 the U.S. Fish and Wildlife Service completed an Interim Wolf Control Plan for the Northern Rocky Mountains of Montana and Wyoming (U.S. Fish and Wildlife Service 1988). Amendment 1 to this plan added Idaho and northeastern Washington. The interim plan and the amendment plans are intended to operate until specific management zones and objectives are established and are intended to be amended to incorporate any subsequent changes in management objectives or direction in the different zones. These plans are based on the concept of wolf control to enhance propagation or survival of the species. Section 10(a) of the Endangered Species Act includes a provision allowing the secretary of the interior to permit acts otherwise prohibited by Section 9 (including the taking of endangered species) for scientific purposes or to enhance propagation or survival of the species. A 1985 decision by the U.S. Court of Appeals for the 8th Circuit in a case pertaining to wolf control in Minnesota stated that this provision allows removing depredating animals or culling of diseased animals from a population (U.S. Fish and Wildlife Service 1988).

The Interim Wolf Control Plan includes guidelines for identifying problem wolves, conducting control actions, and disposing of problem wolves. Controlling problem wolves is expected to demonstrate to the public that the responsible federal agencies would act quickly to resolve depredation problems and thus reduce the hostility toward wolves that would result in illegal and indiscriminate killing. The U.S. Fish and Wildlife Service's biological opinions on the plan found that controlling specific depredating wolves is not likely to jeopardize the continued existence of the wolf. To the contrary, by removing the few wolves that kill livestock and enhancing the survival of nonoffending wolves, the U.S. Fish and Wildlife Service believes its control program will actually contribute to the recovery of the species in the northern Rockies and enhance survival of the species.

Under the Interim Wolf Control Plan, capturing, relocating, or removing wolves would be conducted by qualified federal, state, or tribal personnel under a Section 10 permit, issued by the regional director of the U.S. Fish and Wildlife Service. If the animal cannot be captured alive, and attacks on livestock continue, shooting may be used in accordance with control agency policy and guidelines and in consultation with the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 1988). In the control actions to date in Montana, the actual work has been a cooperative effort between the U.S. Fish and Wildlife Service and the U.S. Department of Agriculture—Animal Damage Control.

If wolves were to recover naturally in the Greater Yellowstone area, or if they were reintroduced—but not as an "experimental population"—the U.S. Fish and Wildlife Service Interim Wolf Control Plan would take effect there. (The plan would also immediately be in effect if previously unknown wolves in the Greater Yellowstone area were to prey on livestock there.) However, if an experimental population is established, provisions for control would likely be as defined in experimental population regulations and state wolf management plans (see next section).

A variety of control methods and devices have been used on the wolf in North America. These methods and devices include steel traps, pits, deadfalls, corrals, snares, set guns, hunting (various approaches), den digging, poisoning, and aerial hunting (Young and Goldman 1944; Lopez 1978). Trapping is the primary method used in Minnesota (Fritts 1982; Fritts et al. 1992). Trapping and darting from a helicopter are the primary methods used in Montana so far. In most Canadian provinces, shooting and trapping by government agents and the public are the most common control methods to protect livestock. Alberta, British Columbia, and Saskatchewan allow limited use by government personnel of strychnine or compound 1080 to protect livestock from wolves. Some methods of wolf control are more appropriate when conducting control that targets problem individuals, whereas others are more appropriate for reducing local populations, as in wolf reduction for ungulate management. Aerial hunting has been the method of choice in the large wolf reduction programs in Alaska (Gasaway et al. 1983; Harbo and Dean 1983). Techniques such as poisoning and aerial hunting are highly controversial even though they can effectively target specific problem wolves. The use of compound 1080 is now banned in the United States, and strychnine is illegal for all aboveground use. M44's, which employ sodium cyanide, are commonly used in coyote control, but they have not been approved by the Environmental Protection Agency for use on wolves. Aerial shooting of problem wolves could be employed by the U.S. Fish and Wildlife Service or its subpermitees under its Section 10 permit. However, the primary methods used in the Greater Yellowstone area are expected to be trapping (modified steel foothold traps; Kuehn et al. 1986), shooting, and live capturing by darting from aircraft in the vicinity of the depredation. Humaneness must be an important element in all control activities if the national public is to accept wolf control (Kellert 1985a, 1985b), especially with the increasing interest in animal welfare (Schmidt 1989a, 1989b).

A major concern of grazing allotment holders and of Animal Damage Control personnel is how the presence of wolves in national forests surrounding Yellowstone National Park would affect coyote control. Coyotes currently are—and will likely continue to be—far more important predators of livestock in Montana than wolves will be (Bangs et al., in preparation). Each year, Animal Damage Control personnel control coyotes on certain allotments that have a history of coyote problems. Rather than operating under permit, Animal Damage Control presents its plans in its annual work plan. Control methods used on forest lands are restricted to aerial hunting, calling, shooting, trapping, and using M44's. The Northern Rocky Mountain Wolf Recovery Plan recommended that Animal Damage Control activities be compatible with wolf management objectives:

> Generally in Zone I, traps for coyote control should be No. 2 (No. 3N with offset jaws in Zone II) and should be checked once every 24 hours. Aerial shooting should be limited to October through May and snares should not be used. Use of toxicants should be limited to those that avoid killing wolves either because of the selectivity of the delivery system or the toxicant (U.S. Fish and Wildlife Service 1987:37).

Prohibiting M44's would be a handicap to current Animal Damage Control operations. These devices are particularly useful where ground conditions make trapping difficult. If Animal Damage Control was prohibited from using M44's each time a wolf might be in the area, efficiency of coyote control would be reduced. Thus, the presence of wolves in the Greater Yellowstone area may indeed restrict the methods that can be used in existing coyote control programs.

Potential Control of Yellowstone Wolf Population Designated as Experimental Population

Significant flexibility in wolf control in the Greater Yellowstone area was provided by the 1982 amendments to the Endangered Species Act (specifically Section 10(j)), which created the experimental population designation. Before 1982, the U.S. Fish and Wildlife Service had the authority to reintroduce threatened and endangered species into unoccupied historical range; however, many attempts to do so were fervently resisted. The reason for resistance was that the U.S. Fish and Wildlife Service lacked the ability to assure other federal agencies, state and local governments, and private landowners that transplanted populations would not disrupt their future land-management options due to the jeopardy prohibition of Section 7 or the taking prohibition of Section 9 of the Endangered Species Act. Such resistance caused the U.S. Fish and Wildlife Service to abandon plans to reintroduce endangered red wolves (*Canis rufus*) to parts of Kentucky and Tennessee in 1984 (Parker 1989). To encourage acceptance of reintroductions, Congress amended the Endangered Species Act in 1982 to include Section 10(j) that allowed the secretary of the interior to designate reintroduced populations as experimental, defined as

> Any population (including any offspring arising solely therefrom) authorized by the Secretary for release under paragraph (2), but only when, and at such times as, the population is wholly separate geographically from nonexperimental populations of the same species (Section 10(j)(1)).

The amendment also made it clear that the term applies to populations derived from endangered or threatened species for which the secretary has determined that a release will further conservation. Section 10(j)(2)(c) gives the U.S. Fish and Wildlife Service more flexibility for managing these populations by providing that all experimental populations shall be treated as threatened species (rather than endangered) regardless of the status of the donor population. Regulations implementing Section 10(j) were published on 27 August 1984 and are codified at 50 CFR Part 17, Subpart H. The few ensuing papers written on the experimental population rule in endangered species management were listed previously (Fritts 1990:1–31).

The experimental population designation has been made or proposed for 10 vertebrate species: red wolf, Delmarva fox squirrel (*Sciurus niger cinereus*), Colorado squawfish (*Ptychocheilus lucius*), woundfin (*Plagopterus argentissimus*), yellowfin madtom (*Noturus flavipinnus*), southern sea otter (*Enhydra lutris nereis*), Guam rail (*Rallus owstoni*), desert pupfish (*Cyprinodon macularius*), Gila topminnow (*Poeciliopsis occidentalis occidentalis*), and black-footed ferret (*Mustela nigripes*). The sea otter reintroduction and experimental population designation was done by an act of Congress (Public Law 99–625, 7 November 1986).

Before designating a population as experimental, the secretary of the interior must determine through the rulemaking process that the reintroduction will further the conservation of the species, the geographical location of the population, and if such a population is essential or nonessential. Designation would include developing proposed special rules to identify geographically the location of the experimental population, procedures for its management—possibly including special activities designed to contain the population—and compliance with the Administrative Procedures Act, which involves public review of the rulemaking and publishing the above in the Federal Register.

Experimental populations must be designated either essential or nonessential. *Essential* refers to a reintroduced population whose loss would be likely to reduce the likelihood of the survival of that species in the wild. Essential populations receive the full protection of Section 7, meaning that federal agencies must formally consult with the U.S. Fish and Wildlife Service on actions that may affect existence of the species in the wild. *Nonessential* refers to an experimental population whose loss would not be likely to appreciably reduce the survival of the species in the wild. Except in national wildlife refuges and national parks, nonessential populations are treated under Section 7 as "proposed species." Thus, federal agencies must only confer with the U.S. Fish and Wildlife Service on activities that could jeopardize the species. In national parks and national wildlife refuges, nonessential populations are treated as threatened species under Section 7(a)(2). Congress intended that most experimental populations be considered nonessential (House of Representatives Conference Report 835).

All experimental populations are treated as threatened species for which the U.S. Fish and Wildlife Service must write special rules concerning prohibited acts. Basically, the writing of special rules provides the opportunity to tailor the reintroduction of an experimental population to specific areas and conditions, including specific opposition. Public acceptance needs have to be balanced with recovery needs. Because few populations have been designated experimental and the process is legally new, no case law exists to review on Section 10(j). Use of the experimental population designation and the nonessential status determination seems to be an option for wolves in the Greater Yellowstone area (Fritts 1990).

The Northern Rocky Mountain Wolf Recovery Plan (U.S. Fish and Wildlife Service 1987) recommended reintroduction of wolves to Yellowstone as an experimental population. This designation has been broadly acclaimed as providing the management flexibility needed to render reintroduction workable (see Tilt et al. 1987 for example). Considerable discussion has occurred about that possibility, and many recent articles and discussions have assumed that wolves reintroduced to Yellowstone would be designated experimental. Nonetheless, some misunderstanding exists among the public and agency personnel about what an experimental population is and how it could be regulated.

In an earlier paper, I examined Congress's intent in amending the Endangered Species Act with Section 10(j) within the context of a wolf reintroduction to the Greater Yellowstone area (Fritts 1990). Congress intended to make more reintroductions possible—that is, to make reintroduction a more viable recovery tool—with the full realization that provision for taking may be necessary to make a given reintroduction possible. The question of taking members of an experimental population is important to potential state involvement in wolf management. The Northern Rocky Mountain Wolf Recovery Plan (U.S. Fish and Wildlife Service 1987) assumed that the experimental population designation in the Greater Yellowstone area would give a broader flexibility that would be adequate to control wolves and even recommended that consideration be given to allowing livestock owners to take depredating wolves if verified depredations occurred on lawfully present livestock on private property and if control actions were limited to within 1.6 km of the depredation site.

The U.S. Fish and Wildlife Service's interpretation of the experimental population designation is that special rules could be written and approved to allow for control of depredating wolves in the Greater Yellowstone area (Fritts 1990). In general, the experimental population rule can provide for taking if a legally supportable rationale exists that the take is consistent with the conservation of the experimental population and is necessary for the successful establishment and maintenance of the population. In deciding where, when, and by whom control can occur, consideration may be given to what is needed to win acceptance and support for recovery—but it also should be legally defensible. Montana, Idaho, and Wyoming would have many advantages in being able to manage wolves under conservation plans or management plans. (Note that the term *conservation plan* would not be the same as a conservation plan used under Section 10(a)(2)(A), with respect to incidental take permits; currently, no precedent is available for a conservation plan under Section 10(j).)

Taking of wolves under special rules for an experimental population would be easiest to justify—and perhaps more acceptable to the general public—if the U.S. Fish and Wildlife Service, Animal Damage Control, or states were doing the taking and it was directed at specific offending wolves. The rule would need a rational basis to support taking wolves by private individuals rather than by government personnel, and that private take is needed to meet the standard of being consistent with recovery. A greater burden of proof of necessity would be needed. Private taking would still be subject to federal guidelines, control, and reporting procedures. (The final rules for the threatened gray wolf in Minnesota and the nonessential experimental red wolf population in North Carolina does require control to be done by state or federal personnel.)

Therefore, allowing livestock owners to kill wolves in the act of depredating or following confirmed depredations is a possibility under special rules for an experimental population in the Greater Yellowstone area, if the U.S. Fish and Wildlife Service can demonstrate that such taking is consistent with conservation of the experimental population and will not adversely affect recovery of the species in the wild. Some control by the public in defense of property would be consistent with local rural sentiment and might go far in winning support among local residents for a reintroduction while having a minimal effect on the wolf population. The effect of such taking on a small recovering wolf population would have to be considered.

In addition to taking wolves for depredation on livestock, another key issue is whether they could be taken if excessive predation occurred on ungulate herds that conflicted with state ungulate management objectives. Controlling wolves for ungulate management is expected to be more controversial than for protecting livestock. Nonetheless, the flexibility could exist for states to integrate management of wolves and their prey. For example, if wolves were severely affecting local herds—and, therefore, their prey base—the states, subject to federal guidelines, could be delegated responsibility for control actions. The control would need to be for the benefit of the wolves (e.g., a declining prey base is not consistent with the long-term survival and sustainment of the experimental wolf population). Hypothetically, such wolf control might take the form of translocation early in wolf recovery and lethal control after some population level was attained.

Developing the proposed rule would be a critical part of designating an experimental wolf population for Yellowstone. A number of complex issues would have to be resolved. These issues include control measures, management zones, taking provisions, measures to keep the population within the defined area, and state involvement. This is where such critical questions arise as how much taking is permissible under Section 10(j) of the Endangered Species Act while still meeting the definition of long-term conservation of the population and to what extent states can manage an experimental population with a plan that provides for some taking. A major task would be preparing wolf management plans by the three states in consultation with federal agencies. Preparing the plans would require some state legislative and commission action to ensure that classification of the wolf in each state is consistent with wolf recovery and that state wildlife agencies could participate in wolf recovery and management. For example, Wyoming's listing of the wolf as a predator would have to be altered. Also, statutes preventing the Idaho Department of Fish and Game from being involved in wolf surveys, research, and management, including the expenditure of funds for these activities, would have to be changed.

If wolves were to naturally recolonize the Greater Yellowstone area, Sections 7 and 9 of the Endangered Species Act would be in full effect, meaning that wolves would be protected by all provisions of the act. Clearly, this scenario offers far less management flexibility than is possible through reintroduction as a nonessential experimental population. Natural wolf recovery in northwestern Montana (Ream et al. 1991) is enhancing the probability of dispersing wolves reaching the Greater

Yellowstone area. Even now the National Park Service and the U.S. Fish and Wildlife Service receive occasional reports of wolf observations from the area. Although these sightings are not thought to indicate a resident population (Weaver 1978:20), the possibility exists that dispersing wolves from Idaho or Montana could reach the area in the next few years and establish a breeding population. Occasional reports of wolf observations are received from southwestern Montana, especially from along the continental divide west of Yellowstone National Park (Ream and Mattson 1982; U.S. Fish and Wildlife Service, Helena, Montana, unpublished data). Numerous reports from various locations in central Idaho have led to the conclusion that a small number of wolves exist there (Kaminski and Hansen 1984; J. Johnston and J. Erickson, U.S. Forest Service, Boise, Idaho, unpublished report). The distance from Glacier National Park to Yellowstone is only 483 km, and from central Idaho to Yellowstone is only 241 km. Travel by wolves from Idaho to Yellowstone National Park would be perilous but entirely possible. Wolf dispersal movements of up to 886 km have been documented (Fritts 1983).

If wolf recovery continues in Montana and Idaho, dispersing wolves would eventually reach the Greater Yellowstone area. Wolves naturally recolonizing the Greater Yellowstone area could not be designated an experimental population under Section 10(j) of Endangered Species Act because the 1982 amendment refers to reintroduced populations. Moreover, a small population there could not be augmented with introduced wolves and be designated experimental because Section 10(j) stipulates that such a population (meaning animals or plants for release) must be "wholly separate geographically from non-experimental populations of the same species." One wolf advocate group (Earth First) has informally stated its intent to reintroduce wolves to Yellowstone National Park if government agencies do not do so. While the prospects of released captive wolves or wolf × dog hybrids being released into the park and forming a wild population seems remote, such an event should not be totally discounted. If such an illegal reintroduction were to occur, it might not be possible to confirm that released animals were not of natural origin; thus they would have to be left in the ecosystem. Interestingly, at least 33% of Wyoming residents surveyed believed that wolves already exist in Yellowstone National Park (Bath 1987b).

The regulation establishing an experimental population must define the area where the species would be found and where it would be identified as experimental. If individuals moved outside the defined area and mingled with nonexperimental individuals of the same species, the experimental designation apparently would not apply. Outside the boundaries of the experimental population area, wolves would be classified as endangered and be afforded all protections of the Endangered Species Act.

Establishing the geographical boundary between experimental and nonexperimental (receiving all protections of the Endangered Species Act) populations would be an important feature of state wolf management plans and the experimental population rule. In a zone management system, the outer perimeter of the outermost zone would define the limits of the experimental population area. In the Greater Yellowstone area it may be advisable to circumscribe a large region to allow management flexibility over a broad area into which wolves might be expected to disperse. This area could extend far to the east and south, but careful consideration of the northern and western extent would be necessary because a wolf population already exists in northwestern Montana.

In the red wolf project, the experimental population regulations apply over a four-county area, and animals that leave the refuge are retrieved (Parker et al. 1986). Retrieval of most wandering wolves in the Greater Yellowstone area does not seem practical, except early in a reintroduction effort when all animals would be wearing radio collars.

A 1985 decision by the U.S. Court of Appeals for the 8th Circuit—in the case of *Sierra Club et al.* v. *William Clark et al.*—has been of concern to state wildlife officials because of the potential effect on the control and management of the wolf in the northern Rockies. Montana, Wyoming, and Idaho have maintained that the decision that prohibited public sport hunting of the threatened wolf in Minnesota would jeopardize the use of public hunting or trapping to control individual wolves from a Yellowstone experimental population that roams outside the primary or core Yellowstone recovery area. This interpretation may not be correct, because Congress intended no connection between the taking of regular threatened species and taking of experimental populations, and the court's opinion explicitly made the same distinction and therefore contained no ruling on taking of experimental populations (Fritts 1990:1-37,1-38).

Example of Red Wolf Reintroduction

Advantages of Experimental Population Designation

Restoration of the red wolf to the wild was recently accomplished using Section 10(j) of the Endangered Species Act (Phillips and Parker 1988; Parker and Phillips 1991; Phillips et al., in preparation). That effort probably would not have been possible without the opportunity to designate released wolves as an experimental population (Parker 1989; Parker and Phillips 1991). In the early 1980's, the U.S. Fish and Wildlife Service attempted to reintroduce the red wolf to the Land Between the Lakes area in western Kentucky and Tennessee—a 68,800-ha recreation area administered by the Tennessee Valley Authority. A technical plan was developed for reintroduction and announced to the public in fall 1983. Resistance soon developed from the farm bureaus, various livestock associations in Tennessee and Kentucky, and owners of small livestock operations in the vicinity. The belief was widely held that presence of a reintroduced endangered species would obstruct local projects and programs and otherwise interfere significantly with lives of local citizens. This was a factor that led to abandoning the plan to reintroduce wolves to the Land Between the Lakes area, even though the area seemed to be biologically suitable.

In 1985 and 1986, the U.S. Fish and Wildlife Service developed a plan to reintroduce red wolves to the Alligator River National Wildlife Refuge in North Carolina. Regulations had been developed by this time for designating experimental populations, and the process had already taken place with three other species. When meeting with the public to explain the plan, U.S. Fish and Wildlife Service personnel were able to stress the management flexibility afforded by the experimental population designation. The U.S. Fish and Wildlife Service was able to address many of the concerns that the public voiced—for example, that hunting and trapping on the refuge would be prohibited due to the possibility of a wolf being inadvertently shot or trapped—when writing special regulations for the population. The flexibility made possible by the experimental population designation was of great value in winning the support of the public and was considered by project personnel to be a major factor in accomplishing the reintroduction. No changes in state laws or regulations were necessary. The red wolf project is a model for demonstrating how the experimental population designation can generate regulations that adequately protect wolves while still respecting the traditions of an area and its people, thereby securing the support of the public. A program is well under way to reintroduce an experimental population of red wolves into the Great Smoky Mountains National Park, largely because of the success of the reintroduction at the Alligator River National Wildlife Refuge (Parker 1990).

Provisions for Control of Red Wolves

Red wolves were introduced as a nonessential experimental population. During the public meetings and before the reintroduction, concern about accidental taking was frequently expressed by local citizens. Hunting and trapping are common in the refuge where the release was to take place with the possibility of accidentally taking a red wolf, even while exercising reasonable caution. North Carolina indicated that it would support the red wolf reintroduction as long as hunting and trapping on the refuge were not affected. Thus, the U.S. Fish and Wildlife Service decided that when taking was unavoidable, unintentional, and did not result from negligent conduct, no prosecution would be undertaken, assuming the taking was reported immediately to the refuge manager (Parker and Phillips 1991). Taking was allowed for educational purposes by federal or state officials or their designees; for scientific purposes; for enhancement of propagation or survival of the species; for zoological exhibition; to aid a sick, injured, or orphaned specimen; to dispose of or salvage a dead specimen; or when an animal represents a threat to human safety (all standard language) or is responsible for depredations to lawfully present livestock

(50 CFR 17.84(c)). The regulation did prohibit members of the public from taking red wolves that prey on livestock or otherwise cause property damage. Individuals suffering such losses must contact the U.S. Fish and Wildlife Service or state officials who are authorized to conduct control. In this circumstance, the U.S. Fish and Wildlife Service did not consider it a burden to local livestock producers for them to report problems to officials rather than to take wolves themselves. Livestock is scarce in the area, and no losses were reported in the first 2 years of the reintroduction (Parker and Phillips 1991).

The special rules apparently have the support of the local public. Two reintroduced wolves have been legally caught in leg-hold traps set by local fur trappers. In both instances, the captures were immediately reported, and red wolf project personnel successfully released the animals. Two of five automobile strikes were reported by the drivers, and investigations indicated the motorists were driving legally. The three nonreported cases were judged to be accidental, and no investigations were initiated (Parker and Phillips 1991). Even though hunters have sighted the wolves on at least 30 occasions, no wolf has been purposely killed to date. This result is extremely significant. Project personnel attribute this result to the fact that traditional uses of the refuge were not curtailed because of the reintroduction program. Again, this result has been possible because of the Section 10(j) amendment to the Endangered Species Act (Parker and Phillips 1991). Although distinct differences exist between red wolf management in North Carolina and gray wolf management in the Greater Yellowstone area, the advantages of the experimental population designation in crafting a reintroduction are clear from this example.

Reintroduction by Legislative Mandate

A legislatively mandated reintroduction of a threatened species occurred recently using the experimental population designation. Public Law 99–625, 100 Statute 3500 (1986) dictated specifications of a plan for the translocation of southern sea otters to San Nicholas Island off the California coast. The law required that the plan be developed by regulation, in cooperation with the appropriate state agency, and that it include the specification of a translocation zone and a management (otter-free) zone and some detail of how the zones would be managed. The U.S. Fish and Wildlife Service was required to make every effort to capture and return any sea otter that moved outside the translocation zone. Any member of the experimental population, while in the translocation zone, would be treated as a threatened species for purposes of the act—Section 7 was to apply only to agency actions that are undertaken in the translocation zone. Any otter within the management zone would be treated as a member of a species that is proposed to be listed under Section 4 of the Endangered Species Act. Taking by the public was prohibited—except that incidental taking within the management zone was not to be treated as a violation. The objective of doing this translocation by legislation and regulation was to guarantee that certain management measures could be implemented without legal challenge. Whether or not the reintroduction will be successful is still not known because many transplanted sea otters leave the release site (Booth 1988; Rathbun and Benz 1991).

A bill that likely would have required reintroduction of wolves to Yellowstone as an experimental population was introduced in the House of Representatives (H.R. 2786) on 28 June 1989. The bill, sponsored by Utah State Representative Wayne Owens, would have required the secretary of the interior to complete an environmental impact statement on the reintroduction of gray wolves to Yellowstone National Park and adjacent public lands by 31 December 1991. Selection of a preferred alternative would have been required within 60 days of completion of the environmental impact statement, and implementation of the decision would have begun within 6 months. Draft amendments would have provided for control of wolves by private landowners, formal public involvement in cooperation with an interagency effort to delineate a Yellowstone wolf recovery area, measures and funding to isolate and contain the experimental population, and provisions for state wildlife management agencies to designate wolves outside the recovery area as big game animals and control wolves when conflicts develop with state game management goals (T. Kaminski, personal communication). The purposes of the bill were to move the wolf reintroduction along through the normal administrative processes, clarify and solidify specific matters regarding wolf management that the authors of the bill considered difficult to resolve through normal administrative processes, and to solidify points of management so they would not be challenged in court. Examples of issues that the authors of the bill felt could best be handled with specific legislative language were involvement of state wildlife agencies in wolf management, description of zones, provisions for control, and participation of the public in control on private land.

Another wolf reintroduction bill (S. 2674) was introduced into Congress in 1990 by Senator James McClure of Idaho. Independent of the Endangered Species Act, that bill mandated the placement of three breeding pairs of wolves in the park and portions of central Idaho and removed them from the endangered species list outside those core areas (exclusive of northwest Montana). This approach would have superseded the normal National Environmental Policy Act (NEPA) process, although public input could have been obtained in another manner. This approach differs from the sea otter legislation and the Owens bill in that it is more of a purely legislative solution to the issue, rather than working within existing administrative mechanisms.

These legislative initiatives could have forced certain guidelines for wolf control on the National Park Service, U.S. Fish and Wildlife Service, and Animal Damage Control. Specific provisions for control would have been written in as law, thereby removing any uncertainties about the ability to manage the population. The NEPA process with an environmental impact statement might have been bypassed (at least with S. 2674) or done in retrospect, as was the case in the sea otter reintroduction, and public input—important in this issue (Bath and Phillips 1990; Peek et al. 1991)—would not necessarily have been heard.

Opposition may be longer-lived if the public is not able to voice its opinion on a matter, such as wolf control, that evokes such strong feelings. Also, the public may be able to offer information and insights that are not apparent to state and federal agencies and contribute significantly to the planning process. Legislation such as the sea otter legislation or the Owens Bill apparently can allow for formal public input, even though stipulations may have already been made on outcomes. One of the primary criticisms of the two wolf reintroduction bills was that going outside normal procedures to accomplish the reintroduction would weaken the Endangered Species Act (Keiter and Holscher 1990). Conservationists especially objected to details of S. 2674 that limited the areas of wolf protection and required delisting outside specified core zones before wolves reach population levels called for in the recovery plan (Cohn 1990).

In November 1990 an amendment to fiscal year 1991 appropriations language directed the secretary of interior to establish a 10-member Wolf Management Committee for the task of developing a wolf reintroduction and management plan for Yellowstone National Park and the central Idaho wilderness. The plan was provided to the secretary of interior and Congress by the required deadline of 15 May 1991. Several elements of the Wolf Management Committee's plan dealt with wolf control (Wolf Management Committee 1991).

The committee's report recommended that Congress immediately designate wolves in Idaho, Wyoming, and Montana (with the exception of the Glacier National Park area) as a nonessential experimental population, effective until 1 July 1993. In the meantime, wolves in the experimental population area would be managed by the Fish and Wildlife Service with ample control for depredations on livestock, including taking by livestock producers. By 1 July 1993, the states would prepare and adopt wolf management plans agreeable to the secretaries of interior and agriculture and governors of the three states. An environmental impact statement and rulemaking process would be conducted during the same period. Following completion of the necessary processes, states would assume primary management authority throughout the area except in national parks and national wildlife refuges. In its report, the committee recommended that states follow specific guidelines in developing management plans. The report recommended reintroduction to Yellowstone National Park and a 5-year evaluation of recovery progress in central Idaho. If a breeding population was not confirmed in central Idaho after 5 years, a reintroduction would be initiated.

Thus, the plan attempted to address concerns about serious effects on livestock and big game. Some of the specific provisions of the plan were (1) allowing livestock operators to kill wolves on private or public land when depredations occurred or when wolves were harassing livestock (subject to reporting provisions and other conditions); (2) compensating for livestock depredations from a publicly administered trust fund; (3) having a regulated public harvest managed by the states after reaching specified recovery levels; and (4) managing wolves in areas where they were conflicting with the state's ungulate management objectives, with management response varying with the stage of wolf population recovery, location, and effect, but with wolf recovery being the underlying theme. For specific language, the reader is referred to the Wolf Management Committee's plan itself, especially pages 4–19. Critics of the plan believe that broad interpretation of point 1 (above) would jeopardize wolf recovery in the Northern Rockies (see Fischer 1991).

Congress took no action on the committee's recommendations (Keiter and Holscher 1990; Strauch 1992). Instead, in November 1991, it directed the U.S. Fish and Wildlife Service, in consultation with the National Park Service and the U.S. Forest Service, to prepare an environmental impact statement concerning recovery of wolves in the Yellowstone area and central Idaho. Appropriations of $348,000 to the U.S. Fish and Wildlife Service and $150,000 to the National Park Service were included, with the stipulation that none of these funds can be used to reintroduce wolves to either area. The environmental impact statement must consider a wide variety of options, and the draft must be completed by May 1993. Wolf control will, no doubt, be a major topic in the development of the environmental impact statement.

Anticipated Control Within Yellowstone National Park

Background and Park Policy

Potential wolf control within Yellowstone National Park would be affected by legislation and resulting National Park Service policy. Control in the park is less sensitive to provisions of the Endangered Species Act than control outside the park. Special rules that would be written for managing an experimental population could also regulate control activities within the park, but the rules would probably reflect park policy.

Yellowstone National Park was created in 1872 when Congress set aside "a public park or pleasuring ground for the benefit and enjoyment of the people." The legislation assigned the new park under the administration of the secretary of the interior, who would be responsible for issuing regulations to provide for the "preservation, from injury or spoilation, of all timber, mineral deposits, natural curiosities, or wonders within said park, and their retention in their natural condition." Other park management functions included developing visitor accommodations, constructing roads and bridle trails, removing trespassers from the park, and protecting "against wanton destruction of fish and game" (16 USC 21–22).

Legislation in 1894 addressed the killing of wildlife within Yellowstone National Park (16 USC 3372). Section 4 of that act stated that "all hunting, or the killing, wounding, or capturing at any time of any bird or wild animal, except dangerous animals, when it is necessary to prevent them from destroying human life or inflicting an injury, is prohibited within the limits of said park . . . ."

The National Park Service was created by the Organic Act in 1916 for the purpose of promoting and regulating the use of the federal areas known as national parks, monuments, and reservations, "which purpose is to conserve the scenery and the natural and historic objects and the wild life therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations" (16 USC 1).

This language lies at the heart of national park system management philosophy, and the principles in the Organic Act still guide National Park Service policy today. Section 3 of the act allowed the secretary of the interior to "make and publish such rules and regulations as he may deem necessary or proper for the use and management of the parks, monuments, and reservations under the jurisdiction of the National Park Service . . . ."

The same section allowed the secretary considerable flexibility in the control of animals: "He may also provide in his discretion for the destruction of such animals and of such plant life as may be detrimental to the use of any of said parks, monuments, or reservations." (Language in this section granted the secretary permission to graze livestock in national parks, but Yellowstone was excluded because several members of Congress expressed concerns that commercial grazing would destroy its value as a wildlife sanctuary.)

Thus, Congress gave the park service permission to establish policy for controlling animals. The National Park Service has exercised this authority in controlling grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), elk, and bison in the park in recent times and in eliminating the wolf from the park earlier. Wolves and coyotes were reported abundant in 1870, but scarce in 1880 because of poisioning activities (Murie 1940:11). By 1889, Superintendent Captain F. A. Boutelle recommended predator control because predators were becoming plentiful along with other animals (Murie 1940:12). In 1915 the military administration of the park was assisted with the killing of the wolves by two U.S. Biological Survey hunters, hired under the authority of a congressional act calling for eliminating predators from all public lands (Weaver 1978:32; Lopez 1978:187). The practice continued when the park passed into civilian hands with the creation of the National Park Service and did not subside until 1935 (Murie 1940; Weaver 1978; Dunlop 1983). Although this policy seems difficult to understand today, it was well accepted in the early years of the park system.

National Park Service policies, including biological resource management, are found in Management Policies (National Park Service 1988). This document will be revised at appropriate intervals to include policy changes. Some local discretion on general policies is permitted. Pages 4.5–4.6 under Biological Resource Management, subheading "Protection of Native Animals," describe current National Park Service policy on control within national parks:

> "Management emphasis will be on minimizing human effects on natural animal population dynamics . . . . Native animal populations will be protected against harvest, removal, destruction, harassment, or harm through human action. Individual animals within a population may be removed only when . . . . removal or control of animals is necessary for human safety and health or to protect property or landscaped areas . . . ."

According to the Management Policies, the park service relies on natural processes to control populations of native species to the greatest extent possible. However, animal populations or individuals can be controlled when they present a threat to property or visitor safety and health. The decision to initiate a control program cannot be arbitrarily made but must be based on scientific information obtained through research. Planning and implementing control actions must comply with established planning procedures, including public review and comment. Where conflicts between humans and animals persist, a determination will be made of whether or not curtailing or modifying visitor use and other human activities might be a desirable alternative to controlling animals. The need for, and results of, controlling animal populations will be evaluated and documented by research studies and in a natural resource management plan.

The document identifies other management measures that may be used, including live trapping for transplants, gathering of research specimens for National Park Service and cooperating scientists, public hunting on lands outside the park, habitat management, predator establishment, sterilization, and destruction by National Park Service personnel or others. In controlling wildlife populations, highest priority is to be given to encouraging public hunting outside the parks and live trapping within parks for transplanting elsewhere.

Situations That Could Warrant Limited Wolf Control in Yellowstone National Park

The only need for control that I can envision within Yellowstone National Park is for occasional nuisance animals and, even rarer and in very special circumstances, chronic depredating wolves that have entered the park. Both occasions for control are expected to be rare. Most wild wolves are extremely shy of humans. Aggressive behavior of healthy wild wolves towards humans is rare (Munthe and Hutchinson 1978; Tompa 1983; Jenness 1985; Scott et al. 1985). Mech (1990) reviewed wolf–human interactions in North America and concluded that the few aggressive encounters documented seem to be either threats, defensive reactions, or some other kind of nonpredatory interactions, and none has resulted in serious injury. Many biologists have studied wolves at close range without being attacked (see Mech 1988 for example) and have removed pups from dens in the presence of adult wolves without incident (Murie 1944; Young 1946; Crisler 1958). Moreover, countless people have lived, worked, and played in wolf habitat without incident. For example, visitors have spent 19,000,000 days in Minnesota's Superior National Forest without a single wolf attack (Mech 1990). Thus, the prospect of wolves injuring humans in Yellowstone National Park is remote. If personal injury were to occur, it probably would be the result of a wolf losing its fear of humans. Some species (notably bears) become habituated to people within parks because animals learn that humans are not a threat and cease to fear them (Herrero 1985). Outside of parks, persecution of animals is more common. This human behavior may help reinforce animals' fear of humans or may select against unwary individuals.

Although wolves avoid humans in most areas, some loss of fear of humans might occur in Yellowstone National Park over a long period. Some individual variation exists in wolves' reluctance to approach people, associated objects, and domestic animals (Woolpy and Ginsburg 1967; Fritts 1982 and personal observation; Mech 1988). Individuals that are least shy (by genetic predisposition) would ordinarily be the ones most likely to be killed and removed from the gene pool. The lack of wolf persecution in Yellowstone National Park and the many people visiting the park could encourage habituation of wolves to humans and park situations in which wolves were perceived as a threat to human safety. (The number of visitors to the park in 1990 totaled 2,857,096; vehicles entering the park totaled 972,809.)

Experiences in other areas suggest that some wolves will be encouraged to approach humans after artificial feeding, as has been the case with bears, but that loss of fear of humans is a slow process for most wolf populations. Some minor habituation to people apparently has occurred in Denali National Park and Preserve, Alaska (L. D. Mech, personal communication), whereas little or no evidence for it has been noted in Isle

Royale National Park in the 40 years wolves have been there (Peterson and Morehead 1980; R. O. Peterson, personal communication). (People inhabit Isle Royale for only 4 months of the year.) Algonquin Park, Ontario, has noted three "tame" wolves since its establishment in 1893 (D. Strickland, Algonquin Park District, unpublished report). G. B. Kolenosky (personal communication) considers the behavior of one of the wolves, killed in 1987, to be that of a released captive wolf. Algonquin is a 7,511-km^2 park where 60,000 people/year travel in the interior, and where 150–300 wolves exist (Strickland and Rutter 1987). Yellowstone National Park is 1.2 times larger than Algonquin but has only 15% the number of backcountry camper-nights (32,279 vs. 211,200 in 1989). Thus, any such incidents should be even rarer in Yellowstone.

Bears that pose an obvious threat to humans within Yellowstone National Park are removed. The National Park Service closely monitors bears in developed areas and provides intensive public information and enforces laws to prevent habituation of bears to people, their foods, and the places people gather. The National Park Service uses a backcountry permit system to ensure that campers talk to rangers and to assign sites through an office that tracks bear reports. This system allows closure of sites for human safety where bears pose a threat, and allows bears the undisturbed use of a temporally important food source. The same systems could also be used to discourage human conflicts with wolves if it becomes necessary. Initially, we do not expect any wolf–visitor conflict.

Loss of fear of humans by coyotes has been widespread in national parks and urban areas where they associate with humans at campgrounds (Carbyn 1989). Coyotes and ungulates within Yellowstone National Park do not show the same fear of humans that they show in areas where they are frequently shot. Habituation of bears to people within the park has been a well-publicized problem (Schullery 1986) but has been reduced because of the strict sanitation measures now enforced (Schullery 1986). All garbage is removed from the park, and visitors are instructed repeatedly to store food and dispose of garbage properly. Visitors are monitored when bears frequent roadside areas to prevent people from intentionally feeding or closely approaching bears. These measures should prevent wolves from becoming dependent on garbage for food—a problem in Italy (Boitani 1982).

Another hazard that could confront park visitors is that of a diseased wolf. Wolves are subject to many diseases and disorders, including rabies (Carbyn 1982a), but the incidence of rabies seems to be rare (Young and Goldman 1944; Rausch 1958; Mech 1970). People have known about rabies in wolves for at least several centuries, and rabid wolves will attack humans, as will any other rabid canid, including dogs. Chapman (1978) reported that rabies decimated a pack of 10 wolves in northern Alaska. An incident of a wolf attacking a man in Canada in 1942 seemed to involve rabies (Peterson 1947). A rabid wolf was reported to have bitten several people at camps on the upper Green River in Wyoming in 1833

(Lopez 1978:71). Rabies has never been documented in wild Minnesota wolves. This disease seems to be more common in wolves in the higher latitudes of this continent; the lowest latitude for which this disease has been documented in North American wolves is about 58° north latitude (L. D. Mech, personal communication). The prospects of wolves becoming infected with rabies in Yellowstone National Park were thoroughly examined by Johnson (1992). He concluded that the chances of rabies infecting reestablished wolves or any other animal in the park were extremely remote because of patterns of geographical distribution of terrestrial rabies, distribution among species, and factors influencing spread of the disease. Rabies has never been reported in the park (Johnson 1992). Clearly, any wolves that did develop rabies would have to be quickly eliminated.

Another situation in which wolves might approach humans is when attacking dogs. Dogs are allowed in Yellowstone National Park campgrounds on a leash; they are not allowed on trails or in the backcountry. Studies in Minnesota and observations in Canada and Alaska have revealed that when wolves are intent on attacking dogs they do not display the usual caution about coming near humans. To the contrary, they frequently cause alarm by their apparent boldness. Most attacks on dogs in Minnesota occurred in the owners' yards and occasionally in the presence of a human (Fritts and Paul 1989). When dogs are killed, they are often eaten (75% of instances in Minnesota), which can amplify the owners' reaction. After killing a dog, individual wolves or wolf packs may deliberately seek dogs for a few days or weeks, causing a cluster of problems. Such episodes could conceivably develop within Yellowstone National Park at residences of park employees or campgrounds.

The National Park Service would be the agency responsible for controlling nuisance wolves within Yellowstone National Park. Before wolves are reintroduced, the park service, in consultation with the U.S. Fish and Wildlife Service, could define nuisance wolves in guidelines patterned after those for the grizzly bear (Mealey 1986). The park could also write procedures for determining management responses to these wolves, as are now in place for the grizzly bear (Yellowstone National Park 1983). Control of nuisance wolves would include capture of the problem individual(s) by trapping or darting. A list of zoos that might accept the wolves would be maintained. If the zoos would not accept the wolf, the animal could be translocated to another part of the park where encounters with humans were less likely. However, translocation may not provide a permanent solution. Translocated wolves often try to return to their capture site or move long distances away from their release site (Henshaw and Stephenson 1974; Weise et al. 1975; Fritts et al. 1984; Fritts 1993). Due to the size constraints of the park, the maximum relocation distance possible is approximately 178 km (diagonal distance) and the greatest within-park distance that a wolf could realistically be taken from its capture site is closer to 121 km. Nuisance wolves captured within the park probably would not be released outside the park. If a wolf were to engage in nuisance behavior after being translocated once, it could be recaptured and humanely euthanized.

Another potential situation in which a wolf might have to be captured or destroyed is in the event of an injury caused by a visitor, such as an automobile strike. As mentioned earlier, 972,809 vehicles entered the park in 1990. The park has 595 km of paved roads. The speed limit is 72 km/h except on a 37-km stretch near the northwestern edge within Montana where it is 88 km/h. The potential therefore exists for wolves to be struck by cars on park roads. Automobile strikes are a fairly common cause of wolf mortality in areas with paved roads; eight studies in the Great Lakes region were reviewed by Mech with the conclusion that vehicle strikes constitute an important mortality factor (L. D. Mech, personal communication). Five of 16 captive-raised red wolves that have died in the Alligator River National Wildlife Refuge in North Carolina were killed by vehicles, making vehicles the single most important cause of death. To reduce vehicle collisions, the North Carolina Department of Transportation has erected red wolf crossing signs. Local radio stations air public service announcements alerting motorists to the possible presence of red wolves along the highways, especially during tourist season (Phillips et al., in preparation). Reintroduced wolves born in the wild may be more susceptible to automobile strikes soon after release than those that have had more time to become familiar with the area.

Wolves are occasionally injured severely but not killed outright by the impact of an automobile. If that happened within Yellowstone National Park, humane euthanization of the wolf would be appropriate (assuming complete recovery is unlikely). Euthanasia of wolves in this situation is authorized by language in the Endangered Species Act and by National Park Service regulations and policy. Mention of these circumstances can also be covered in special rules for an experimental population, as was done with the red wolf (50 CFR 17.84 (c)).

Additional guidance applicable to wolf control within the park is found in the National Park Service's *Natural Resources Management Guidelines* (National Park Service 1991) that states

> Predators are part of the natural ecosystem. No native predator will be destroyed on account of its normal utilization of any other park animal.
>
> Control of predators that are killing livestock or game animals shall be practiced outside of the park's boundaries. Entry into the park for the purpose of controlling predators will not be permitted.

> The National Park Service will cooperate with the control of predators that are causing financial damage, for example, by controlling any human influenced attractant in the park that is exacerbating the problem (for example, garbage) or by reporting a predator's departure from the park.

Recognizing these guidelines as guidelines, consideration might be given to authorizing special agents to take specific identifiable wolves that had persistently killed livestock outside the park but eluded capture by taking refuge inside park boundaries (or if their capture outside the park was not possible for some reason). Such action would have to be done in conjunction with an approved management plan. Because of distance from the park to livestock allotments and logistical considerations, such a scenario is very unlikely. Trapping near the depredation site is the principal method of wolf control expected. Early in wolf restoration efforts, all or most wolves in the Greater Yellowstone area would be radio-collared, possibly with radio-controlled capture collars (Mech et al. 1984, 1990; DelGiuduce et al. 1990).

If a radio-collared wolf were known to depredate, the radio could be useful in the capture of the individual and conceivably used to follow a wolf into the park. Based on control efforts involving radio-collared wolves in Alaska, a segment of the public might view such use of collars as an unfair advantage to the control agents and object to the action.

Another possible situation in which control could occur within the park is in the unlikely event that a local population of prey is about to become extinct because of wolf predation. If that highly improbable situation arose, the park would want to intervene, but in such a manner as to have minimal effect on the wolves involved. Both these issues could be addressed in the special rules for an experimental population, if reintroduced wolves were so designated.

In summary, the only wolf control inside Yellowstone would be that necessary to deal with nuisance animals and to possibly take specific individuals that were persistently killing livestock outside the park—but could not be captured outside the park—or to aid injured or sick individuals. Nuisance behavior would be defined and rules established for controlling nuisance wolves, much like those in place for grizzly bears. Few wolves are expected to require control. National Park Service personnel would conduct the control. The type and extent of control that would be needed is permissible within the present National Park Service statutes, regulations, and policies and could be included in the special rules that would be written for an experimental population, if reintroduced wolves were so designated.

Wolf Control Outside Yellowstone National Park

Situations That Could Warrant Wolf Control

With the exception of limits on grazing and hunting in Grand Teton National Park and on lands administered by the U.S. Fish and Wildlife Service, Greater Yellowstone area public lands outside Yellowstone National Park are managed for multiple use, and it is here that conflicts are possible between wolves and livestock producers, wildlife managers, and hunters. Although national parks were founded on principles of preserving natural features, historic objects, and wildlife for public enjoyment, Congress has mandated that national forests be managed for multiple uses, including recreation, wildlife, grazing, mining, oil and gas drilling, watershed protecting, timber cutting, and wilderness. The Endangered Species Act nonetheless requires all federal agencies to carry out conservation (recovery) programs for endangered and threatened species and to ensure that agency actions are not likely to jeopardize the continued existence of listed species or degrade or destroy their critical habitat. In addition to these differing management objectives inside and outside of Yellowstone National Park, the involvement of, and potential for conflict among, several federal and state regulatory agencies add to the complexity of reaching a satisfactory compromise on the issue of wolf control outside of Yellowstone National Park. Section 7 consultation would not be an issue outside the park if wolves are designated as nonessential and experimental. (Within the park, formal Section 7(a)(2) consultation will be necessary.) Wolf management should not lead to land-use restrictions, such as those required for grizzly bear management, due to the biological and behavioral differences between the two species. Biologically, wolf recovery should be easier to accomplish because the reproductive rate of wolves is such that the loss of an individual (or even a pack) will be of minor significance compared to the loss of a single reproducing female grizzly bear. Moreover, the reproductive potential of wolves is such that recovery levels may be reached much faster. The two primary circumstances that may require some form of wolf control outside the park are depredation on livestock and excessive predation on big game.

Depredation on Livestock

Wherever wolves and domestic animals have coexisted in North America, some degree of depredation has occurred; the Greater Yellowstone area would be no exception. Historically, the severity of this problem in the West probably has been grossly overstated (Lopez 1978:182). Nonetheless, livestock depredations are a primary reason that wolves were eliminated from the West less than a century ago (Young and Goldman 1944; Lopez 1978).

Scientists have only recently inquired objectively into the actual nature and extent of wolf depredations on livestock. The number of depredations has been low in Minnesota, Alberta, and British Columbia where this problem has been documented in detail (Fritts and Mech 1981; Dorrance 1982; Fritts 1982; Bjorge and Gunson 1983, 1985; Gunson 1983; Tompa 1983; Fritts et al. 1992). In the first 10 years of wolf recovery in Wisconsin, three depredations involving two sheep and three dogs have occurred (R. P. Thiel, personal communication). Verified complaints of depredations in Minnesota during 1975–89 averaged 32/year, and an average of 24 farms were affected annually (about 1 out of every 300 farms in the wolf range). During winter, cattle and sheep are confined or their movements are restricted to fields near farm buildings, but in late April or May they are released to graze in open and wooded pastures until about October. Cattle (mostly calves), sheep, and turkeys are the most common domestic prey of wolves in Minnesota. Verified losses of cattle and sheep from 1979 through 1989 averaged 25 and 47 annually (Fritts et al. 1992). From 1977 through 1989, the highest annual cattle losses claimed by farmers in Minnesota were 4.5/10,000. Highest sheep losses claimed were 26.6/10,000. Wolf depredations on livestock were highly seasonal; cattle losses peaked in May, and sheep losses peaked in July through September. The magnitude of the losses was related to animal husbandry practices and to the severity of the winter before the attacks (Fritts 1982; Mech et al. 1988; Fritts et al. 1992). Most wolves fed on wild prey even when the wolves lived near livestock. Although the effect on livestock production in Minnesota as a whole was very small, each year a few individual producers were seriously affected. During 1979–89, an average of 43 wolves/year were captured and 36/year (2% of the winter population) destroyed in Minnesota out of a population of 1,500+. Both depredations and number of wolves controlled increased over these periods (Fritts et al. 1992). Most indices of the depredation problem, as well as the number of wolves controlled, were higher in 1990 and 1991 than in previous years (W. J. Paul, unpublished data).

Most depredations on livestock in Canada occur in Alberta and British Columbia because of the overlap of wolf range and livestock operations in those two provinces (Dorrance 1982; Carbyn 1983). In Alberta during 1972–81, there was an annual average of 140 wolf depredation complaints, of which approximately 44% resulted in compensation. During 1974–80, 365 indemnity payments were approved: 67% confirmed, 18% probable, and 15% missing (Gunson 1983). Bjorge and Gunson (1983) studied the relations between wolves and cattle on remote grazing leases in the Simonette River area of northwestern Alberta during 1976–80. An average of 1,885 cattle/year grazed in an area occupied by 27 to 29 wolves. An annual average of 3.2% of these cattle were lost to all causes. Known wolf kills and maulings for the 5 years totaled 16 and 51, respectively. Annual known losses and maulings from wolves averaged 3.2 (0.17%) and

10.2 (0.54%), respectively; however, it was unlikely that all kills were detected. Wild ungulates formed the bulk of the diet there, even though wolves had free access to cattle. The primary control method by government personnel was poisoning with strychnine. In Alberta, shooting and trapping were the main methods used by the public. An average of 88 wolves/year were removed out of a population of perhaps 5,000 during 1972–80 (Gunson 1983). During 1980–88, an average of 46 wolves/year (range, 17–109) were taken by Alberta Fish and Wildlife personnel during depredation control (J. R. Gunson, personal communication).

In British Columbia during 1978–80, an average of 144 wolf depredation complaints were confirmed each year (Tompa 1983). Some of the complaints involved harassment, missing animals, and maulings, in addition to kills. Verified wolf-related losses of all stock in the province were consistently less than 0.1%. An average of 152 wolves/year was controlled during 1978, 1979, and 1980 out of a provincial population estimated at 6,300. Poisoning, shooting, and trapping were the main control methods used (Tompa 1983). During 1985–89, an average of 100 wolves/year were taken on depredation control activities (R. Archibald, personal communication).

Depredations on livestock have occurred in Montana since wolves began recolonizing that state (Bangs et. al, in preparation). In 1980, a lone adult male killed several cattle and sheep over several months near Big Sandy, Montana, before it was killed by an Animal Damage Control trapper. In 1987, a pack of 7 wolves killed 6 cattle and 10 sheep on the Blackfoot Indian Reservation just east of Glacier National Park. Evidence exists that wolves had been present on the reservation for years. Individual wolves had been illegally killed there previously, and evidence was found in 1987 of earlier den use. Four of the wolves involved in the 1987 incident were killed and two were placed in captivity. A pack of at least five wolves west of Kalispell, Montana, were thought to have killed a minimum of three cattle in summer 1989. Four members of the group were captured and translocated in 1989. A surviving pup from the 1989 litter killed four calves at the same ranch in spring 1990 before being killed by Animal Damage Control personnel; a companion of that wolf subsequently killed another calf before apparently leaving the area. In spring 1991, a group of four 11-month-old wolves killed two steers in an area about 56 km northwest of Missoula, Montana. Average annual losses in Montana during 1987–90 were 3.5 cattle and 2.5 sheep in an area where a minimum of 75,000 cattle and 11,000 sheep graze.

No depredations on farm animals by reintroduced red wolves have been reported since the U.S. Fish and Wildlife Service began releasing them in 1987 in North Carolina. However, little livestock is raised in the area (Parker and Phillips 1991; M. K. Phillips, personal communication).

In the Greater Yellowstone area, the greatest potential for depredation on livestock would be on the grazing allotments in each of the six national forests that surround Yellowstone National Park. Slightly more than half of these national forests are open to cattle and sheep grazing. Of the 708 allotments, only 81, or 11.4%, are in or partly within wilderness areas near the park (N. A. Bishop, personal communication). Considering the Greater Yellowstone area as a whole (including the park), about 44% is open to grazing, with grazing occurring primarily in portions of forests most distant from the park (Fig. 1). Livestock numbers on 708 allotments in 1989 were 74,868 cattle, 120,609 sheep, and 1,231 horses (Table 1). The number of sheep on allotments in the Greater Yellowstone area exceeds that on farms in Minnesota, but the number of cattle is much smaller. Based on the Minnesota studies, sheep are more likely to be preyed on by wolves than are cattle and horses. Therefore, the greatest depredations may occur in the Targhee National Forest, which had 93,129 sheep (89 permits) on allotments in 1989, followed by the Shoshone, which had 12,489 sheep (11 permits). The density of livestock, particularly sheep, on public and private land southwest of Yellowstone National Park may cause the potential for conflicts to be higher there than on other sides of the park. On the other hand, it is uncertain whether wolves would be able to inhabit the park's southwestern corner because of deep snow and absence of a year-round prey base (Koth et al. 1990).

Most livestock in the Greater Yellowstone area is not placed on grazing allotments until at least mid-June. For cattle, the average annual date ranges from 13 June on the Bridger–Teton Forest to 3 July on the Gallatin and averages 26 June for the six forests combined. The average time in the national forests is 101 days/year (Table 2). Calving occurs before annual placement. In Minnesota, 80% of cattle losses to wolves are calves, and depredation on cattle peaks in May when most calves are still small (Fritts et al. 1992). Approximately 43% of verified depredations on cattle in Minnesota occur before 26 June. Larger calves and adult cattle are more capable of withstanding wolf attacks. Therefore, the possibility exists that depredations on cattle by wolves in the Greater Yellowstone area would be minor because most calves are already past the size of greatest vulnerability when they are released into the national forests. On the other hand, cattle losses peak in mid- to late summer in Alberta and British Columbia (Gunson 1983), and two of the three recent livestock depredations by wolves in Montana occurred in late summer (Bangs et al., in preparation).

Sheep arrive at national forests later than cattle, with forest averages ranging from 3 July in Gallatin National Forest to 17 July in the Beaverhead National Forest and averaging 10 July for the six forests combined. Sheep are present in the forests for a briefer period than cattle ($\bar{x}$ = 67 days vs. 101 days; Table 3). Unlike cattle, which are unguarded, sheep are accompanied by herders who keep them moving to prevent overgrazing. The presence of herders may deter depredations by wolves (Curnow 1969:36). Wolf depredation on domestic sheep peaks in July through September in Minnesota (Fritts et al. 1992), when the sheep are present on the national forests in the Greater Yellowstone area. Because

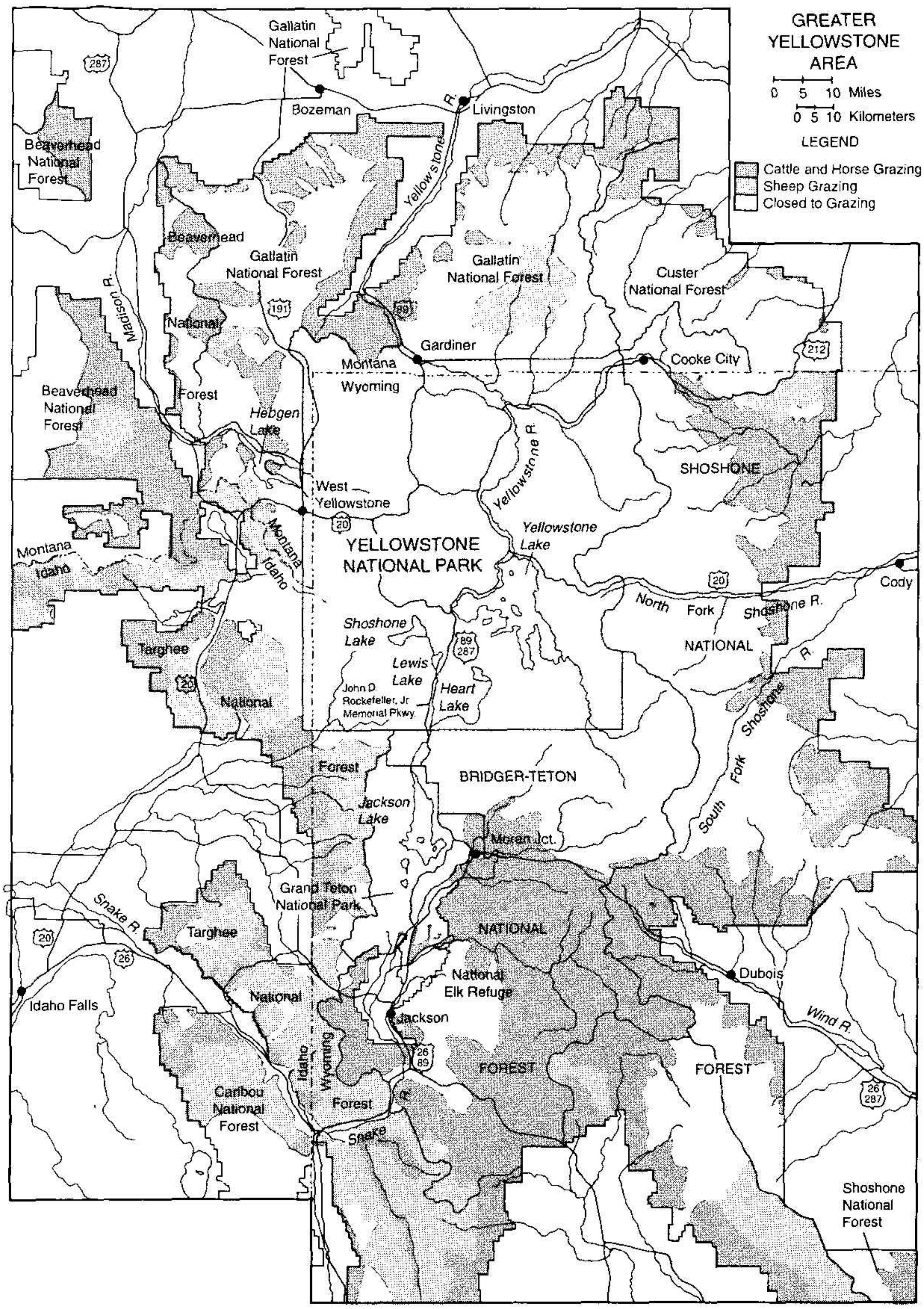

Fig. 1. Areas grazed and areas closed to livestock grazing in the Greater Yellowstone area.

depredation on sheep usually involves more individuals killed over a shorter period than cattle (Fritts et al. 1992), it would be especially important to implement control measures promptly when sheep are being killed.

Predator losses on Greater Yellowstone area grazing allotments run less than 1% for cattle and about 5% for sheep. About half of all live-

Table 2. Average dates that cattle arrive on and depart from grazing allotments in national forests in the Greater Yellowstone area (1989).

National forest	Average arrival date	Average departure date
Beaverhead	6/27 (178)[a]	9/30 (273)[a]
Gallatin	7/3 (184)	10/6 (279)
Custer	7/1 (182)	10/3 (276)
Bridger–Teton	6/13 (164)	10/15 (288)
Targhee	6/25 (176)	9/30 (276)
Shoshone	6/26 (177)	10/8 (281)
Average	6/26 (177)	10/5 (278)

[a] Figures in parentheses are Julian dates. Average time on allotments is 101 days.

Table 3. Average dates that sheep arrive on and depart from grazing allotments in national forests in the Greater Yellowstone area (1989).

National forest	Average arrival date	Average departure date
Beaverhead	7/17 (198)[a]	9/15 (258)[a]
Gallatin	7/3 (184)	9/11 (254)
Custer	no sheep	no sheep
Bridger–Teton	7/6 (187)	9/30 (273; 2 permitees)
Targhee	7/10 (191)	9/15 (258)
Shoshone	7/16 (197)	9/4 (247)
Average	7/10 (191)	9/15 (258)

[a] Figures in parentheses are Julian dates. Average time on allotments is 67 days.

stock losses are thought to be due to predators, and coyotes probably are the primary predator. Bears and eagles (*Aquila chrysaetos* and *Haliaeetus leucocephalus*) also kill some domestic animals (Congressional Research Service 1986:90). Wolves are known to kill coyotes (Carbyn 1982b). Conceivably, an established population of wolves in the Greater Yellowstone area could lead to a reduced coyote population and fewer coyote depredations on livestock in some areas, but it is doubtful that wolf recovery would cause an appreciable reduction in livestock losses caused by coyotes.

Indemnity programs exist for livestock lost to wolves in Minnesota (Fritts 1982; Fritts et al. 1992), Alberta (Gurba 1982; Gunson 1983), Ontario (Kolenosky 1983), and Italy (Boitani 1982). Defenders of Wildlife, a private environmental group, has established a compensation fund for depredations by wolves in the northern Rockies (Fischer 1989) and currently has over $100,000 in the fund (H. Fisher, personal communication). Although dealing with instances of missing livestock is a common difficulty, compensation programs are generally deemed successful and well worth the cost. Relations with the agricultural community are unquestionably strengthened by these programs (Gunson 1983; Fritts et al. 1992). Nine Montana ranchers have been paid about $11,000 through July 1991 (H. Fischer, personal communication).

Nonlethal methods of reducing losses of livestock to wolves might play some role in the Greater Yellowstone area. For example, modifying livestock husbandry practices (Fritts 1982; Tompa 1983) and using guard dogs (Coppinger 1987) might reduce losses in some situations, although implementing such measures may be difficult on remote pastures.

Because wolves may follow prey as they migrate between winter and summer range, a problem that does not exist in most other areas of North America may arise. Some of the original Yellowstone wolves seemingly followed ungulates in their altitudinal migrations to and from summer and winter ranges (Weaver 1978:18). Even if denning on or near ungulate winter range in the Greater Yellowstone area turns out to be common, considerable elk winter range exists where wolves could den within Yellowstone National Park, and those areas would likely be preferred denning areas, as in the past (Weaver 1978:18 and personal communication). If wolves follow elk to wintering areas in lower elevations outside the park, the wolves might remain there after elk return to summer range. Wolves breed in late February and pups are born in late April at the latitude of Yellowstone National Park. Pups are not mobile enough to travel far until midsummer. Wolves, therefore, might not be able to move to ungulate summer range until midsummer and could prey on local livestock if natural prey is scarce (Curnow 1969:33; Edgar and Turnell 1978:76). This scenario is what might have happened in a depredation incident east of Glacier National Park in 1987 if the wolves involved were from the park (their origin is unknown).

Some depredation on pets, especially dogs, is a possibility in the Greater Yellowstone area outside the park (see section on situations that could warrant limited wolf control in the park). From 1979 through 1987, officials confirmed 28 instances of wolves wounding or killing dogs in Minnesota. Wolves killed at least 24 dogs and wounded 10; 14 of 19 dog carcasses examined were partially or fully eaten. Most attacks occurred near the dog owners' yards. During attacks on dogs, wolves appear oblivious to humans (Fritts and Paul 1989).

If wolves become established in the Greater Yellowstone area, some individuals will eventually prey on livestock and others will threaten the welfare of livestock and pets. The number of depredations cannot be predicted, but probably would be small if findings in Canada and Minnesota are representative (Mack et al. 1992). A risk analysis for livestock in the Greater Yellowstone area should be done. Losses probably would be low at least during the early years of recovery because wolves would be few and the prey would be abundant. Experience shows us that, whatever the number of losses, they would be given a high degree of attention by the news media, and the public attitude toward the wolf would suffer, at least in the agricultural community. Even an occasional depredation could result in an inflated perception of the wolf as a livestock predator and lead to profound concern in ranching communities. Human responses to losses from wolves dwarf reactions to losses to other predators.

Wolf control is imperative when depredations on livestock occur. Provisions must be in place to deal quickly and effectively with problem wolves, both to solve the local problem and to avoid public perception of government inaction. Leaving problem wolves in the population may exacerbate the level of depredations in the long run. Wolves that kill livestock should not be the building blocks of a Greater Yellowstone area wolf population.

Predation on Ungulates

Predation on big game is another major factor leading to intolerance of the wolf (Mech 1970). Wolves coevolved with their prey, resulting in a good match between ability of wolves to successfully hunt and that of their prey to escape. While wolves are adept predators, their prey is, on average, adept at detecting and eluding them. This balance in capabilities has allowed ungulates to persist over the millennia despite constant predation by wolves and other animals and has been a major factor in developing and maintaining the anatomical, physiological, and behavioral adaptations of ungulates that makes hunting them "sport."

Experiences elsewhere have shown that reducing the number of wolves to increase hunter opportunity is more controversial than control to protect domestic animals. Alaska and the western Canadian provinces have been the sites of debate and litigation on this issue over the past several years (for examples, see Harbo and Dean 1983; Haber 1988; Williams 1988; Kerasote 1989). State and provincial wildlife agencies have been censured for controlling wolves, and data used to support control has been criticized by other wildlife professionals and conservation groups.

Even wolf biologists disagree about the effect that wolves have on populations of their ungulate prey. The effect is difficult to measure and difficult to distinguish from other factors influencing population dynamics. Many years of study may be necessary to assess the effect of wolf predation. Apparently, wolves have different effects in different circumstances (for examples, see Mech 1970; Mech and Karns 1977; Connolly 1978; Fritts and Mech 1981; Gasaway et al. 1983; Keith 1983; Taylor 1984; Messier and Crete 1985; Theberge and Gauthier 1985; Van Ballenberghe 1985; Gauthier and Theberge 1987; Bergerud and Ballard 1988; Peterson and Page 1988; Fuller 1989). Other sections of this monograph address that question as it pertains to Yellowstone, but the question cannot be answered definitively until the wolf is present and may then require many years of study. Any effect may not be perceptible for some time. Return of wolves to the Greater Yellowstone area would provide a rare opportunity to add greatly to the understanding of how wolves influence an ecosystem, and that opportunity should not be wasted (R. J. Taylor and C. J. Walters, Utah State University and University of British Columbia, unpublished report).

Research into wolf ecology in some areas of North America has suggested that, at least in certain circumstances, wolves can reduce ungulate populations (see Gauthier and Theberge 1987 for review) and opportunities for hunters. This situation would occur, for example, after some other environmental factor—such as weather, habitat deterioration, or overhunting—has already reduced ungulate levels. In these circumstances, wolves can accelerate the rate of decline of a prey population and suppress it for longer and at a lower level than would be the case in the absence of wolves. Such conditions are not normal in North America. Wolves, bears, and hunters often seek the same prey without driving the ungulate populations to low levels. For example, the wolf has returned to the Kenai Peninsula in Alaska in recent times with no perceptible effect on ungulate levels or hunting regulations. In fact, a successful caribou reintroduction was conducted subsequent to wolf recovery (Kenai National Wildlife Refuge, unpublished data).

Wildlife managers may legitimately try to restore suppressed ungulate populations to a former higher level or raise harvest levels. This is not normally a concern inside Yellowstone National Park because of National Park Service management objectives. It is a concern outside the park because hunting of big game is widespread in the national forests, wildlife refuges, and private land in the Greater Yellowstone area.

In addressing wolf predation on a herd that is declining, state wildlife agencies will have at least five options available: (1) reduce the hunting kill; (2) shift hunting pressure from females to males; (3) reduce wolves; (4) do #1, #2, and #3; or (5) do nothing. The public response to option 3 can be predicted. Given the case history in Alaska and elsewhere, some hunters will demand wolf reductions. A large segment of the public will oppose reduction of wolves at nearly every level, but especially if it is justified on the basis of providing more ungulates for the hunter (Van Ballenberghe 1989). From a biological standpoint, wolf reduction can occur if it is done in such a way that the survival of the overall population is not jeopardized.

Because some populations of prey that may be used by wolves are already harvested at nearly maximum sustained yield (Vales and Peek 1990), reduction of wolf populations in some areas of the Greater Yellowstone area may become biologically prudent. To reintroduce the wolf is to interject a new variable into the already complex task of managing populations of ungulates outside the park. Wolves should be managed in ways compatible with state objectives for ungulate management, consistent with the long-term conservation of the wolf. Wolf and ungulate management cannot be treated as separate issues but must be considered together, as recognized by the Northern Rocky Mountain Wolf Recovery Plan (U.S. Fish and Wildlife Service 1987:36).

The foremost problem in controlling wolves for ungulate production would be determining or defining the exact circumstances in which wolf reduction should be practiced (Theberge and Gauthier 1985; U.S. Fish and Wildlife Service 1987:33). Criteria must be established in advance for determining if or when control should begin and when it should end so that these decisions are not made subjectively. The location of the control work and numbers of wolves to be taken would need to be clearly identified and enforced for the desired results to be achieved. Criticism of and litigation over killing wolves can be expected in the absence of data that show the action would have the desired effect on the ungulate population. Thus, fairly in-depth understanding of the relation between wolves and their prey in the Greater Yellowstone area would be important. On the other hand, enough studies of wolf control have occurred in Alaska and Canada to allow some generalizations and guidelines without definitive data each time wolves are to be controlled (Wolf Specialist Group, International Union for Conservation of Nature and Natural Resources, Species Survival Commission 1984). A study of wolves and their prey before each control effort for ungulate management in the Greater Yellowstone area should not be necessary or is not reasonable.

Control Options and Management Zones in the Greater Yellowstone Area

In a simple sense, the possibilities for intensity of wolf control in the Greater Yellowstone area could be portrayed as points along a continuum (Fig. 2). The continuum theoretically could stretch from very intensive control, including allowing taking of wolves by the public immediately outside the park boundary, to essentially no control anywhere within the area. Historically, the level of wolf control practiced in the Greater Yellowstone area was at the intensive control end of the continuum (Lopez 1978; Weaver 1978). Control programs of past eras in the West had the objective of eliminating the wolf, and control methods were used that will not be seen again (besides the fact that we are now dealing with a national park).

As we move toward less control, the potential for conflicts with livestock production and big game management increases. A management

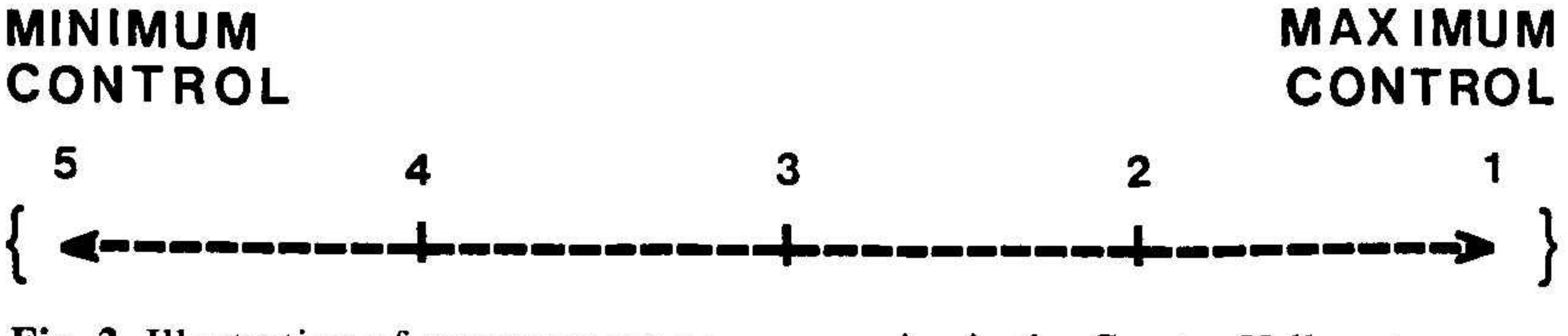

Fig. 2. Illustration of management zone scenarios in the Greater Yellowstone area as a continuum.

scheme toward the right end of the scale should mean fewer conflicts but may also mean longer time to reach population recovery, lower overall population size, and greater risk to the population. Wolf control could have various demographic and genetic effects, depending on the size and composition of the wolf population (Boyce 1990). As pointed out by Boyce, the probability of extinction is strongly related to the size of the overall wolf population, which in turn is dependent on the size of the area (zone) in which wolves are allowed to exist without control. For example, if wilderness areas and national forests surrounding Yellowstone were included in the recovery zone, the total number of wolves could be much higher and the population much more secure (Boyce 1990). The degree of control that is optimal for balancing opposing objectives and interests in the Greater Yellowstone area would seem to lie somewhere between the ends of the continuum.

A thorough risk assessment of the effects of wolf control on a small recovering wolf population in the Greater Yellowstone area could shed light on the advisability of different control levels. If control were too intensive, the population might have to be augmented with further releases to ensure recovery goals are reached. For example, a strategy could be implemented whereby wolves taken in control activities in the early stages of recovery would be replaced with additional wolves.

Decision analysis may be a useful tool in helping managers make difficult control-related decisions in which there seems to be a trade-off between meeting wolf recovery goals and resolution of wolf conflicts (Maguire 1986; J. Weaver, personal communication). This decision-making process may be especially useful in the early stages of recovery.

Management zones (U.S. Fish and Wildlife Service 1987), if used in the Greater Yellowstone area, could provide different management (control) in different areas or in different circumstances to meet specific goals and objectives (Fig. 3). Management zones would be distinct areas where wolves would be managed differently based on such factors as biological suitability of the habitat, the need for protection, and potential for conflicts with human economic endeavors. A number of assumptions are inherent in the zone management concept: (1) places exist where wolves belong and places they do not belong because of potential conflicts with man; (2) adequate habitat to support a viable population should exist in the zone or zones where the species is afforded most protection; and (3) the species should receive high priority in the central zone (i.e., zone with most protection, but other activities are of higher priority in the outer zone[s]). Zone management of wolves may or may not be preferable in the Greater Yellowstone area. The Northern Rocky Mountain Wolf Recovery Plan (U.S. Fish and Wildlife Service 1987) recommended management by zones and assumed zones would be developed during a NEPA-type process. Three zones were recommended as follows in the recovery plan for each of the three Northern Rocky Mountain Wolf recovery areas (in-

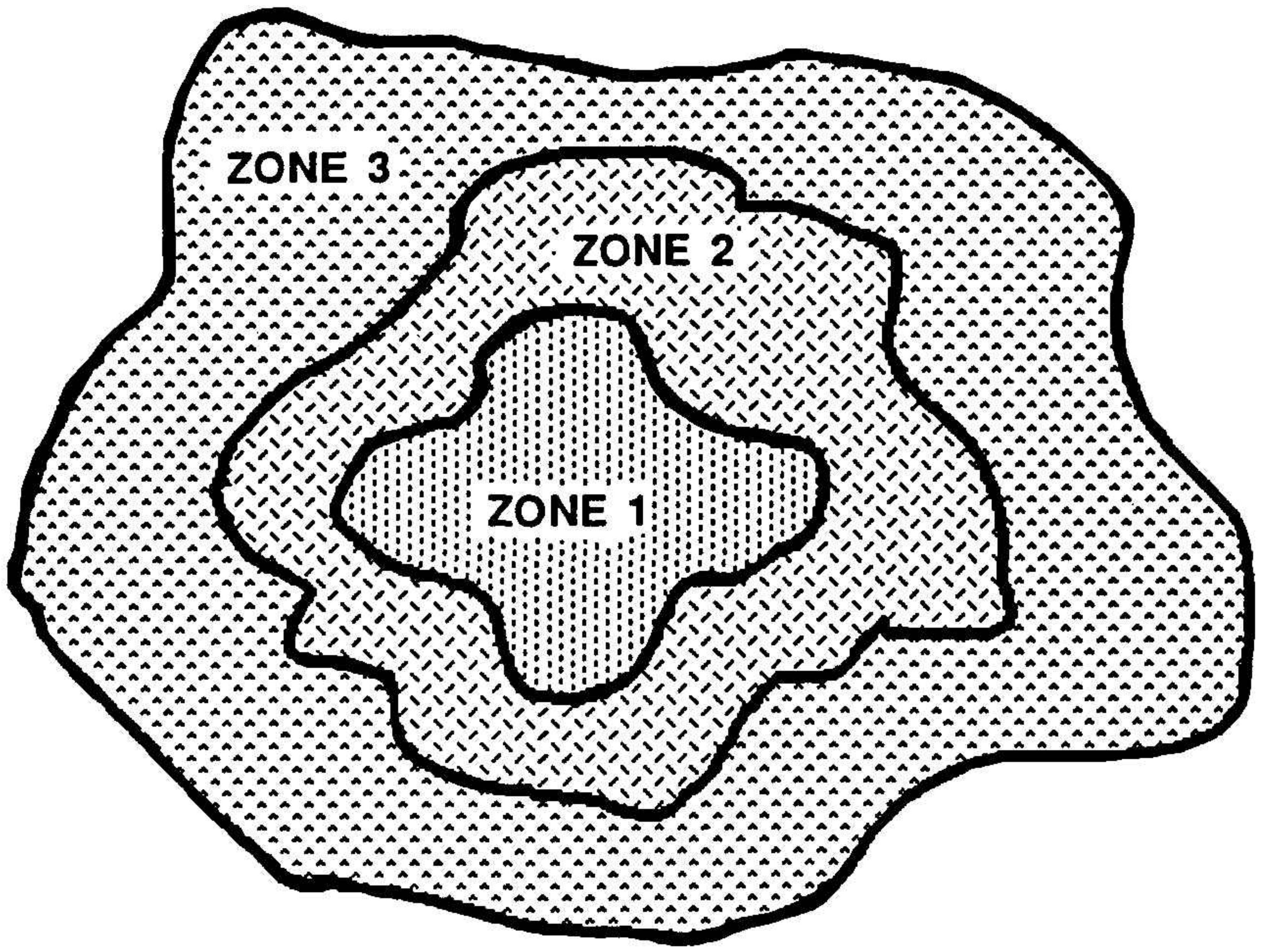

Fig. 3. Hypothetical zone management option for wolves in the Greater Yellowstone area. (Note: The outside boundary of zone 3 defines the experimental population area. Wolves outside that zone would receive all protections of the Endangered Species Act of 1973, as amended.)

cluding the Greater Yellowstone area); the extent of control was expected to be greater in the higher-numbered zones:

Management Zone I: This zone should contain key habitat components in sufficient abundance and distribution on an annual basis to sustain 10 breeding pairs of wolves. It should generally be an area greater than 7,770 contiguous square kilometers with less than 10% private land (excepting railroad grant lands) and less than 20% subject to livestock grazing.

Management Zone II: This zone should be established as a buffer zone between Zones I and III. It should contain some key habitat components but probably not in sufficient abundance and distribution on an annual basis to sustain a viable wolf population. Zone II boundaries may be changed according to demonstrated wolf population and habitat needs, provided the change does not bring wolves into conflict with existing livestock areas or allotments.

Management Zone III: This zone contains established human activities, such as domestic livestock use, or other human activities or developments in sufficient degree to render wolf presence undesirable (U.S. Fish and Wildlife Service 1987:31).

Zone management of wolves has increased in popularity recently in Canada and Alaska. Several agencies have zone management systems in the planning stage. These are described primarily in internal documents, and little implementation has occurred to date. Limited zone management of wolves has been applied in Minnesota (50 CFR 17.40(d)), although not as recommended by the Eastern Timber Wolf Recovery Team (U.S. Fish and Wildlife Service 1978). Five management zones are recognized in Minnesota, but the only meaningful difference in management is between zone 1 and zones 2, 3, 4, and 5. Control of wolves can occur in the event of significant depredations on lawfully present domestic animals in zones 2, 3, 4, and 5. Management zone 1, consisting of 11,624 km^2 in the northeastern corner of Minnesota, was set aside as a sanctuary because it is important as wolf habitat, relatively undeveloped, few people live there, and the potential for conflicts is minimal. No wolf control occurs there. The only type of conflict that has emerged in zone 1 is depredations on dogs. The Eastern Timber Wolf Recovery Team proposed a regulated public taking in some areas of Minnesota, particularly zone 4, but the taking has never occurred. No taking for purposes of ungulate management occurs in Minnesota.

In the Greater Yellowstone area, the area of greatest priority for wolves is clearly Yellowstone National Park. Most discussions of reintroduction and wolf recovery in the area have focused on the park itself. However, the park boundary is not a biologically meaningful boundary, and there is no guarantee that management priority (complete or near complete legal protection) for wolves in the park alone would be adequate to allow a secure population to develop and persist over time (Yellowstone National Park et al. 1990). The chances of full recovery are higher if wolves have access to key ungulate winter ranges outside the park (Boyce 1990). Although wolves have sustained themselves for decades in areas much smaller than Yellowstone (e.g., Isle Royale National Park, Michigan, and Riding Mountain National Park, Manitoba), they have not had to contend with extensive prey migration in those areas. The designated wildernesses and national forests outside of the park provide a buffer—although an imperfect one—between the park and most economic interests in the area that wolves might affect. Thus, the Greater Yellowstone area may be well suited to some geographically defined management zone system using three or more zones. The most obvious zone scenario would include management within the buffer area (Zone 2 in Fig. 3) between the park and the zone most distant from the park.

If zones are defined, consideration will have to be given to whether administrative, physiographic, or biological lines or some combination of these should be used. Major factors to be considered in defining zones are size of area necessary (and type of management therein) to support a viable wolf population, distribution and seasonal movements of prey, distribution of livestock allotments, and distribution of areas of potential conflict with state ungulate management objectives. Another consideration is whether to allow for some movement of wolves outside the park in winter because they may follow their prey outside the park. Possibly, some packs could follow prey to lower elevations in winter and establish dens in lower elevations, thus not return to the summer ranges of their prey until midsummer. Careful attention would have to be given to the number of zones. Fewer zones may mean simplified management with increased ease of understanding for the public and agency personnel (J. Weaver, personal communication) but less fine-tuning of management.

Another consideration in defining zones is whether wolves should be protected over a greater area during population establishment with contraction to a smaller area after full recovery is accomplished and more is understood about the biological requirements and behavior of wolves in the Greater Yellowstone area. From the standpoint of wolf reestablishment, the highest priority should be given to provision of sufficient year-round resources to support a viable population of wolves. Although what constitutes a viable population is debatable (Conner 1988), an effort to restore wolves to the area is improvident if the population fails in a few years.

When considering management and management zones for wolves, we must also consider who would be authorized to conduct wolf control. In previewing this question as it relates to the Greater Yellowstone area, a broad range of possibilities can be envisioned, similar to the continuum depicted earlier for intensity of control (Fig. 2). Five distinct "who scenarios," going from less control to more control, are as follows:

1. No one authorized to engage in control activities, except government officials in the event of disease, threats to human life or safety, and nuisance behavior;
2. Control by state or federal agents only;
3. Control by state or federal agents and livestock operators;
4. Control by state or federal agents, livestock operators, and the public through a regulated harvest; or
5. No restriction on who can engage in wolf control.

Five of the more obvious management zone scenarios of the numerous possibilities that exist for wolves in the Greater Yellowstone area were discussed by Fritts (1990). Some of the possible variations of each scenario were discussed, and the effects of each scenario were presented in the form of biological and administrative or socioeconomic advantages and disadvantages. Each scenario assumed that wolves would be introduced to Yellowstone as a nonessential experimental population and that, outside zone 1, management consistent with the conservation of the experimental population would be implemented by the states of Montana, Wyoming, and Idaho under a management plan developed with the federal agencies. Those scenarios used administrative boundaries for zones while trying to emphasize the biological requirements of the wolf. Other approaches may be equally or more valid. The following standard terms were used:

Zone 1: Geographical area at center of Greater Yellowstone area of sufficient size and prey base to meet biological requirements of wolves and ensure survival and recovery (10 breeding pairs). Wolves would be almost totally protected within the zone. No control would occur in the park except for occasional taking of nuisance or injured animals by park personnel. Wolves occurring outside the park (if the zone extends outside the park) would be managed by the states of Idaho, Montana, and Wyoming. (Note that, in this discussion, zone 1 is defined as an area in which no taking of wolves occurs for controlling livestock depredations or predation on big game species. However, there is no reason that such taking could not be permitted in zone 1 if the taking were consistent with recovery goals.)

Zone 2: Area, in general surrounding zone 1, that may be important to the wolf population as a buffer between zones 1 and 3. A moderate degree of protection for the wolf in this zone would enhance recovery objectives in zone 1. Emphasis of wolf management would focus on state big game management objectives and wolf–livestock conflict resolution. Wolves would be managed by the states of Idaho, Montana, and Wyoming under a management plan consistent with the survival of the species, and wolves would be controlled only in response to confirmed depredations on domestic animals or declining ungulate populations and only by federal or state agents.

Zone 3: Area, generally outside zone 2, considered not vital to wolf recovery and containing a high enough level of human activities that conflict management must be a major priority. Wolf management would focus on preventing conflicts with livestock production and ungulate management objectives. Wolf numbers and distribution would be managed by the states of Idaho, Montana, and Wyoming under a conservation–management plan consistent with the long-term survival of the species. The plan would likely include regulated hunting and provision for public to take wolves on private and possibly public land in the act of depredating or after documentation of depredation on livestock. Taking by federal or state officials would also be authorized.

An important point is that the outermost zone would represent the outer extent of the area in which management as an experimental population could occur. The outer boundary of the outside zone demarcates the area with the most extensive wolf control from a surrounding area of full wolf protection under the Endangered Species Act. Consequently, delineation of that zone would warrant greater attention than if a nonexperimental population was involved.

All five management zone scenarios would provide wolves with complete protection inside the park, except that taking by park personnel could occur under extraordinary circumstances such as disease, threats to human life and safety, and nuisance behavior (Fritts 1990). Outside the park, hypothetical special rules for managing the experimental population would range from few restrictions on the taking of wolves anywhere outside park boundaries (one extreme) to no taking by federal or state agencies in the park or on any Greater Yellowstone area lands in response to depredation on livestock or excessive predation on ungulate herds, including no taking by the public on public or private lands (the other extreme). Whether wolf management under each of those scenarios would be consistent with conserving an experimental population would have to be considered.

Two zone options that do not fit the continuum model were also discussed (Fritts 1990). One option would provide complete protection for wolves within the park plus winter ranges of selected migratory elk herds that summer in the park. That approach would address the potential problem of wolves needing the elk that winter outside the park. The boundary of zone 1 (complete protection) could flex seasonally to encompass some of the migrating herds. Another scenario could be fashioned after management of the grizzly bear in the Greater Yellowstone area (Fritts 1990; Fig. 4).

A large array of options for wolf control and management zones are available for the area, and each option has many variations. With progressively more control, the potential for depredation on livestock and conflicts with state ungulate management decreases, but the risk to the wolf population increases, time to recovery and delisting increases, and the likelihood of reaching recovery level (10 breeding pairs) decreases. Conversely, with less wolf control, the potential for conflicts increases, but the risk to the wolf population decreases, time to recovery and delisting is reduced, and the likelihood of reaching recovery is increased.

Every possible scenario offers advantages and disadvantages, depending on the priority under consideration. Each management scenario could have many variations to provide for special concerns. Because so many possibilities are available, the opportunity exists to reach agreement on a management arrangement that would satisfy the biological needs of the wolf and allow recovery and delisting while satisfying most concerns of most interested parties. Public input may be extremely beneficial on these issues. Zone management usually invokes strong public interest, and we know the public is already highly interested in the issue of wolf reintroduction to Yellowstone. More complete agency and public involvement could be advantageous in fully defining control options and management zones and in determining whether zones should be used.

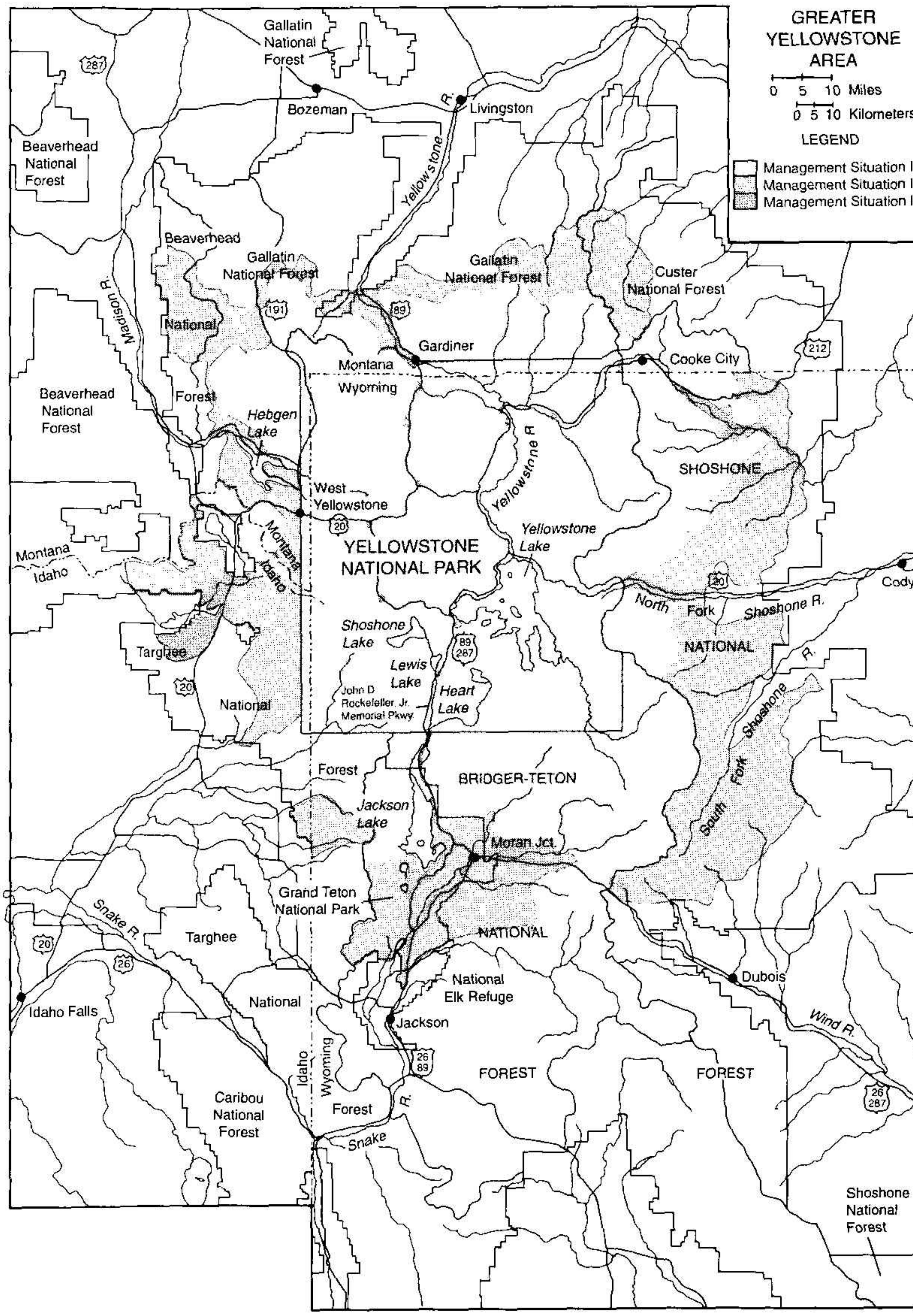

Fig. 4. Grizzly bear management zones in the Greater Yellowstone area.

Summary and Conclusions

The Greater Yellowstone area has considerable potential as a wolf recovery area because of its size, wildness, and abundance of prey. As with most other areas where wolves might be restored, potential for conflicts with economic endeavors exists, producing opposition to wolf restoration. Potential conflicts of greatest expressed concern will take place outside the park and involve primarily livestock production and big game hunting. Wolf control is normally controversial, and in the Greater Yellowstone area, that controversy will be exacerbated by intense national interest. Reintroduction is generally supported by residents of Montana, Wyoming, and Idaho; but support is weakest among people living closest to the Greater Yellowstone area, especially ranchers. These individuals have the greatest potential to have a direct adverse effect on wolf recovery. Different interest groups have different expectations about the degree of conflicts wolves will cause and have different views on the intensity of control that will be needed. Nonetheless, the public generally supports wolf control, favoring humane methods. Major methods expected to be used in the area are trapping, shooting, and live-capture using helicopters. Wolf control will occur, whether legal or illegal. Legal control is focused, more humane, and selective, whereas illegal control is random, unfocused, and nonselective. The price of wolf recovery is occasional control.

Actual conflicts are expected to be infrequent both inside and outside the park. Those that occur will receive intensive media coverage. The need for control is expected to be negligible inside the park and limited mainly to occasional control of nuisance animals by park personnel, as is now true for grizzly bears. Human safety will rarely be an issue. Translocation may be the major control approach within the park. Control activities in the park can be conducted under existing legal authorities.

Control is more complicated outside the park because of the multiple uses of public lands and the different jurisdictions involved. A need for control is envisioned in response to depredation on livestock and on big game species in special circumstances where wolf predation is conflicting with state ungulate management. The need for wolf control, the extent of control exercised, and the effect on the wolf population will be points of contention in the Greater Yellowstone area. State involvement in wolf management is highly desirable for a variety of reasons.

The legal basis for wolf control outside the park is strongly related to how wolves get to the Greater Yellowstone area, whether by natural recolonization through dispersal from Montana or Idaho, reintroduction without being designated experimental, reintroduction as a nonessential experimental population, or reintroduction brought about by specific legislation or action of Congress, possibly including use of the experimental population designation. Legal authority exists under Section 10(a) of the Endangered Species Act to control problem wolves when that control enhances the survival of the species. The control actions to date in Montana were based on that authority. Plans are in place that would allow implementing the same type of control in the area if wolves were to naturally recolonize or were reintroduced but not as an experimental population. The probability of natural recolonization is low but is increasing as the wolf population in Montana increases and expands southward.

Greater management flexibility is possible if reintroduced wolves are designated an experimental population under Section 10(j) of the Endangered Species Act. Congress intended the experimental population designation for difficult reintroductions—such as wolves in Yellowstone—where opposition would need to be specifically addressed. Special management rules written for Yellowstone wolves would spell out details of control, possibly including taking by members of the public in some circumstances. States could implement wolf management within their borders, but under Section 10(j) of Endangered Species Act, ultimate authority for the experimental population and its management would rest with the U.S. Fish and Wildlife Service. If a reintroduced population were designated experimental and nonessential, potential land-use restrictions would be less of an issue. Federal agencies would only have to confer informally with the U.S. Fish and Wildlife Service on activities that might jeopardize the species (except in national parks and national wildlife refuges). A jeopardy ruling would not prohibit the federal agency from committing resources to the proposed activity.

If special legislation mandated a reintroduction, that legislation would likely define details of control. Two bills introduced into Congress, one in 1989 and another in 1990, addressed reintroduction to Yellowstone but had different approaches to wolf management in the Greater Yellowstone area. Neither passed Congress. A plan developed by a congressionally mandated wolf management committee had still another approach to control and that plan was not acted on by Congress. An environmental impact statement currently in progress may determine the ultimate approach to wolf control in the Greater Yellowstone area.

The degree of control allowed would affect the size, distribution, and viability of the wolf population. If control is too intensive, a population might never reach a viable level or the full recovery level (defined as 10 breeding pairs), but conflicts would be the lowest imaginable. If the intensity of control is too low, the wolf population might thrive, but the level of conflicts might become excessive and local support for the wolf could deteriorate. Management zones may be the answer to tailoring specific control provisions to specific areas and thus balancing the biological needs of the wolf with socioeconomic considerations. A detailed wolf management plan might be difficult to craft in advance of wolves occupying the area because of uncertainty about how wolves would use the Greater Yellowstone area (e.g., whether they would require areas outside the park to sustain a population).

Wolves can occupy the Greater Yellowstone area with minimal effect on human endeavors, particularly if modern wildlife management techniques are applied. Wolf control in the area is expected to be especially controversial because of its visibility to an interested American public that is largely urban based. Education on wolves, including the realities of wolf control, should be given high priority in advance of wolf restoration to the Greater Yellowstone area.

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Predicting the Consequences of Wolf Recovery to Ungulates in Yellowstone National Park

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Abstract. A stochastic predator–prey model was developed to simulate the probable consequences of gray wolf (*Canis lupus*) recovery in Yellowstone National Park. Abundant prey in the park enhances the probability that wolves could be reestablished. Wolves could reduce prey by 10–30%, with elk (*Cervus elaphus*) as the principal prey species. Under assumed sigmoidal functional response, wolf predation could dampen the substantial fluctuations of park ungulate populations caused by variations in climate. Consequences of wolf recovery to native ungulates will depend on management practices. Killing wolves that leave the park and poaching within the park reduce the total number of wolves occupying the park, increase the risk of extinction for the wolf population, and increase the number of ungulates. Increasing the area included within the recovery zone will reduce the probability that wolves will go extinct during the century following reintroduction. Hunting ungulates outside park boundaries is compatible with wolf recovery in the park because no hunting is allowed inside the park, culling rates outside the park are not high, and compensatory mortality and natality permit moderate levels of hunting as well as predation. The WOLF program is user friendly to encourage use by individuals who are unfamiliar with computers but who wish to learn about predator–prey dynamics.

In this paper, I present results of a simulation model that was designed to predict the probable consequences of gray wolf (*Canis lupus*) reintroduction on ungulate populations in Yellowstone National Park. Because future management activities are uncertain, the model allows the user to choose several possible management scenarios. By manipulating such alternatives, the user of the model can explore the consequences of different management actions. These actions include culling wolves that leave the park, addressing poaching inside the park, and continuing to allow hunting of bison (*Bison bison*) and elk (*Cervus elaphus*) north of the park.

Any such model must incorporate the natural variability of the weather, because climate can have enormous consequences on any ecological process. Therefore, the model is a stochastic one—that is, the model contains random variation in climatic variables. Such stochastic model structure is important because it helps to educate the user about the im-possibility of precisely predicting the consequences of wolf recovery. The purpose of this model is not to offer recommendations about whether wolf recovery should take place but rather to provide resource managers with an additional tool that will assist them in making such a decision.

According to Kellert (1980, 1986), education is probably the most significant contributor to favorable attitudes toward wildlife (also see Noss 1989). Public education is an important future use for this model. Numerous scientific investigations of predator–prey relations exist, but the principles underlying this body of scientific knowledge are not widely known by the American public. I hope that this user-friendly program will be used by students, park rangers, resource managers, politicians, and the general public.

Methods

I developed a dynamic systems model that is composed of stochastic difference equations where certain parameters are entered directly or indirectly by the user. This model is used to project wolf and ungulate populations for 100 years into the future. The core model is programmed in Turbo Pascal and has been entitled WOLF. To run the model requires less than 96 kilobytes of RAM, and screen drivers have been included so that the model should run on a DOS-based computer having any standard graphics capability. The program has been tested on over 20 different microcomputer configurations and was compatible with each. It is available in both 5¹/4-inch and 3¹/2-inch disk formats, and none of the software is copy protected. Users are welcome to copy and distribute the program without my permission.

A priority in developing the model was that the model be interactive. To my mind, the closest approximation to reality for populations in a seasonal environment is a system of differential equations with seasonality imposed by continuous-time oscillations—that is, sinusoidal forcing functions (Boyce and Daley 1980). Difference equation models are usually inadequate characterizations of nature because mortality seldom approximates a discrete-time process, and reproduction is almost always a function of resources integrated over some previous time. Nevertheless, continuous-time models require considerable computation time that would render them ineffective for interactive use; thus, difference equations were used. The model was stable in deterministic runs, which suggested that the discrete-time simplification did not substantially complicate the behavior of the model.

Additionally, the age structure was collapsed so that the program would run in a reasonable length of time. Although predation mortality may vary among ages, this age structure essentially has the consequence of scaling predation rates and creating lags in population fluctuations. To evaluate the consequences of age structure, I performed simulations using a Lefkovitch (1965), nonsenescent, age-structured matrix to monitor juveniles, yearlings, and adults. Predation and density dependence were incorporated as in the WOLF program but specific to age classes. These complications to the model did not alter the qualitative behavior of population projections.

Ungulate Population Dynamics

Six species of ungulates in Yellowstone National Park would be prey for wolves (Houston 1982; Despain et al. 1986). In the order of their population biomass, these species are elk, bison, mule deer (*Odocoileus hemionus*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), and pronghorn (*Antilocapra americana*). In addition, several species of smaller mammals and birds that live there may form a portion of the diet of wolves; occasional white-tailed deer (*Odocoileus virginianus*); and mountain goats (*Oreamnos americanus*); but I do not anticipate that these will be major prey items (Singer 1991). Beavers (*Castor canadensis*) are important summer prey for wolves in Alaska (Boyce 1974), Minnesota (Frenzel 1974; Van Ballenberghe et al. 1975; Fritts and Mech 1981; Fuller 1989), Isle Royale (Peterson 1974, 1977), Ontario (Voigt et al. 1976; Theberge and Strickland 1978), and Manitoba (Chadwick 1987), but beavers are not abundant in Yellowstone.

Investigations by Houston (1982), Merrill et al. (1988), and Merrill and Boyce (1991) provided background information on the population of elk and bison in Yellowstone National Park, which forms the structural basis for ungulate populations in program WOLF. Elk is the most abundant ungulate in the park; therefore, an understanding of the population dynamics of elk is critical for any model of wolf recovery in Yellowstone.

Survival and fecundity for both elk and bison are density dependent (Fowler and Barmore 1979). In addition, summer forage production has significant influences on population dynamics for each of these species (Merrill et al. 1988; Merrill and Boyce 1991), and severe winter weather can result in high mortality (Houston 1982). Survival of elk calves is a function of both winter climate and population density (Sauer and Boyce 1979, 1983; Boyce 1989).

Following Houston (1982), Picton (1984), and Merrill and Boyce (1991), a modified Lamb's index for winter severity was calculated from temperature and precipitation measurements for December through March at Mammoth, Wyoming. When both temperature and precipitation are average, Lamb's index is 0. Integer additions or subtractions to the index are made for each standard deviation from mean temperature and precipitation. Increased precipitation contributes to Lamb's winter severity index, whereas increased temperature decreases the index.

Mean and variance of green herbaceous phytomass (kg/ha) was estimated annually for 1971–88 from Landsat imagery and was related to elk and bison per capita population growth rates (Merrill et al. 1988). High quality summer forage can increase reproduction by enhancing the condition of the dam and favors rapid growth and subsequent survival of calves (Merrill and Boyce 1991).

The influence of winter severity and summer range production on per capita growth rates was estimated using multiple linear regression. Here, the per capita population growth rate, $r(t)$ is defined as

$$r(t) = ln\{[N(t+1) + H(t+1)]/[N(t) - LGH(t)]\} \tag{1}$$

where $N(t)$ is the winter population count minus adult males in year t (see Houston 1982),
$LGH(t)$ is the elk kill during the late Gardiner hunt (Montana state hunting unit 313) in year t, and
$H(t+1)$ is the harvest from unit 316 in Montana during year $t+1$.

The following model was fitted using least squares procedures:

$$r(t) = r_0 - b_1 N(t) - b_2 L(t) + b_3 P(t) \tag{2}$$

where b_i's are regression coefficients,
r_0 is the potential population growth rate,
$L(t)$ is Lamb's index of winter severity, and
$P(t)$ is green herbaceous phytomass during summer.

This regression model can be rewritten as a difference equation for predicting the dynamics of elk populations:

$$N(t+1) = N(t)exp[r_0 - b_1 N(t) - b_2 L(t) + b_3 P(t)] \tag{3}$$

where $L(t)$ and $P(t)$ are independent random normal variables. By using mean values of climate and herbaceous phytomass, this model collapses to a difference equation approximation of the logistic model with $N(t)$ ultimately converging on carrying capacity, K, where $r(t) = 0$. By setting $ln[N(t+1)/N(t)] = 0$ in equation 3, we can solve for $K = r_0/b_1$.

For elk, fitting data to equation 2 accounted for more than 88% of the variance in per capita growth rates ($P < 0.001$). An estimate for r_0 was based on Eberhardt's (1987) analysis of the northern Yellowstone elk herd. The winter census of elk on the northern range of Yellowstone National Park is plotted with a logistic fit to data in Fig. 1. Similarly, the proportion of cow elk with calves at heel was correlated with green herbaceous phytomass and population size. To apply this model of elk population dynamics to the entire park, carrying capacity for elk (K_{elk}) was increased above the estimates for the northern range to include elk wintering in other portions of the park (see Cole 1983; Boyce 1989; Singer 1991).

The model fitted for bison was similar to that for elk (Merrill et al. 1988). For both species, a linear model fit $r(t)$ as a function of $N(t)$ better

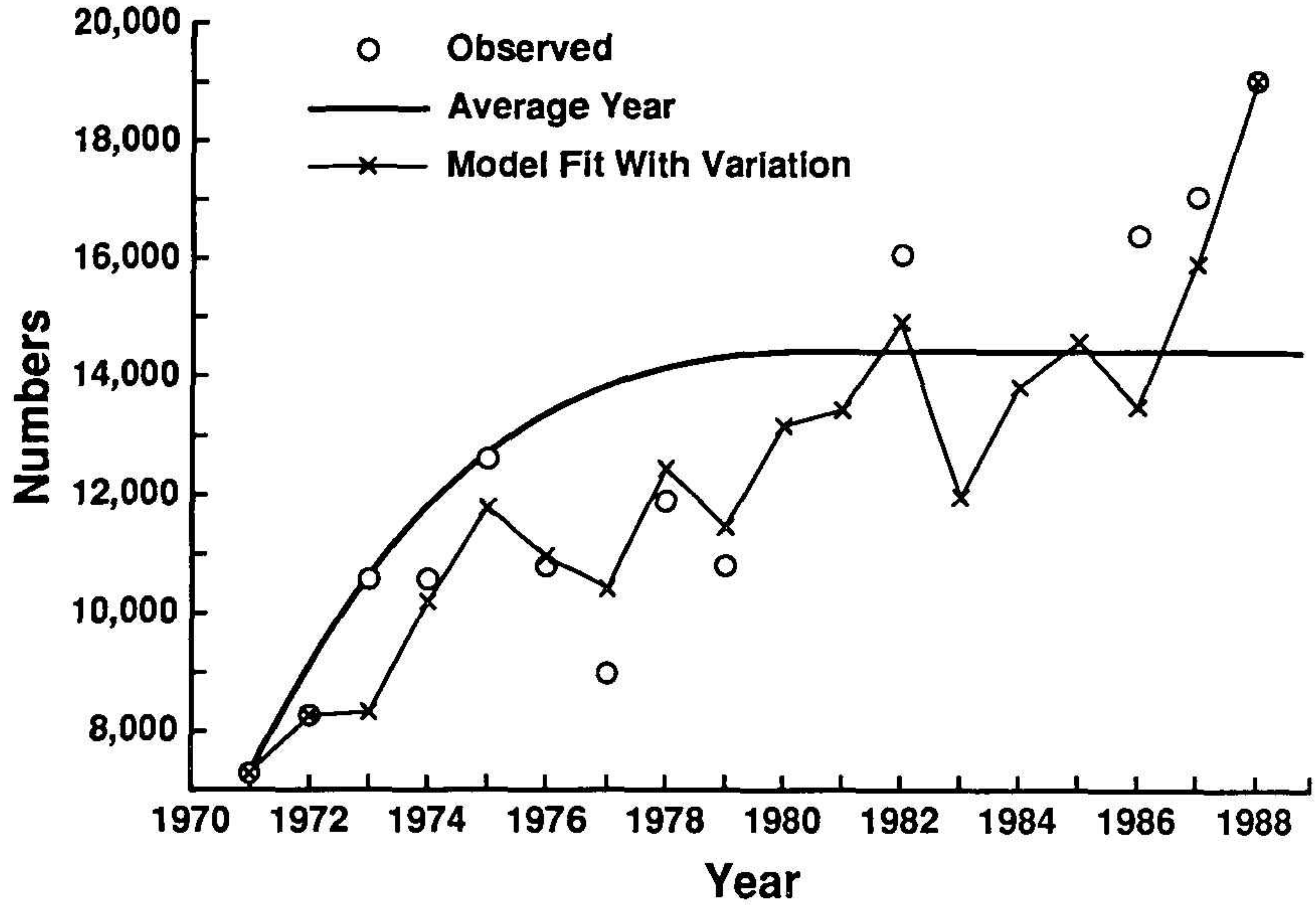

Fig. 1. Observed winter census of elk in Yellowstone National Park plotted with a logistic fit to the data (*solid line*). *Asterisks* (*) indicate the counts predicted from equation 3 using observed values of winter severity and summer phytomass (from Merrill and Boyce 1991).

than a concave one, despite the usual tendency for vertebrates to have concave density dependence (Fowler 1987; Boyce 1989). Frances Cassirer (University of Idaho, personal communication) suggested that this linearity may be a consequence of recent range expansion by both bison (Meagher 1989a, 1989b) and elk (Houston 1982) on the northern range, which would tend to flatten the density-dependent function. Another consideration is that a linear model may well provide an excellent fit over the range of observed values, but for still lower $N(t)$'s it is unlikely that $r(t)$ can get any larger. Therefore, I set an upper limit to r for each species.

A detailed model for moose and deer is not described because empirical data are inadequate. I estimated carrying capacity for moose and deer based on approximations of population size in recent years and estimated r_0 for these species from literature reports (Wallmo 1981). A value of r_0 for moose was reduced to 0.2 due to heavy hunting pressure outside the park (Singer 1991).

Bighorn sheep and pronghorns were not included in the simulation model. Few of these animals live in Yellowstone National Park; therefore, their influence on wolves would be small. Bighorn sheep are not expected to be influenced by wolf recovery because they usually escape from wolves by staying near cliffs or other rugged terrain (Cowan 1947; Murray 1987). Pronghorns are not likely to suffer heavy wolf predation either because they winter near the town of Gardiner, Montana, where people may keep wolves away.

Stochastic Variation

At our current state of understanding, it is not possible to predict climatic variation among years. I will presume, therefore, that climatic variation is stochastic with mean and variance comparable to that which has occurred during the past 50 years. For example, this results in a Lamb's index with an average of 0 and a standard deviation of 6.5. I employed a random number generator based on adding 12 uniform random values to obtain a normal distribution.

Fires of 1988

Ungulate population dynamics are expected to be affected by the large fires of 1988, and generally the ungulates included in the WOLF program are known to increase after their habitat has burned (Boyce and Merrill 1991). To incorporate the effects of the 1988 fires, a literature review formed the basis for a maxima function simulating range improvements for both elk and bison in the park (Boyce and Merrill 1991). For elk, the carrying capacity in year t is assumed to follow the function

$$K_{elk}(t) = 168t\,exp(-0.2t) \tag{4}$$

and similarly for bison

$$K_{bison}(t) = 253t\,exp(-0.3t). \tag{5}$$

Detailed justification for these functions is provided by Boyce and Merrill (1991).

Predation

Only predation by wolves is incorporated into the WOLF program, although other predators on ungulates occur in Yellowstone National Park, including coyotes (*Canis latrans*), cougars (*Felis concolor*), black bears (*Ursus americana*), and grizzly bears (*Ursus arctos*). Bears occasionally can be significant predators on elk (Schlegel 1976; Singer and Harting 1988) and other ungulates (Singer 1987). Predation by bears and other carnivores is not explicitly incorporated into these simulations, although predation is assumed to be a component in past changes in ungulate populations.

Wolf Life History

The gray wolf is the largest species of wild canid, with males occasionally exceeding 50 kg (Mech 1974). Wolves once lived in most of North America but are now substantially reduced in distribution. Large populations still exist in Canada and Alaska, and recently wolves have appeared in Glacier National Park, Montana, but the only clearly viable population in the contiguous 48 states occurs in northern Minnesota (Mech 1970, 1974).

Several den sites were recorded in northern portions of Yellowstone before the extirpation of the wolf. Average litter size for wolves in

Yellowstone National Park was 7.8, ranging from 5 to 14 pups ($N = 10$; Weaver 1978). Sexual maturity in wolves may occur at 2 years, although in most areas they do not breed until age 3 (Mech 1974) and sometimes not until age 4. The age at first breeding may vary with the maturity and density of the wolf population. Reproductive rates for wolves in Alaska average 1 pup per wolf per year (Chapman 1977). Most packs only produce 1 litter per year, but when food is abundant, 15 to 20% of the packs in Alaska were observed to bear two litters—that is, each pack included two breeding females (Haber 1977; Ballard et al. 1987).

Social behavior of wolves imposes density dependence that can influence the upper limit to population density. In undisturbed populations, approximately 60% of the mature females breed, whereas upwards of 90% may breed in populations heavily hunted by people (Rausch 1967; Pimlott et al. 1969) or in rapidly increasing populations (Fritts and Mech 1981). Clearly, density dependence is an essential component of any realistic model of wolf population dynamics (Packard and Mech 1983).

In this model, pack size in Yellowstone National Park is assumed to be seven or eight wolves. A high rate of dispersal and reproduction at minimum age, however, may result in smaller mean pack size for several years during wolf establishment (Fritts and Mech 1981:25–26). Kill rates are lower for small wolf packs (Van Ballenberghe 1987). Furthermore, the kill rate per wolf tends to decline as pack size increases from four wolves, and pack size has been observed to be larger where little human hunting of wolves occurs (Peterson et al. 1984), as would probably be the case within Yellowstone National Park. I have not incorporated these effects related to pack size variation into the model.

For estimating maximum wolf densities, I assumed that no interstitial spaces between packs exist when population density is high (Messier 1985; Ballard et al. 1987). Wolf territories may be larger and packs smaller during the colonizing phase of wolf recovery than after large numbers of wolves have been established (Ream et al. 1991). During winter, all wolf packs are expected to be restricted to ungulate winter ranges in the park. The principal winter range in Yellowstone National Park is the 830-km^2 northern range (Houston 1979). Adequate numbers of ungulates may occur to support wolves in the Madison–Firehole area (Cole 1983) and perhaps along the upper Yellowstone River south of Yellowstone Lake (Boyce 1989).

Wolves require approximately 3.2 kg/day of food in the winter, and 3.6 kg/day are required for successful reproduction (Mech 1977; Weaver 1979). I am not aware of any information on the density of elk necessary to sustain wolves, although Messier (1985) reported that moose densities lower than 0.2 moose/km^2 were inadequate to support wolves. Large portions of the interior of Yellowstone National Park are virtually devoid of ungulates in winter and could not support wolves through that season.

Functional Response

Key structural features of any predator–prey model are functional and numerical responses. The functional response is predicted by an equation that generates the per capita rate at which prey are captured as a function of the number of prey available to the predators. For mammals, functional responses are usually logistic (S-shaped) often labeled a Type-III functional response (Holling 1959). For wolf predation, a logistic functional response is justified by the statistical analysis of Garton et al. (1990) and Mech's (personal communication) observation that prey switching may occur. The form of such a functional response is

$$F_i = C_i N_i^2 \Big/ \left(1 + \left[C_i \left(1/F_{\max}\right) N_i^2\right]\right) \tag{6}$$

where F_i is the number of the i-th prey species taken per predator per unit time,
C_i is a scaling constant,
N_i is the number of ungulates, and
F_{max} is the asymptotic maximum number of prey killed per predator for large populations of prey.

In Table 1, I summarized all of the population and functional response coefficients for each of the four species of ungulates modeled in the WOLF program. Note that the carrying capacities for ungulates are equilibrium population levels that eventually would be attained in the absence of wolves. The carrying capacity for each of the ungulate species tracks the responses to fire as derived from equations 4 and 5.

Average kill rates vary depending on the species and density of prey. Mech and Frenzel (1971) reported an average kill rate of 1 deer per 18

Table 1. Population, functional response, and numerical response coefficients for each of the four ungulate species modeled in program "WOLF."

Species[a]	r_0[b]	r_0/K[c]	W[d]	P[e]	C[f]	F_{max}[g]	R[h]
Elk	0.43	2.7×10^{-5}	0.0233	0.00036	2.0×10^{-7}	25	0.075
Bison	0.23	9.2×10^{-5}	0.0079	0.0002	1.5×10^{-7}	10	0.13
Moose	0.2	2.5×10^{-4}	0.01	0.0001	1.5×10^{-7}	20	0.09
Deer	0.4	1.3×10^{-4}	0.009	0.0003	2.5×10^{-7}	110	0.015

[a] Elk = *Cervus elaphus*; bison = *Bison bison*; moose = *Alces alces*; deer = *Odocoileus* spp.
[b] r_0 = potential per capita population growth rate.
[c] K = winter carrying capacity for Yellowstone.
[d] W = coefficient scaling the response to winter severity.
[e] P = response to green herbaceous phytomass.
[f] C = functional response coefficient, scaled to preference.
[g] F_{max} = maximum number of prey killed given unlimited prey abundance—usually determined by satiation.
[h] R = numerical response coefficient, scaled to the body mass of each prey species.

days (2.5 kg/wolf/day), whereas on Isle Royale, Michigan, Mech (1966) observed that 1 moose was killed per 45 days (6.3 kg/wolf/day). This value is remarkably close to Keith's (1983) review of the results of five North American studies in which he calculated 1 moose killed per 41 days. The highest kill rate observed was 1 moose/1.8 days for a pack of 8 to 10 wolves during a 35-day period (Peterson 1977). This rate would yield an F_{max} of 22.5 moose per year, but wolves couldn't likely sustain such a high kill rate through an entire year.

In Banff and Jasper parks, Alberta, midwinter consumption rates of elk were estimated to range between 0.14 and 0.2 kg per kg of wolf per day (Weaver 1979). In Riding Mountain National Park, Manitoba, where wolves were feeding extensively on elk, Carbyn (1983) noted daily consumption by wolves to average 0.21 kg of prey per kg of wolf. If wolf mass averages 40 kg, this yields approximately 8.4 kg/wolf/day, or the equivalent of about 14 elk/wolf/year.

Wolves prefer elk over moose as prey, and elk are killed at a one-third higher incidence relative to their abundance (Carbyn 1983). This higher predation rate on elk probably occurs because they are more vulnerable than moose. Even small wolf packs have been observed to kill elk (Carbyn 1983), whereas moose are often tested a few times before one is attacked (Mech 1966, 1970).

The maximum rate at which wolves can kill elk is 25 per year for each wolf, which forms the upper asymptote of the functional response curve (Fig. 2). This rate is higher than typical maximum consumption rates for wolves, because I presume that some surplus killing may occasionally occur (see below). Because elk are expected to be more abundant than other ungulates, they will dominate wolf diets. Therefore, wolves are expected to switch to different prey only in isolated circumstances, such as for bison in winter in the Firehole area.

For functional response estimation, I assumed that bison are more difficult prey for wolves to kill than are elk. Yet, in northern Canada, wolves have successfully hunted bison, the largest of North American land mammals (Carbyn and Trottier 1987). Most susceptible are yearling bison that are no longer under the defense of their dams, although in one study, proportionately more bulls than other age and sex classes were taken by wolves (Oosenbrug and Carbyn 1983). Bison actually may be slightly easier prey for wolves than are moose, especially in snow where moose can maneuver better with their long legs (Telfer and Kelsall 1984). For the WOLF program, I have scaled preference for bison (C_{bison}) at 67% of that for elk, but because they average more than twice the body mass of elk, the maximum possible kill rate under high densities (F_{max}) is 10 bison/wolf/year (Table 1).

Data on moose and deer in Yellowstone National Park are meager compared to those available for elk and bison. Therefore, many of the parameters are based on literature survey. More research has probably been

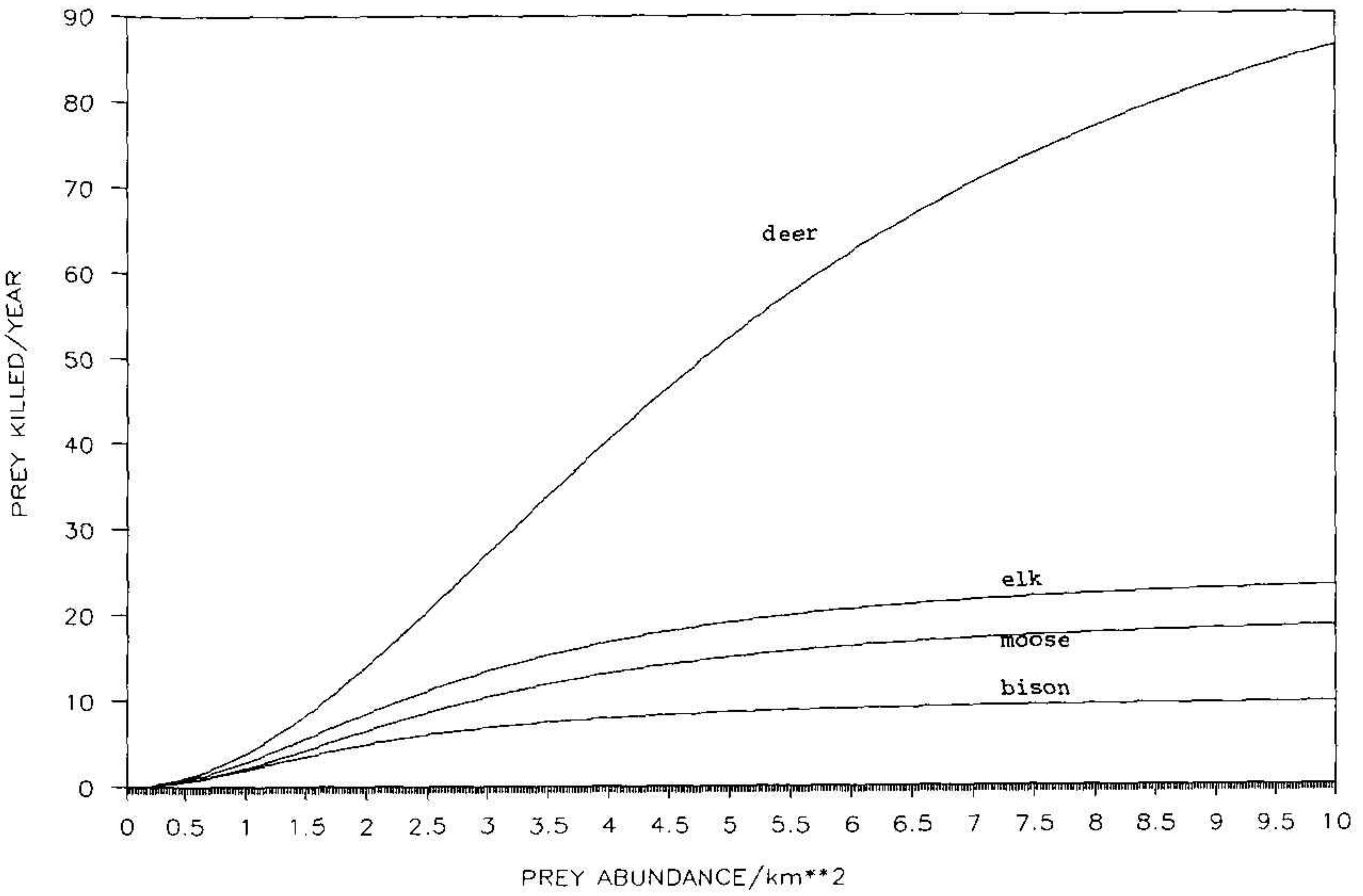

Fig. 2. Logistic functional response curves for four species of ungulates.

done on wolf predation on moose than on other ungulates (see Mech 1966; Crete et al. 1981; Gasaway et al. 1983; Messier and Crete 1985; Ballard et al. 1987). Based on the Canadian studies of Carbyn (1974, 1983), I have assigned a preference for moose that is 0.67 that of elk and deer. Because Shiras moose are slightly larger than elk in Yellowstone National Park, I have assumed $F_{max} = 20$.

I assumed that deer are 1.3 times as preferred as elk after Cowan (1947); however, many more elk spend winter in the park than deer. When scaled for their smaller body size, I estimated a F_{max} of 110 deer killed per wolf per year when deer are extremely abundant. At densities observed on the northern range, we can expect an average of less than 2.5 deer killed per wolf per year averaged over all wolves in the park. On the northern range, approximately 700 to 1,000 mule deer winter in the vicinity of Gardiner, Montana, where human developments may frighten wolves away. I modeled this refugium as a step function, whereby wolf predation cannot reduce the deer population below 700 animals.

Numerical Response

The numerical response, as opposed to the functional response, describes the rate at which captured prey are converted into predator offspring. Again the numerical response is presumed to be a logistic function for mammalian predators and is calculated as a simple multiple of the functional response at equation 6.

For wolf population growth, I use a multiple-species numerical response function, where $N_{wolf}(t + 1)$ is the number of wolves in year $t + 1$, which is a function of the abundance of each prey species, and the number of wolves at time t:

$$N_{wolf}(t+1) = N_{wolf}(t)exp\left\{\left[\sum R_i F_i(t)\right] - \left(r/K_{wolf}\right)N_{wolf}(t) - 0.68\right\} \quad (7)$$

where the R_i's in front of the F_i's are scaled proportionately to the mean body mass for each prey species (see Table 1). The portion of equation 7 within square brackets represents the numerical response. The constant r in the density-dependent term is assumed to be 0.6. Although I believe that this model performs well given the distribution of prey abundances in Yellowstone, if alternate prey were to become significant proportions of the diet, it may be necessary to develop a more complex model to limit joint handling time (i.e., after the form of the multispecies disc equation [Walters et al. 1981]).

K_{wolf} is the carrying capacity for wolves determined by territoriality, which in turn is a function of the prey available to wolves in Yellowstone National Park. I estimated territory size for Yellowstone based on the review by Walters et al. (1981) of the effect of prey biomass on wolf territory size. In the model, minimum territory size for packs is 130 km^2. Even for resident wolves, it is assumed that territories may be as much as 50% outside the maximum compression elk winter range outlined by Houston (1982). In most years, considerably more area than the maximum compression elk winter range will be part of the winter range for ungulates. On average, the model assumes that each pack might occupy 65 km^2 of the 830 km^2 on the northern range, setting a K_{wolf} on the northern range of approximately 12 packs.

When all species of prey are at population sizes near their carrying capacities, and N_{wolf} is near zero, the wolf population will attain a maximum population growth rate comparable to the r_0 term for ungulates (see equation 3). For wolves, litter sizes are large, and consequently, potential population growth rates can be higher than for ungulates. Ballard et al. (1987) observed a finite growth rate of 2.4 in Alaska, although this growth was likely due in part to immigration. For the WOLF program, wolves have a potential growth rate of 1.8. This rate means that during the initial growth phase, the wolf population could attain an increase of 80% per year once a stable age distribution is reached.

Scientists are currently debating the mechanisms that create logistic-shaped functional and numerical response curves (Caro 1989). The logistic shape has been verified empirically, and the concavity of the right-hand side of the curve (see Fig. 2) is generally agreed to be a consequence of predator satiation (Holling 1959; Taylor 1984). The debate concerns the convex portion of the curve where prey densities are less than at the inflection point at $F_{max}/2$. Traditionally, scientists claimed that the convex portion of the curve is a consequence of the predator developing a search image. For example, wolves might locate certain prey more accurately at a cost of missing other prey items (Krebs 1971). But the convex part of the curve also may result from wolves learning where to hunt, learning how to handle a new prey species better, learning to accept unfamiliar prey, or learning to adjust their search rate (Allen 1989; Caro 1989). For purposes of this modeling effort, however, the mechanisms do not matter as long as the shape of the functional and numerical response curves is appropriate.

Surplus killing by wolves is known to occur, particularly of young prey or other vulnerable animals (Eide and Ballard 1982; Miller et al. 1985). Carbyn (1983) documented that wolves killed more elk than they needed in late winter, because wolves have improved mobility on crusted snow and elk are in a weaker condition at the end of winter. One might suggest that surplus killing by wolves would be heaviest in years with a high Lamb's index, although wolves have a difficult time maneuvering through deep powdery snow. Years of abundant prey may also be years when surplus killing is more prevalent. Yet, in northwestern Minnesota, two-thirds of the deer taken by wolves were in low-density deer areas, apparently where deer were more vulnerable (Fritts and Mech 1981).

To anticipate surplus killing by wolves in this draft of program WOLF, I increased the maximum potential kill rates in the functional responses for each ungulate species (see equation 6; Table 1). Surplus killing might also be interpreted as a waste of prey of approximately 10% when prey are abundant. But such waste serves as carrion for scavengers and decomposers.

Program Options

The WOLF program offers seven options for the user. For each option, a screen describes available alternatives. Next, I list the alternatives for each option and explain the consequences resulting from the choice of each alternative. Because the alternatives are numerous, I present a justification for the default selection for each choice for the purpose of comparing simulation results (Table 2).

Table 2. Default responses to options in program "WOLF."

Option	Default alternative
Winter severity	Average winters
Migratory behavior	Partial migrations
Elk hunt	Continue elk hunt
Conflicts with humans	Wolves avoid humans
Legal wolf culls	Wolves culled outside park
Poaching in park	Low poaching mortality
Inoculum size	30

Option 1: Weather Conditions
The screen reads

> Mild winters from 1981–1988 allowed ungulate populations to grow in the park. This option allows you to select weather conditions equal to the average observed during this century, or you may select 10% more severe, or 10% milder than average. This last alternative may be appropriate if the greenhouse effect should begin to warm the planet.
>
> Choose one of the following and type the number of your choice: 1 = AVERAGE WINTERS; 2 = SEVERE WINTERS; 3 = MILD WINTERS.

Choosing severe or mild winters results in a winter severity index that is increased or decreased by 10%. The standard deviation in winter severity remains exactly the same; only the mean is changed. Increased winter severity reduces ungulates over the long run, which ultimately reduces wolves as well. The opposite is true for mild winter conditions. Although a strong case for global warming might be made, I think that the most plausible selection for this choice is that average weather will continue.

Option 2: Migratory Behavior of Wolves
The screen reads

> In some regions wolves are known to migrate in pursuit of prey, like some caribou herds. We cannot predict if wolves will follow elk and bison or if they will remain on winter ranges year-round. The most likely scenario seems to be moderate levels of migration, becoming more pronounced over the years as the wolves become acclimated to the Yellowstone ecosystem.
>
> Choose one of the following and type the number of your choice: 1 = NONMIGRATORY; 2 = PARTIALLY MIGRATORY.

Migratory behavior increases potential carrying capacity for wolves on their winter range. For nonmigratory wolves, the carrying capacity (K_{wolf}) is set at 150 wolves, whereas it is set at 200 for partially migratory wolves. The nonmigratory wolf carrying capacity was estimated from Fig. 3, assuming that at least half the wolf territories would occupy ungulate winter range as outlined by Houston (1979). The consequence of selecting the migratory behavior alternative is an increase by six packs in the carrying capacity for wolves in the park.

Partial migrations are likely to develop rapidly as wolves seek prey that migrate seasonally (Shoesmith 1979; Boyce 1991). Apparently such

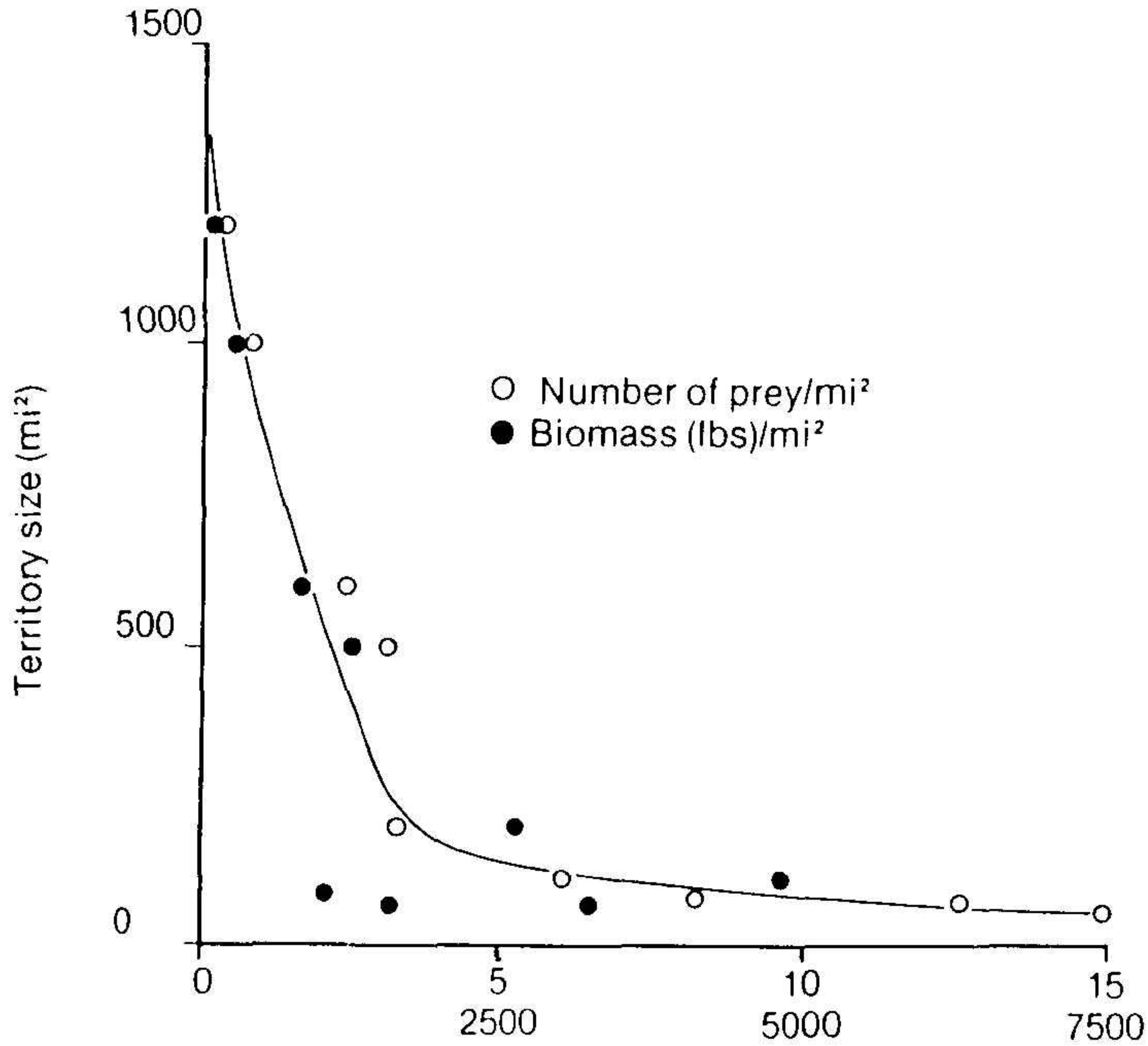

Fig. 3. Wolf territory size as a function of prey biomass (from Walters et al. 1981; data from Pimlott 1967, Pimlott et al. 1969, Clark 1971, Kolenosky 1972, Carbyn 1974, Peterson 1974, Van Ballenberghe et al. 1975, and Walters et al. 1981).

seasonal movements by wolves occurred historically (Weaver 1978). My default choice here is partial migrations.

Option 3: Elk Hunt

The screen reads

> Currently, the Montana Department of Fish, Wildlife, and Parks manages winter elk and bison hunts in the Yellowstone River Valley immediately north of the park. Particularly in severe winters, hunter kill of elk may be sizable. In future years, permits for the late hunts will be limited to 700. For this simulation, you are afforded the responsibility of continuing the elk hunt or ending it.
>
> Choose one of the following and type the number of your choice: 1 = END THE ANNUAL ELK HUNT; 2 = CONTINUE THE ANNUAL ELK HUNT.

In program WOLF, additional elk are added to the population each year if the user ends the hunt. Background data are based on an elk population that has been hunted, and hunting mortality probably contributes to density-dependent mortality in the herd (i.e., elk movements out of the park are more likely when population size is high, thereby exposing elk to more hunters in those years). The Montana Department of Fish, Wildlife, and Parks will likely discontinue hunting if elk numbers dip to low levels. Therefore, I have set a lower threshold of 5,000 elk below which the hunt will be stopped automatically even if choice 2 is selected.

Future permit quotas are set at 700 elk. Assuming 78% mean hunter success and 10% crippling loss, the total number of elk killed by hunters during the late hunting season will average approximately 600 animals.

I think that closing the hunt near Gardiner would be impolitic, and therefore, the most plausible choice is 2—to continue the hunt.

Option 4: Will Wolves Avoid Humans?
For this choice, the screen reads

> Experiences in northern Minnesota suggest that wolves will usually avoid contact with humans. However, occasionally wolves lose the fear of people and encounter ranchers, campers, and others who might harm wolves. We are unsure how wolves in Yellowstone would behave. What is your guess?
>
> Choose one of the following and type the number of your choice: 1 = WOLVES WILL AVOID HUMANS; 2 = CONFLICTS WITH HUMANS WILL BE FREQUENT.

If choice 2 is selected, I have arbitrarily increased the wolf mortality rate by 15%. This rate includes both illegal poaching and a higher level of damage control killing.

Wolves will certainly encounter people, at least occasionally, and dispersing wolves sometimes will kill livestock (Fritts et al. 1984). Indeed, when the wolf population becomes saturated, we may anticipate 15 to 25% dispersal of wolves out of the park each year (L. David Mech, personal communication). Yet, because native prey are so abundant in the Yellowstone ecosystem, the default is choice 1.

Option 5: Will Legal Wolf Kills Be Allowed?
The screen reads

> A possible management option is to kill wolves leaving Yellowstone National Park to lessen conflicts with ranchers and to leave more game for hunters. It is also possible that legal sport hunting or trapping of wolves will be allowed. You may select total protection for wolves except for repeat offenders, or you may opt to kill wolves once they leave Yellowstone National Park.

> Choose one of the following and type the number of your choice: 1 = WOLVES WILL BE KILLED; 2 = WOLVES WILL ENJOY TOTAL PROTECTION.

If killing is selected for choice 5, wolf mortality will increase by 15%. The magnitude of this value is largely arbitrary.

I suspect that it is inevitable that wolves will be killed if they leave the recovery zone. The choice here, however, may not be so much whether wolves will be culled outside the recovery zone, but rather where the boundary of the recovery zone will occur. If the recovery zone boundary is Yellowstone National Park, then choice 1 is appropriate. However, if the recovery zone is expanded to include wilderness areas and other portions of various national forests surrounding Yellowstone National Park, choice 2 may be the more appropriate selection.

For a default choice here, I have used 1—culling will occur when wolves leave the park.

Option 6: Will Poachers Kill Wolves?
The screen reads

> A difficulty that may face wolf recovery is poaching. Public education and strict enforcement can reduce the poaching on wolves. In this option you may speculate on how many park wolves will be poached during the next 100 years.
>
> Choose one of the following and type the number of your choice: 1 = POACHING OF WOLVES WILL OCCUR AT 20% OF TOTAL WOLF POPULATION; 2 = LITTLE POACHING WILL OCCUR.

Here, if the poaching choice is selected, the consequence will be an increase in the wolf mortality rate by 20%. I am optimistic that illegal poaching could be controlled within the boundaries of Yellowstone National Park; therefore, my choice would be 2.

Option 7: Number Of Wolves Released?
The screen reads

> Please enter the number of wolves that will be initially released into the park. The inoculum of wolves must be greater than or equal to 5 and less than or equal to 30.
>
> Enter the number of wolves to initially introduce.

The inoculum size can be critical because when fewer wolves are released, a good chance exists that none will settle in the park. I agree with L. David Mech (personal communication) that an initial release of

30 wolves will offer a reasonable chance that wolf recovery would be effective, and releases of young wolves may be best. However, it may be difficult to obtain this many wolves in 1 year, and thus for logistical reasons releases may need to be spread over a longer period. Furthermore, it may be necessary to supplement the wolf population in early stages of wolf recovery if an early inoculum does not appear to be persisting.

Spatial Distribution of Wolf Packs

The final screen of the model is a map of Yellowstone National Park showing the anticipated locations of wolf packs in the park, depending on the average number of wolves projected through the next century. The appropriate map is accessed by the core Turbo Pascal program. Each of 20 maps was generated by digitizing a photocopy of a map of Yellowstone using a Houston Instruments High Pad digitizer. Maps were enhanced using FREELANCE and stored individually to be accessed depending on the number of wolf packs calculated to exist in the park.

Results

Ungulate Population Dynamics Without Wolves

Perhaps the most striking outcome of ungulate population projections under the WOLF program is the high variance through time in population size. Yet, this result is empirically based. Variation in winter severity causes substantial population fluctuations in all ungulates in the greater Yellowstone ecosystem, and such fluctuations are well documented (Meagher 1971, 1973; Houston 1982). For example, elk numbers in 1989 decreased by an estimated 8,000–10,000 because of density dependence, hunting, drought, fire, and slightly above-average winter severity (Singer and Schullery 1989; Singer et al. 1989; Boyce and Merrill 1991).

Average population sizes for elk and wolves tend to be lower in the stochastic model simulations than for deterministic calculations using the same parameter values (Table 3). Lower populations are due to reduced long-term population trajectories in stochastic simulations (Boyce 1977) as well as to the general concavity of the population growth rate in these density-dependent models (see Boyce and Daley 1980).

Effects of Wolves on Ungulate Populations

Elk

The outcome of the simulations depends on a large number of variables under the control of the program user. Nevertheless, under all possible management scenarios—except those resulting in wolf extinction—the existence of wolves in the park will result in fewer prey over the long

Table 3. Responses to program alternatives in program "WOLF."

Option	Alternative	Elk[a]	Bison[a]	Moose[a]	Deer[a]	Wolf[a]
		Mean population size[b]				
Default	—	12,634	2,263	774	2,878	76
	Proportional response from program alternatives					
Climate	Mild winters	0.06	0.03	0.062	0.01	0.17
	Severe	–0.057	–0.03	–0.062	–0.009	–0.16
Migratory behavior	Nonmigratory	0.04	0.017	0.008	0.022	–0.16
Elk hunting	Stop hunting	0.073	–0.01	–0.007	–0.021	0.17
Conflicts with humans	Frequent	0.068	0.03	0.012	0.038	–0.26
Wolf culls	None	–0.066	–0.02	–0.012	–0.034	0.26
Poaching	20% Poaching	0.094	0.042	0.017	0.054	–0.36
Inoculum size	24	0.001	0	0	0.001	0
	18	0.003	0.001	0	0.002	–0.01

[a] Elk = *Cervus elaphus*; bison = *Bison bison*; moose = *Alces alces*; deer = *Odocoileus* spp.; wolf = *Canis lupus*.

[b] The mean population size for comparison of alternative responses are from deterministic projections with default alternatives as listed in Table 2.

term. For elk the model predicts a reduction in population size of 15–25% over the next 100 years. A typical simulation from the WOLF program using default alternatives is presented in Fig. 4. Elk population response to various program options is summarized in Table 3.

No combination of choices yields devastating consequences to elk populations in the park. The reason is that social factors limit wolf densities (Packard and Mech 1980) such that the wolf population cannot attain total numbers high enough to wipe out the elk herd.

With wolves present, elk populations still undergo substantial population fluctuations; however, wolf recovery can reduce the variance in population size for elk. For the default options, a reduction in the coefficient of variation of mean elk population size in excess of 30% (n = 30) occurs. However, this result is dependent on the shape of the functional response. I also conducted simulations using a multispecies disc equation (as used by Walters et al. 1981) and found the variance in population size to increase under wolf predation.

Bison

Overall, wolves are not expected to be nearly so effective at preying on bison as on elk and deer, at least in areas where elk and deer are also available. Therefore, wolf recovery will influence bison dynamics less than elk. With the default option, the average bison population will be less than 10% lower with wolves than without wolves (see Fig. 5). Bison population response to each of the program options is summarized in Table 3.

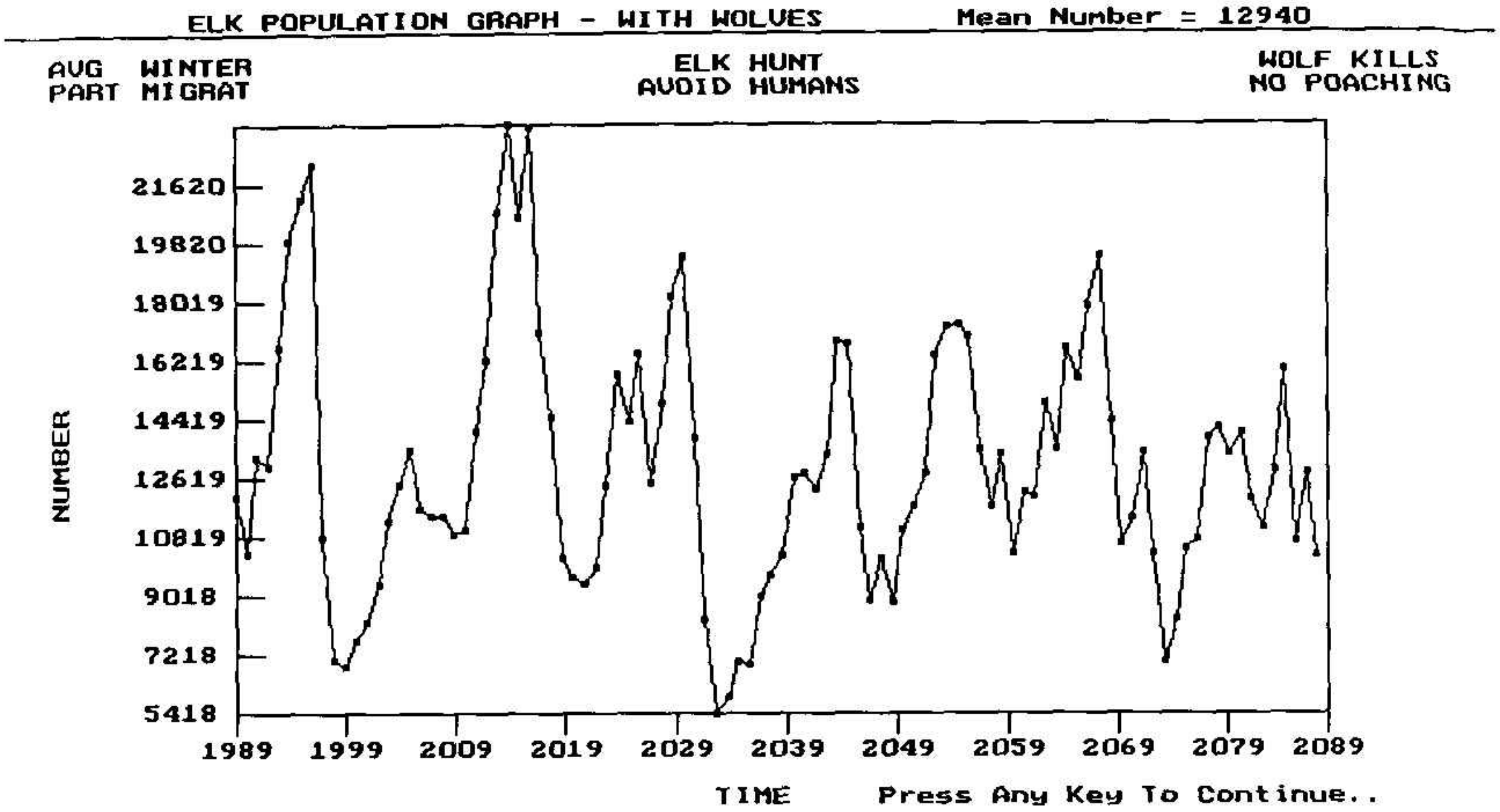

Fig. 4. Typical population projection for elk using default alternatives defined in Table 2.

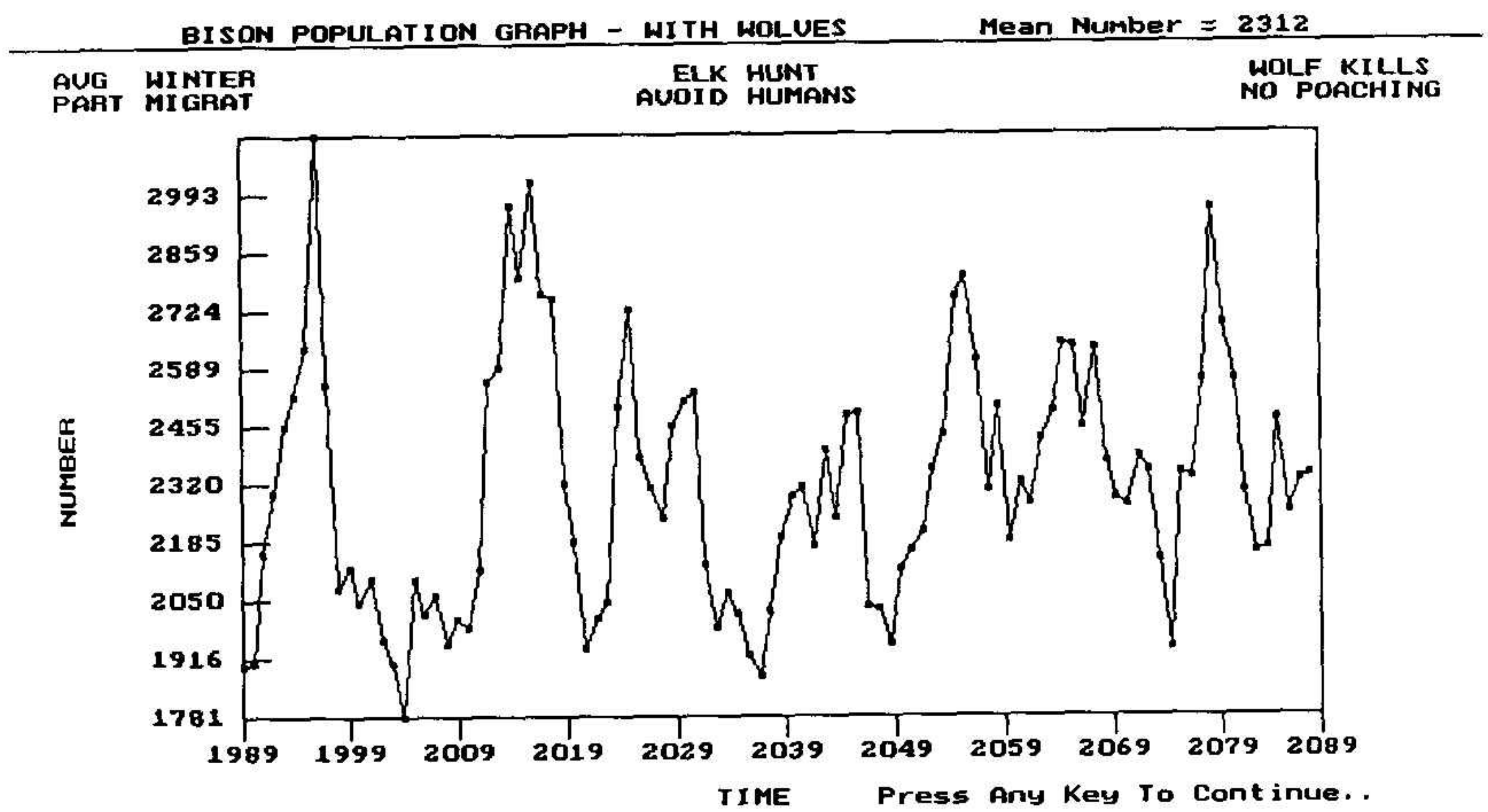

Fig. 5. Typical population projection for bison using default alternatives defined in Table 2.

As with elk, simulation results indicate that a reduction in the variance in bison numbers occurs after wolf recovery. But because predation on bison will be less than on elk, the reduction in the coefficient of variation in mean bison population size is projected to be less than 10% under the default options. Again, the variation in bison numbers resulting from wolf predation is dependent on the assumption of a logistic functional response.

Moose

The empirical data base for moose in Yellowstone National Park is much less complete than for bison or elk, so we cannot be as confident about the effects on moose resulting from wolf recovery. Nonetheless, because few moose winter in the park, they will not have major ramifications to the overall behavior of the predator–prey system. None of the management alternatives offered in program WOLF create more than a 10% change in the moose population (Table 3), but greater effects may occur in the face of heavy hunting pressure on moose in Montana—and different assumptions about the functional responses could alter the effects of wolves on the wintering moose population.

Simulation results predict that wolf recovery will cause a reduction in moose numbers by less than 5% (Fig. 6), although this may be overly conservative. Again, a major concern is that portions of the park's moose population seem to be heavily hunted when they leave the park (Singer 1991). Consequently, the effects of wolf recovery may be greater on moose than other potential prey if current rates of hunting are sustained.

Mule Deer

Although wolves preferred mule deer slightly more than elk, fewer deer than elk are killed by wolves simply because there are fewer deer. The effect of wolf predation on both mean population size and variance in population size of mule deer is intermediate between that of elk and bison. Simulations suggest at least a 10–15% reduction in mule deer numbers and a reduction in the relative variability in deer numbers, reflected by a decline in the coefficient of variation in mean numbers by 20–25%. The number of mule deer from a typical run from the WOLF program is

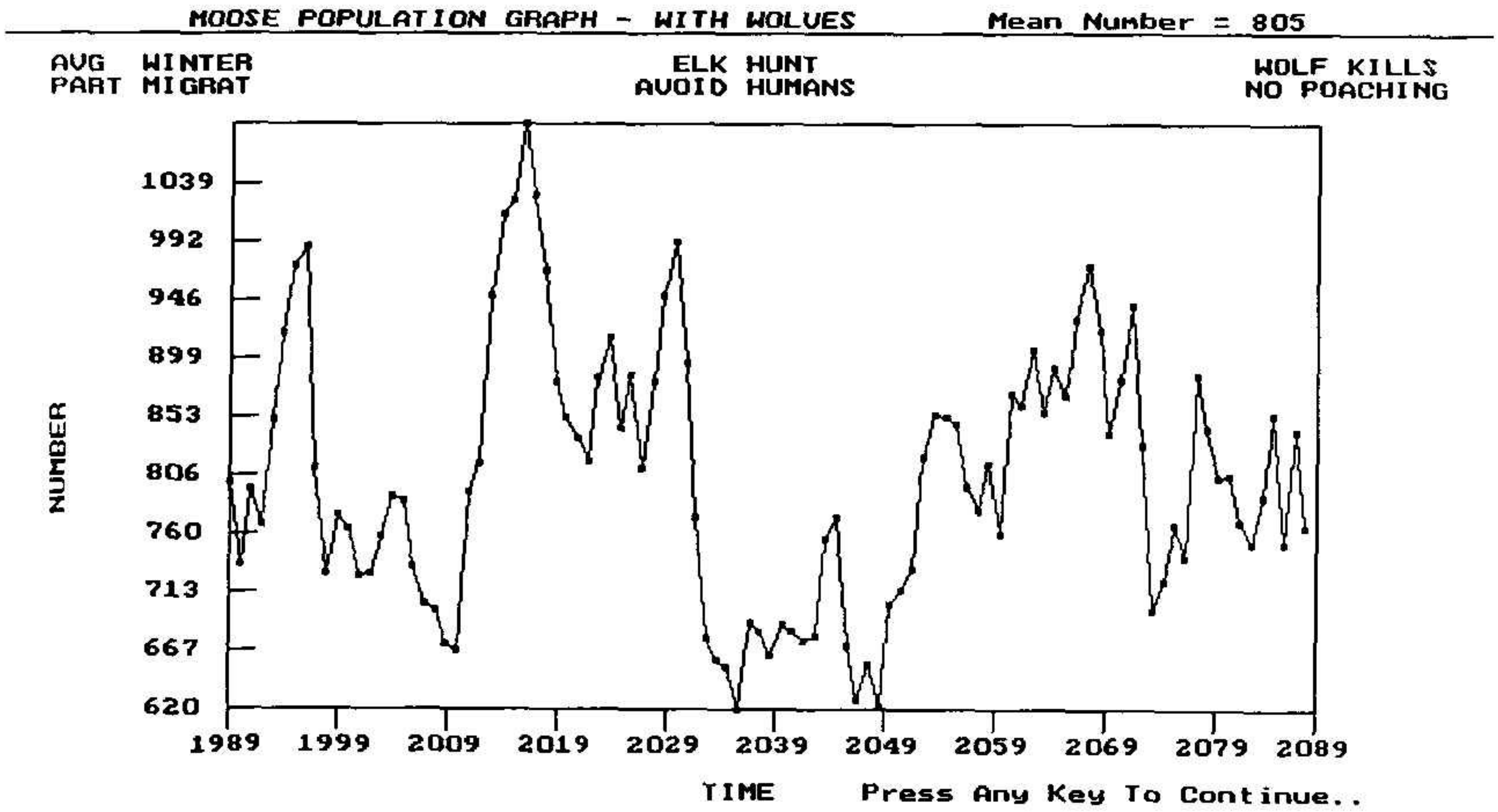

Fig. 6. Typical population projection for moose using default alternatives defined in Table 2.

presented in Fig. 7. The response of deer numbers to different management alternatives is presented in Table 3.

When building the model, I was concerned that deer may be extirpated by wolves, yet I thought that local extinction of deer was unlikely because there should always be some deer near the town of Gardiner, Montana (where a number of deer spend the winter now). Therefore, I constructed a refugium in the WOLF program to ensure that wolves did not reduce deer numbers below 700. As it turned out, however, wolf predation on deer is not likely to drive deer numbers anywhere near the refugium level.

Wolf Population Dynamics

Under most management scenarios, the model shows between 50 and 120 wolves in Yellowstone National Park during the century following reintroduction. Three of the options offered the user of the WOLF program involve an increase in the mortality rate for wolves from frequent conflicts with man, culling outside the park, and poaching within the park. Future wolf populations are highly sensitive to these options (Table 3). If the user chooses to increase mortality in all three options, the survival rate for wolves would be

$$(1-0.15)(1-0.15)(1-0.2)=0.578 \tag{8}$$

of that occurring without the human-induced mortality, and the wolf population will decline and, in most scenarios, become extinct within a few years. These results are consistent with the observations of Keith (1983)

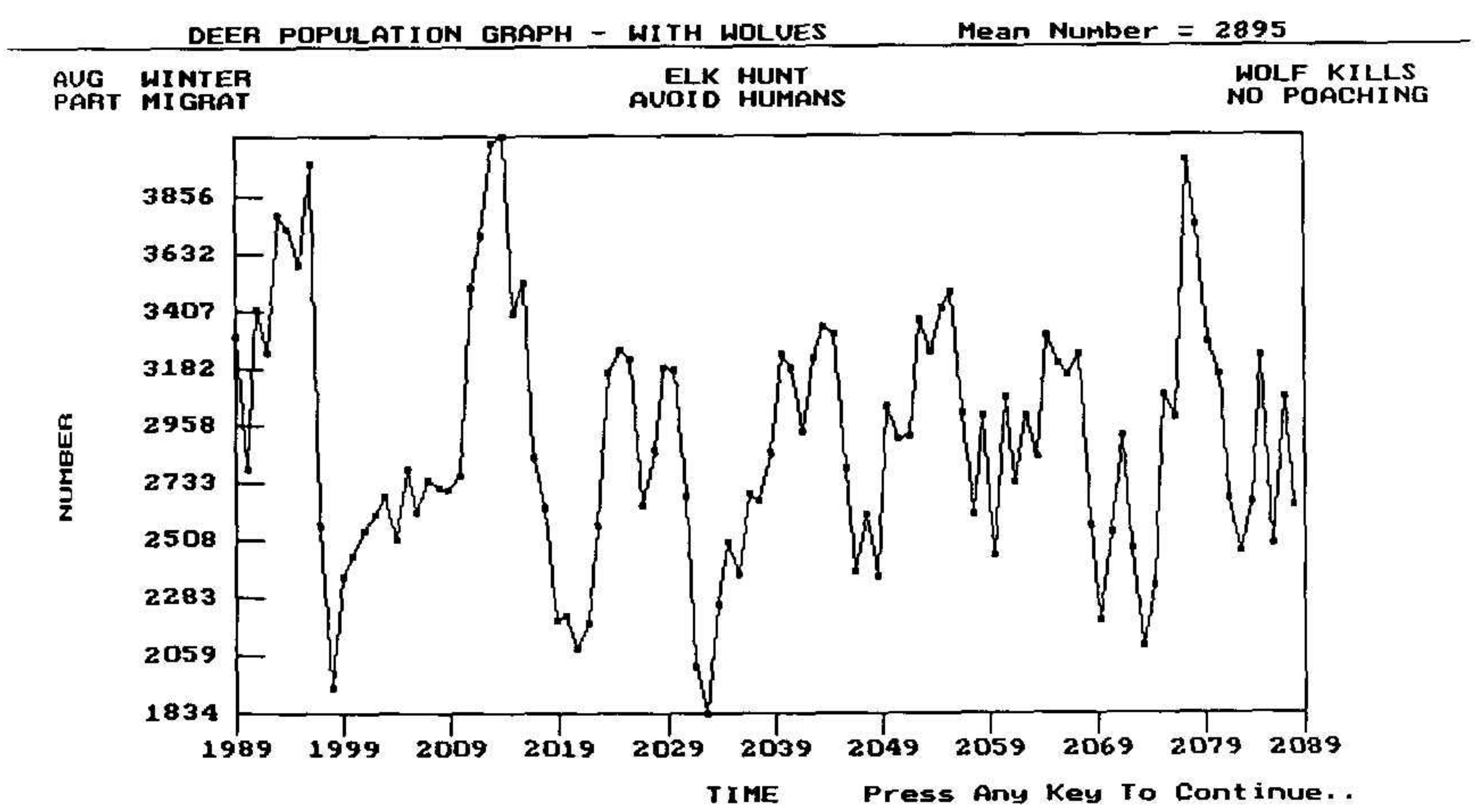

Fig. 7. Typical population projection for deer using default alternatives defined in Table 2.

and Ballard et al. (1987) that wolf kills by man in excess of 40% caused a decline in wolf populations.

Users of program WOLF will note low-frequency oscillations in the number of wolves (Figs. 8 and 9). These fluctuations are suggestive of nonlinear dynamics typical of some predator–prey systems. In deterministic simulations, no such oscillations appear, and the system converges on equilibrium. Apparently, the stochastic variation is great enough to destabilize the system temporarily. The population then undergoes tran-

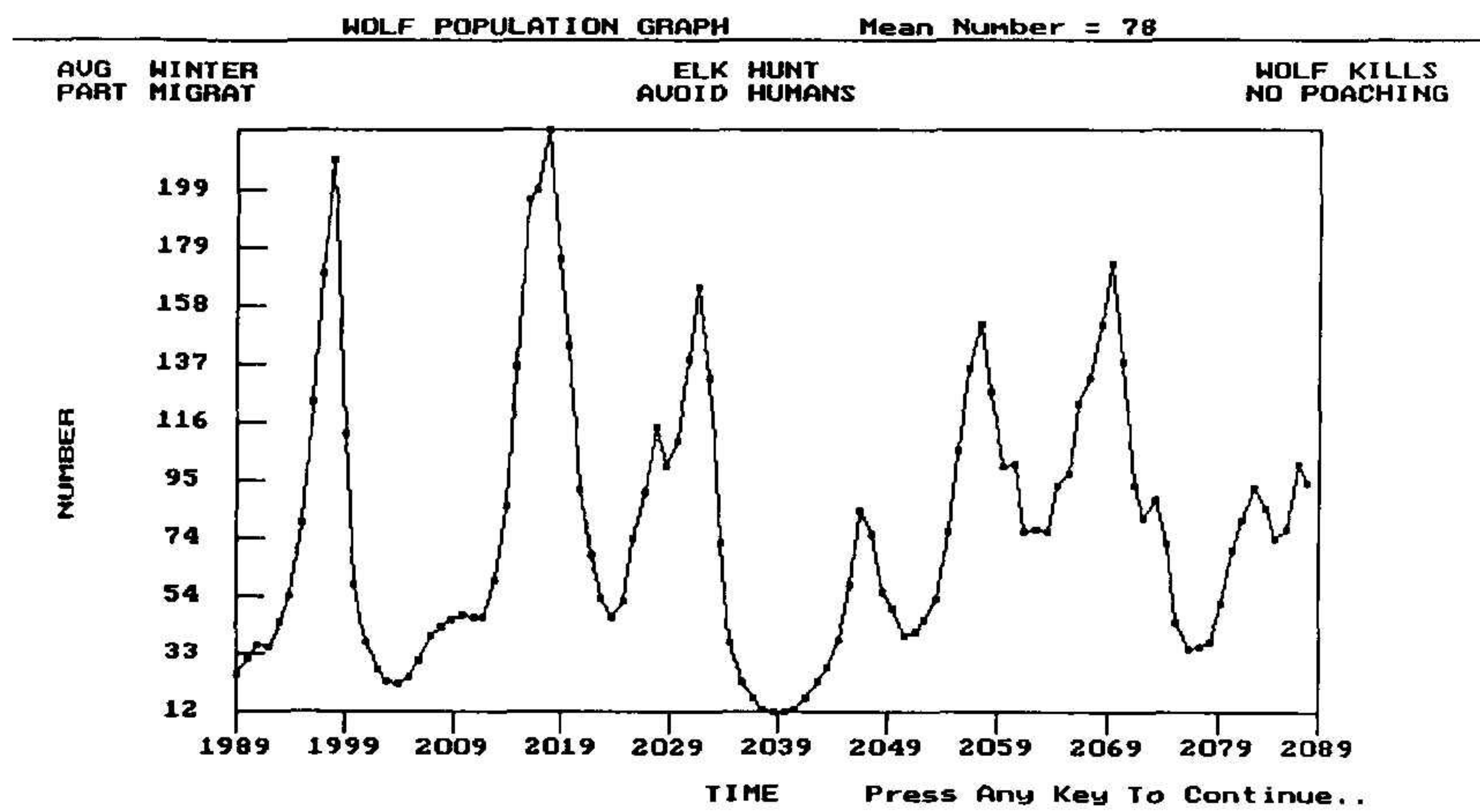

Fig. 8. Typical population projection for wolves using default alternatives defined in Table 2.

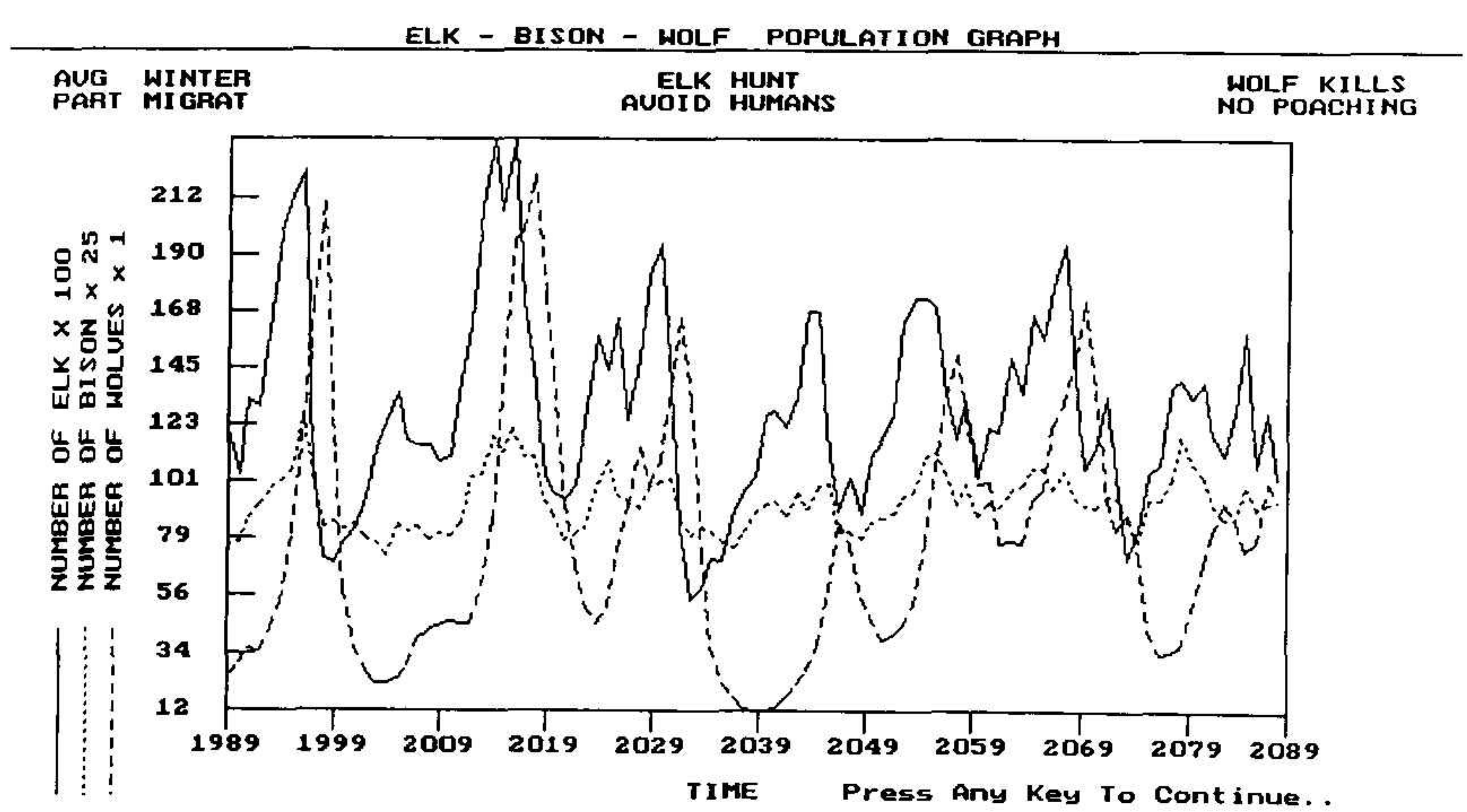

Fig. 9. Population projections for elk, bison, and wolves using default alternatives defined in Table 2. Superimposing the three primary species illustrates how wolf populations lag behind peaks and troughs of abundance of their prey.

sient motion back toward a stochastically varying equilibrium. New methods are developing that reveal nonlinear versus stochastic contributions to system dynamics (Sugihara and May 1990).

Spatial Distribution of Wolf Packs

The maps showing the distribution of wolf packs throughout Yellowstone were based on the current winter distribution of ungulates within the park and the historical distribution of wolf observations and den sites as reported by Weaver (1978). Because most wintering ungulates are on the northern range, we expect that most wolf packs will be there as well. An example of one of these maps corresponding to a wolf population with an average of 78 wolves in 9 packs is presented in Fig. 10.

Sensitivity Analysis

To understand the behavior of the WOLF program requires an appreciation for the sensitivity of various inputs. I performed a sensitivity analysis focusing on variables of ecological significance and variables for which we did not have reliable estimates (Table 4).

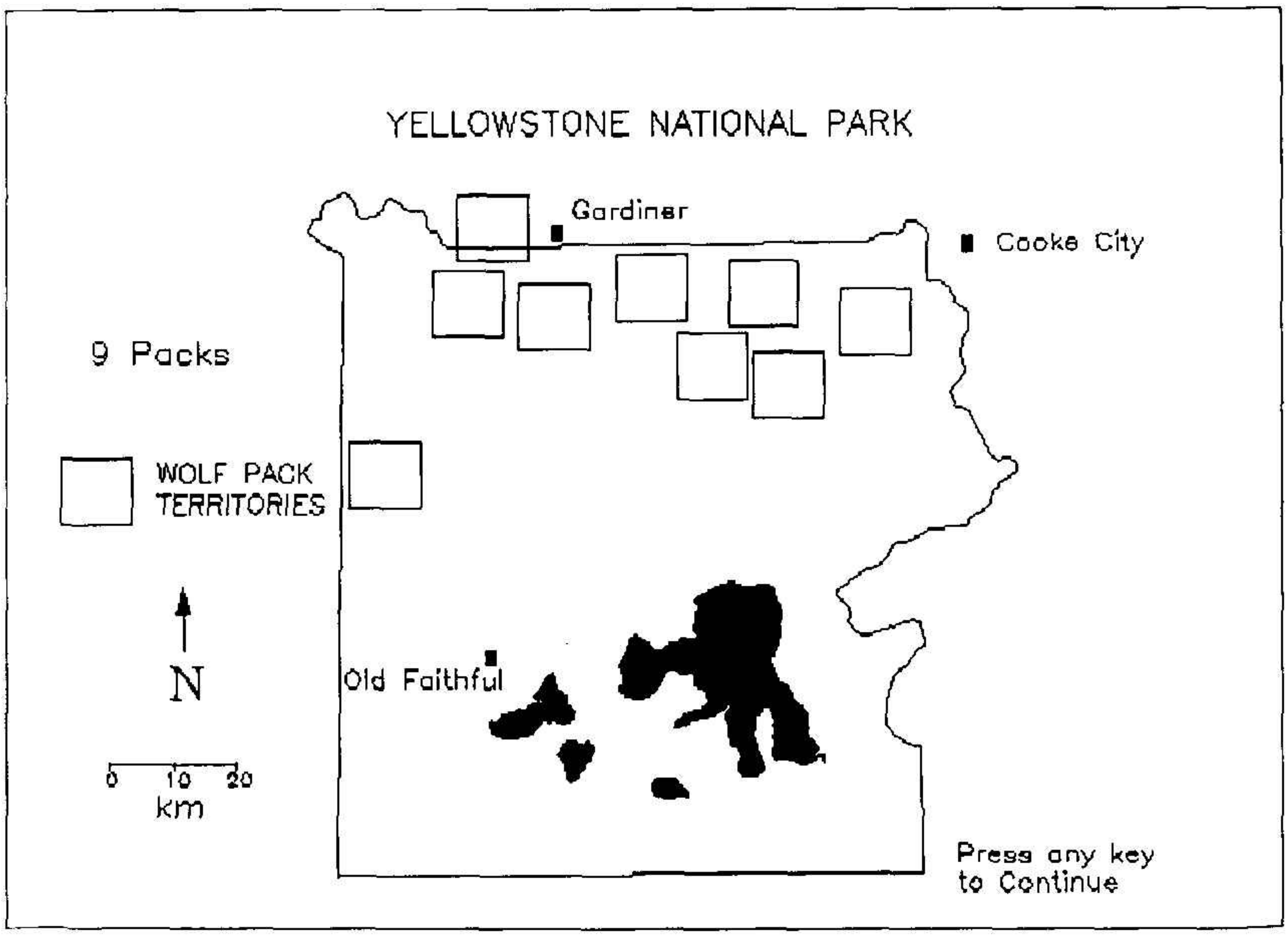

Fig. 10. Map of Yellowstone National Park showing postulated positions for 9 wolf packs in the park, containing a total average population of 78 wolves. The *shaded areas* are major lakes in the park. (Color graphics on the computer screen are more attractive.)

Table 4. Sensitivity analysis of selected variables (see Table 1) in program "WOLF."

Variable	Elk[a]	Bison[a]	Moose[a]	Deer[a]	Wolf[a]
	Mean population size[b]				
Default (n = 30)	12,634	2,263	774	2,878	76
Deterministic	13,067	2,244	779	2,833	89
	Perturbation responses[b]				
F_{max}(elk)	0.0811	0.024	0.009	0.03	–0.213
F_{max}(bison)	0	0.001	0	0	0
F_{max}(moose)	0	0	0	0	0.011
F_{max}(deer)	0	0	0	0	0.011
F_{elk}	0.053	0.014	0.006	0.018	–0.125
F_{bison}	0.006	0.023	0.001	0.003	–0.022
F_{moose}	0.001	0	0.009	0	0
F_{deer}	0.001	0	0	0.029	0
r_0(elk)	–0.031	0.008	0.003	0.01	–0.068
r_0(bison)	0.001	–0.02	0	0.001	0
r_0(moose)	0	0	–0.006	0	0
r_0(deer)	0.001	0	0	–0.026	0
R_{elk}	0.096	0.043	0.018	0.055	–0.363
R_{bison}	0.007	0.003	0.001	0.004	–0.022
R_{moose}	0.001	0	0	0	0
R_{deer}	0.002	0	0	0.001	0
K_{elk}	–0.132	0.037	0.015	0.047	–0.325
K_{bison}	0.011	–0.17	0.001	0.006	–0.044
K_{moose}	0.001	0	–0.183	0.001	–0.011
K_{deer}	0.003	0.001	0	–0.171	–0.022
K_{wolf}	0.032	0.014	0.005	0.018	–0.125
r_{wolf}	–0.032	–0.01	–0.006	–0.017	0.125
μ_{wolf}[c]	–0.054	–0.02	–0.01	–0.028	0.216
Phytomass constant[d]	–0.005	0.001	–0.003	–0.004	–0.011
Phytomass exponent[e]	0.016	0	0.009	0.011	0.045
Bison phyto constant	0.001	0	0	0	0
Bison phyto exponent	–0.001	0.012	–0.001	0	0.011

[a] Elk = *Cervus elaphus*; bison = *Bison bison*; moose = *Alces alces*; deer = *Odocoileus* spp.; wolf = *Canis lupus*.

[b] The mean population sizes for comparisons of perturbation responses are based on deterministic projections. All perturbations entailed a decrease in the parameter value by 20%. Perturbation responses are expressed as a proportion of the state variables before perturbation.

[c] μ_{wolf} is the last term in equation 7 from text.

[d] Phytomass constant is the first numerical value in equation 4.

[e] Phytomass exponent is the numerical value in the exponent of equation 5.

In general, the population dynamics for wolves and elk govern the overall behavior of the model. Populations of ungulates and wolves are relatively unresponsive to perturbations of the functional and numerical responses for bison, moose, and deer, whereas all species react to perturbations in elk functional and numerical responses. In particular, a 20% reduction in F_{max} results in a 21% decline in the mean number of wolves. Similarly, a 20% reduction in the R_{elk}—the numerical response parameter—causes a 36% reduction in wolf numbers.

Parameters that triggered the greatest responses in ungulate population size were the carrying capacities for the respective species, K_i's. The response to fires could vary greatly without substantially changing either ungulate or wolf numbers.

The empirical basis for estimation of the functional response parameters, the F_i's, is probably weakest. Fortunately, population projections were relatively insensitive to perturbation of the F_i's, suggesting that substantial errors in estimation may not be of serious consequence to the outcome of population projections. In other words, the model is reasonably robust to variation in functional response curve placement.

Sensitivity analysis based on proportional perturbations of parameters tends to obscure the fact that some of the parameters may be relatively invariant in nature. For example, K_i's for ungulates vary enormously in response to climatic influences on seasonal range conditions. In contrast, whether F_{max}'s or F_i's vary much at all is unknown. It is not only the proportional responsiveness to perturbation that matters in understanding the structure of the model, but also the ecological interactions that create variation in the parameters.

Discussion

My view of population regulation in the ungulates of Yellowstone National Park does not differ substantially from the nonlinear plant–herbivore model described by Caughley and Lawton (1981). Because I had inadequate information to develop a complete plant–herbivore model, a trophic level is missing in the WOLF program. Because several species are incorporated into the model, it is complex. Complex models, especially when driven by seasonal forcing (Inoue and Kamifukumoto 1984), can yield complex dynamics. However, our analysis of elk and bison population dynamics for the northern range herds showed no evidence of such complex dynamics—and indeed, both species showed stable dynamics, contrary to the model presented by Eberhardt (1987). Population fluctuations were attributable to stochastic variation in winter severity and summer range phytomass but not due to inherent instability in the dynamics for either elk or bison.

Wolf population trends in program WOLF are similar to those characterized by Packard and Mech (1980, 1983). Specifically, population regulation in wolves results from both social and nutritional variables. Pack territoriality sets an upper limit to wolf population size that is attained only when prey abounds.

Consequences of Management Alternatives

Potential Conflicts With Hunting

One of the major concerns about wolf recovery is the possibility that predation on ungulates will substantially reduce populations of hunted game, especially elk, moose, deer, and bighorn sheep (Zumbo 1987). Simulation results indicate that although we will see a reduction in the number of these mammals, hunting need not be reduced. Rather, the result will be lower populations of ungulates. In the same fashion that density dependence ensures sustained-yield hunting, moderate predation by wolves results in compensatory mortality and natality.

Under the default alternatives, the WOLF program projects that terminating the late Gardiner hunt in Montana will only increase the wintering population of elk in Yellowstone by 7%. Interestingly, this increase in the elk population is accompanied by a 20% reduction in the coefficient of variation in mean elk numbers. These changes occur because of the way I modeled the elk hunt. For program WOLF, I presumed that the Montana Department of Fish, Wildlife, and Parks will continue to annually issue 700 elk permits for the late Gardiner hunt. This number would only change if the population of elk fell below 5,000, whereupon the elk hunt would be temporarily discontinued. In reality, it seems probable that if elk numbers again become exceptionally high, as they were in 1988, the number of permits will be increased again. This increase would result in a density-dependent effect that would tend to stabilize elk numbers in the same fashion that wolves do.

Examples exist where conflicts between hunting and wolf predation have been sufficient to merit reductions in hunting opportunities (Mech and Karns 1977; Gasaway et al. 1983; Keith 1983; Gunson 1986). The reason I expect hunting reductions may not be necessary in the Yellowstone area is that hunting is forbidden within the boundaries of Yellowstone National Park. Wolf predation on ungulates tends to be highest during the late winter when the prey are most vulnerable (Carbyn 1974, 1983), and therefore the consequence of predation on transient summer herds will not be as great. In addition, during summer, ungulate populations in the park more than double, and predation would be distributed over many more animals.

An alternative perspective on the consequences of human hunting of ungulates on ungulate–wolf interactions is that wolf numbers may be reduced (Table 3). Carbyn et al. (1987) believed that wolf numbers in Riding Mountain National Park were not as high as they could be because of hunting by humans outside the park. According to the WOLF program, terminating the late Gardiner hunt would allow an increase in the wolf population by 10–15%, but this is not proposed or anticipated in reality.

Anticipating what would happen if wolves were to follow elk migrating south of Yellowstone is difficult. Most of the elk in the Jackson elk herd migrate to winter feeding grounds, including the National Elk Refuge near Jackson. This migration would lead the wolves to farms and ranches where wolves would be imperiled. At most, one pack of wolves might survive winters by preying on elk and moose (and cattle) in the Buffalo Fork valley. I suspect that many wolves migrating into Jackson Hole would be killed. The same fate would probably befall wolves that followed elk summering on the Bechler Plateau in the southwestern corner of Yellowstone National Park and that migrate to the Sand Creek area in Idaho.

Controlling Dispersers

One of the management alternatives that has been suggested to minimize conflicts with local livestock growers is to kill wolves that leave the park. The consequence will be to increase the mortality rate for wolves in the park, especially among packs whose territories cross the park boundary. This mortality will increase the probability of extinction for wolves, although whether this is a significant factor determining the success of the recovery effort will depend on the other management choices.

Poaching

I incorporated poaching as an option in the WOLF program because local ranchers have told me that when wolves are released in the park, they will take it on themselves to poison them. Such poaching could be a serious problem and could reduce the chances that wolf recovery succeeds. Poaching would be much more of a threat to the continued survival of wolves in the park than legal killing of wolves outside the park, because legal killing would not threaten wolves in packs whose entire home range was within Yellowstone.

Initial Inoculum

Inoculum size will influence the success of wolf recovery. Vagaries of the environment and of the behavior of wolves require that a fair number of wolves be released if a reasonable number are to establish territories. United States Senator James McClure of Idaho has proposed releasing three pairs of wolves (Thuermer 1989), which my model suggests would have only a modest chance of surviving. However, the more wolves that are released initially, the greater the number of conflicts that are likely to arise with ranchers. Wolves are likely to disperse after their release (Fritts et al. 1984). Perhaps a higher risk of extinction is an acceptable price to pay for greater public acceptance of the wolf recovery program. Also, the McClure proposal allows for additional releases of wolves if the original three pairs are lost.

Recovery Zone for Wolves

My simulations only attempt to include ungulates and wolves within Yellowstone National Park. The probability of success for wolf recovery could be argued to depend in large part on the management that takes place outside the park. For example, if wilderness areas and other portions of national forests surrounding the park are included in the recovery zone, the total number of wolves in the Yellowstone ecosystem could be much higher. Along with this increase in carrying capacity for the wolves comes a lower probability of extinction.

Based on the sketchy data available, I am reluctant to offer an exact estimate for the probability of extinction of wolves in the greater Yellowstone ecosystem. Simple models exist that predict how expanding the recovery zone will affect wolves in the greater Yellowstone ecosystem.

A variety of approaches have been used to model extinction. Small populations disappear, on average, more quickly than larger ones, for which the effect of chance events (demographic stochasticity) may be negligible. Depending on the selection of program options, simulations using the WOLF program fairly frequently end with the wolf population becoming extinct. Clearly, wolf recovery for Yellowstone is not assured.

Perhaps the simplest of the extinction models is the birth–death model of MacArthur (1972:121–126), which shows that the expected time to extinction is approximately

$$E(T_{ext}) = (1/bN)(b/\mu)^N \tag{9}$$

where b and μ are instantaneous birth and death rates, and N is population size.

As the area of the recovery zone increases, the potential population of wolves, N, will increase. As can be seen from equation 9, the time to extinction will increase exponentially with increasing N.

For wolves, I have used $b = 0.8$ and $\mu = 0.68$ (see equation 7). Thus, for $N = 20$, the expected T_{ext} is only 1.6 years. For $N = 40$, this increases to $T_{ext} = 20.8$ years; with $N = 60$, $T_{ext} = 357.8$. For yet larger N, T_{ext} becomes exceedingly large. At $N = 80$, we calculate $T_{ext} = 6{,}923$ and for $N = 100$, $T_{ext} = 142{,}895$. Yet, this model only embraces the contributions of demographic stochasticity to extinction and naively ignores environmental stochasticity (Shaffer and Sampson 1985), which is large in Yellowstone National Park.

Other investigations using more realistic models that focus on environmental stochasticity have reported that the expected time to extinction varies with the logarithm of initial population size (Sawyer and Slatkin 1981) or with the logarithm of carrying capacity (Leigh 1981). For relatively small areas, increases in area dramatically slow the march to extinction. Again, the implication is that increases in the recovery zone area will increase the wolf population size and carrying capacity. This enlarged recovery zone will thereby have the effect of protecting wolves from extinction.

In none of these discussions have I addressed the issue of genetic constraints on viability for a reintroduced wolf population. Depending on management policies, the population of wolves in Yellowstone may be low enough that inbreeding could threaten the population (Ralls et al. 1986). I do not view this issue as serious, however, because inbreeding may be avoided by releasing a single breeding wolf into the population each generation (Lande and Barrowclough 1987). Yet, such releases may often be unsuccessful because outsiders seldom have an opportunity to join a wolf pack.

Research Needs

One of the products of modeling is the identification of weaknesses in our empirical understanding of systems. To understand the effect of wolves on ungulate populations in Yellowstone National Park, the obvious research need is to release wolves into the park—but this experiment is not currently possible, and other research needs exist.

Elk and bison in Yellowstone have been monitored closely, and although our understanding of the population dynamics of these two species is still rudimentary, we at least have a basis for simple models. Our understanding of moose and mule deer in the park, however, is fragmentary. My simulation results suggested that, under certain conditions, both of these species might suffer substantial losses from wolf predation and, therefore, we need to learn more about the habitats, distribution, and abundance of these ungulates.

Mule deer are of concern because in winter they concentrate on private lands north of the park. Also, deer are a preferred prey by wolves, and populations wintering in the park may be substantially reduced by wolves. Additional baseline data on mule deer distribution and movements are necessary to anticipate the consequences of wolf recovery.

The moose population in the greater Yellowstone ecosystem is not well known. Because moose frequent riparian areas near roads in Yellowstone National Park, viewing and photography of moose are important to park visitors. Moose are important prey for wolves in other areas (Mech 1970; Van Ballenberghe 1987), but they are more difficult to kill than elk or deer (Carbyn 1983) and therefore are less preferred. Nevertheless, there is particular concern about the possible consequences that wolves may have on moose because of the heavy hunting of moose outside the park, especially in Montana (Singer 1991). Still, moose colonized the northern range when wolves were present (M. Meagher, personal communication). Better information on moose numbers and ecology in the Yellowstone area is needed before we can project the consequences of wolf recovery.

To understand the ecology of the northern range, we need to better understand the plant–herbivore interactions. In particular, the role that ungulates play in plant succession and community structure must be understood in response to concerns that the range may be overgrazed (Chase 1986; Kay 1987; Chadde and Kay 1991; Ruediger 1991). Understanding the dynamics of the plant–herbivore system will require dissection of the foraging functional response for ungulates (e.g., Spalinger et al. 1988), especially for elk.

Should wolf recovery take place, implementing a vigorous program of monitoring to verify predictions of this model will be of utmost importance, and one of the more important things to study during wolf recovery is the mechanisms that shape the functional response of wolves to prey abundance and availability (Allen 1989; Caro 1989).

Conclusions

We cannot know the exact sequence of events that will occur after wolf recovery. This unpredictability was the reason for my constructing a stochastic model that never yields the same result twice. With the highly variable climate in Yellowstone National Park, large confidence intervals surrounding any projections for animal populations in the park are certain to exist.

Computer simulations indicate that wolf recovery will result in a reduction in both the mean and variance in ungulate numbers. But this does not imply that management problems associated with elk and bison populations in the park will disappear. For example, the number of bison on the northern range will not be so reduced that bison will stop leaving the park in the winter (Meagher 1989a, 1989b). Also, we will continue to observe substantial mortality of ungulates during severe winters, although the magnitude should be less with wolves present.

The perception that the northern range is overgrazed (Chadde and Kay 1991; Ruediger 1991) may change after wolf recovery. Ungulates will continue to concentrate on the same ranges, because these are places where less snow accumulation leaves forage more available. Yet, these areas probably have been heavily grazed by ungulates since the Pleistocene, and recent palynological (pollen analysis) evidence suggests that there have been no unusual trends in vegetation on the northern range during the last 11,000 years (Whitlock et al. 1991).

I have not attempted to model livestock conflicts resulting from wolf recovery. After wolves have become established, however, we might expect approximately 15 to 25 wolves to disperse from Yellowstone National Park each year. We can be reasonably certain that some of these dispersing wolves will kill livestock from time to time. The most severe conflicts may follow initial release because translocated wolves are likely to disperse (Fritts et al. 1984). When wolves kill livestock, control of problem animals probably will occur as it has in Montana in recent years (Bangs 1991).

Wolves will compete for game with hunters, and there will be differences of opinion as to whether wolves or hunters should be given priority. Hunters have mixed opinions on whether wolf recovery is good or bad.

When I was organizing the conference entitled "Examining the Greater Yellowstone Ecosystem" in spring 1989, I spoke with several members of the Wyoming Guides and Outfitters Association. I was surprised to learn that the association has no official policy on wolf recovery because members disagree about the issue. Some members reflect Zumbo's (1987) view that hunting opportunities may decline as a consequence of competition between hunters and wolves. Others, however, see benefits from wolf recovery. One guide believed that his business depended on providing clients with high-quality wilderness experiences in the Teton wilderness—and what could be a higher quality wilderness experience than to hear wolves howling the evening before embarking on a remote-country elk hunt?

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Population Models for Elk, Mule Deer, and Moose on Yellowstone's Northern Winter Range

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Abstract. We developed population models for elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and moose (*Alces alces*) inhabiting Yellowstone's northern winter range. Models were developed using available harvest, mortality, and sex and age classification data in a PC-based program, POP-II. Most of the available data were for elk using the northern range, followed by mule deer and moose. We estimated that the elk population continually increased during the 1970's to a peak of about 21,000 animals in winter 1987–88. The population then declined to about 17,500 elk in early winter 1988–89 and to about 17,000 elk in early winter 1989–90. We estimated that the mule deer population also increased during the mid-1970's to a peak of about 3,300 in late winter 1987–88. The mule deer population declined to about 2,600 in late winter 1989–90. We estimated that the population of moose on the northern range increased from approximately 366 animals in winter 1975–76 to 432 in winter 1989–90.

Aerial counts of elk (*Cervus elaphus*) may only tally 40–85% of the elk actually present (Samuel et al. 1987; Bear et al. 1989). The National Park Service, Yellowstone National Park, the Montana Department of Fish, Wildlife, and Parks, and the U.S. Forest Service are responsible for managing the northern Yellowstone elk herd. These agencies need reliable estimates of elk numbers for management. Work has been ongoing to develop population estimates for elk on the northern range using a sightability (observability) model (Singer et al. 1988). The sightability model provides one estimate of elk population size. Wildlife managers may find a second, independent estimate of elk numbers useful. The proposed wolf (*Canis lupus*) reintroduction into Yellowstone National Park increases the need for estimating mule deer (*Odocoileus hemionus*) and moose (*Alces*

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alces) numbers because these species could be wolf prey. Developing mark–recapture or sightability models for moose and mule deer is currently not possible. We used existing harvest and population classification (young/female and adult male/female) data to develop population estimates of mule deer and moose.

We used the computer program POP-II (Fossil Creek Software, Inc., Fort Collins, Colorado) to generate elk, mule deer, and moose population estimates. Advantages of POP-II are that (1) the program is relatively inexpensive, (2) the program uses existing population trend and harvest data, and (3) the program operates on a personal computer.

We compiled harvest, reproductive, mortality, and sex and age classification data for elk, mule deer, and moose occupying Yellowstone's northern winter range. We provide first-time population estimates for mule deer and moose and provide a second, independent, population estimate for elk on the northern range for comparison to sightability population estimates (Singer et al. 1988). We also identify voids in the data that limit using POP-II for ungulate population estimates.

Study Area

Houston (1982) describes the ownership, geology, vegetation, and climate of Yellowstone's northern range. From 1980 to 1990, 7 of 10 winters were milder than normal (Farnes 1991). Changes in landownership have taken place since the 1970's. The U.S. Forest Service, the Montana Department of Fish, Wildlife, and Parks, and the Rocky Mountain Elk Foundation have purchased land on northern portions of the winter range. Since 1986, these land acquisitions have totaled 40.5 km^2 (N. Bishop, National Park Service, Mammoth, Wyoming, unpublished data). The largest areas were purchased in 1989 (Dome Mountain properties) and 1990 (OTO ranch). Additional smaller land exchanges and purchases are pending.

Methods

Data used for generating population estimates were obtained from unpublished National Park Service files (1966–90), Mack et al. (1990), Houston (1982), Montana Department of Fish, Wildlife, and Parks progress reports, and F. J. Singer (National Park Service, Mammoth, Wyoming, unpublished data).

The POP-II program (Bartholow 1988) uses the following data: number of age classes, initial population proportions for sex and age classes, beginning population size, preseason and postseason mortality rates, preseason and postseason mortality severity indices, age and sex of the hunter harvest, relative harvest rates among age classes, wounding loss, reproductive rates, and sex ratios at birth. Harvest rates among age classes, wounding loss, and sex ratios at birth are user-defined constants in the program. Except for these constants and initial population proportions and beginning population size, the remaining variables can change each year in accordance with the data collected. Preseason and postseason mortality rates, preseason and postseason mortality severity indices, and wounding loss are variables not required for program operation. We describe specific values and assumptions used to model each ungulate species in the following sections.

Elk Option 1

Biological Years of Operation

For Option 1, we began the model in biological year 1975 (June 1975–May 1976) because in this year, the elk population seemed to stabilize following the last major elk removal by the National Park Service in 1968 (Houston 1982:66–68). The 1975–76 winter was the first time the Montana Department of Fish, Wildlife, and Parks reinstated a late hunt to harvest elk migrating outside Yellowstone National Park. Model simulation only extended to biological year 1989 (June 1989–May 1990).

Number of Age Classes

Houston (1982) listed 22 age classes (0.5 to 21+) for female elk and 16 for males. Our model contained only 17 age classes because few male elk live beyond 15.5 years (Houston 1982), and elk pregnancy rates substantially declined beyond 16.5 years.

POP-II allows the user to determine what age classes should be considered subadults. We considered calves as subadults.

Population Proportions for Sex–Age Classes

Initial age class proportions are required for POP-II. Using Houston's (1982) survivorship table, the proportions of elk in each age class were calculated. We then used a multiplying factor to get the bull and calf ratios in Houston's table to equal the observed bull and calf ratios in biological year 1975. After adjusting the bull and calf number segments, the percentage of each age class that contributed to the population was calculated and entered into POP-II (Table 1).

Estimated Beginning Population Size

We estimated the beginning total population, assuming 90% of the elk were seen during the highest total count (11,665) in winter 1974–75. Our estimated population was 12,961 elk. This high-presumed sightability in 1974–75 is supported by the following four winter counts averaging 0.73 (Table 2) of the POP-II estimated population, a realistic figure for the 1975–79 counting intensity. From elk classifications of 1974–75 (167 total elk/100 cows), the maximum number of cows able to give birth was 7,761. From the calf/cow ratio given for 1975–76 (29:100), the total num-

Table 1. Age class composition of the northern range elk (*Cervus elaphus*) herd for 1975–1976, as modified from Houston's (1982) survivorship curve.

Age class		Houston's data (number)		Calculated percent composition[a]			
POP-II	Actual	Males	Females	Number of males	Percent of total	Number of females	Percent of total
1	0.5	1,000	1,000	1,440	9.12	1,440	9.12
2	1.5	361	677	365	2.31	677	4.29
3	2.5	339	664	342	2.17	664	4.21
4	3.5	335	662	338	2.14	662	4.19
5	4.5	330	660	333	2.11	660	4.18
6	5.5	325	656	328	2.08	656	4.16
7	6.5	309	652	312	1.98	652	4.13
8	7.5	261	643	264	1.67	643	4.07
9	8.5	197	640	199	1.26	640	4.06
10	9.5	155	637	157	0.99	637	4.04
11	10.5	114	628	115	0.73	628	3.98
12	11.5	94	621	95	0.60	621	3.93
13	12.5	63	609	64	0.41	609	3.86
14	13.5	35	596	35	0.22	596	3.78
15	14.5	23	555	23	0.15	555	3.52
16	15.5	10	521	10	0.06	521	3.30
17	16.5	0	501	0	0.00	501	3.17
Total	—	3,951	10,922	4,420	—	11,362	—

[a] Calculated values were obtained by adjusting calf/cow and bull/cow ratios from the survivorship curve to equal the ratios for biological year 1975 (June 1975–May 1976). Correction factors used were 1.01 for each male age class 1.5 years or older and 1.44 for the calves. Percentages were calculated from total adjusted elk numbers.

ber of calves produced was 2,251. Total adult elk plus calves yielded an estimated 15,212 elk for the beginning population for biological year 1975.

Natural Mortality

No data have been collected on preseason (before hunting season) mortality for adults, and we assumed little occurred during summer and early fall (Houston 1982). Preseason calf mortality estimates are not needed for POP-II models because the winter calf/cow ratios estimate the number of calves in the winter population.

Houston's (1982) age-specific mortality was used in POP-II's postseason mortality. After test runs of the model, we increased bull mortality and slightly decreased cow mortality (Table 3), because higher bull mortality was observed in many elk and red deer (*C. elaphus*) populations approaching carrying capacity (Anderson 1958; Peek and Lovaas 1968). The age-specific mortalities entered into the model partially corrected for unreasonable bull/cow ratios generated during previous model test runs.

Table 2. Comparison of the yearly elk (*Cervus elaphus*) population estimates from the POP-II models and the actual number of elk counted during total count survey flights.

Year	Actual number of elk counted	Date counted	Pop-II models Option 1	Pop-II models Option 2	Option 1 adjusted to date of count[a]	Estimated proportion of herd counted	Sightability model estimate
1971–72	8,215	12/2–4/71	—	11,279	—	—	—
1972–73	9,981	12/9–10/72	—	11,804	—	—	—
1973–74	10,529	1/3–6/74	—	12,531	—	—	—
1974–75	12,607[b]	12/29–31/74	—	13,167	—	—	—
1975–76	12,014[c]	12/17–18/75	14,590	12,791	15,797	0.76	—
1976–77	8,980[d]	1/23–24/77	14,305	13,021	13,305	0.67	—
1977–78	12,680	12/20–21/77	14,547	13,357	15,350	0.83	—
1978–79	10,838[e]	12/29–30/78	15,294	14,108	15,364	0.71	—
1979–80	No count	—	15,716	14,504	16,203	—	—
1980–81	No count	—	16,610	15,371	16,743	—	—
1981–82	16,019[f]	1/6–7/82	16,684	15,449	17,699	0.91	—
1982–83	No count	—	18,075	16,794	19,523	—	—
1983–84	No count	—	19,184	17,927	20,837	—	—
1984–85	No count	—	19,930	19,231	21,136	—	—
1985–86	16,286	12/19–20/85	21,056	21,430	22,115	0.74	—
1986–87	17,007	12/10/86	18,982	19,462	19,825	0.86	19,300[g]
1987–88	18,913	1/19/88	21,491	21,636	21,706	0.87	22,018[f]
1988–89	8,739[d]	4/14/89	18,267	17,501	20,619	0.42	18,133[f]
1989–90	14,829	1/18–19/90	17,420	17,333	17,843	0.83	19,118[h]

[a] The late hunt harvest was added to the POP-II Option 1 estimate so comparisons could be made with the actual elk count.
[b] Includes 89 elk counted outside Yellowstone National Park on 12/29/74.
[c] Includes 349 elk counted outside Yellowstone National Park on 12/14/75.
[d] Census conditions were poor and counts are not believed accurate.
[e] Includes 520 elk counted outside Yellowstone National Park by G. Erickson (Montana Department of Fish, Wildlife, and Parks).
[f] Singer 1990.
[g] Singer et al. 1988.
[h] J. Reardon, National Park Service, Yellowstone National Park, personal communication.

Mortality Severity Indices

Mortality severity indices can be used when adverse weather conditions cause higher than normal mortality. Mortality severity indices act as a multiplier to basal death rates. We did not use preseason mortality severity indices in any of the models. Postseason mortality severity indices were not incorporated into the preliminary model for subadults because a poor relation was observed between known winter mortality of calves and winter severity indices (Coughenour and Singer, Yellowstone National Park, Wyoming, unpublished data). Overwinter mortality of adults compared to winter severity was unknown, and postseason mortality severity indices were not used in the model.

Table 3. Age class mortality rates for northern range elk (*Cervus elaphus*) from Houston (1982) and the adjusted overwinter mortality values used in the POP-II model.

Age class		Age class mortality rate			
		Houston's data		POP-II values	
POP-II	Acual	Males	Females	Males	Females
1	0.5	0.639	0.323	0.20	0.10
2	1.5	0.061	0.019	0.05	0.00
3	2.5	0.012	0.003	0.05	0.00
4	3.5	0.015	0.003	0.05	0.00
5	4.5	0.015	0.006	0.10	0.00
6	5.5	0.049	0.006	0.20	0.00
7	6.5	0.155	0.014	0.30	0.00
8	7.5	0.245	0.005	0.40	0.00
9	8.5	0.213	0.005	0.50	0.00
10	9.5	0.265	0.014	0.60	0.00
11	10.5	0.175	0.011	0.70	0.00
12	11.5	0.330	0.019	0.80	0.00
13	12.5	0.444	0.021	0.80	0.00
14	13.5	0.343	0.069	0.80	0.05
15	14.5	0.565	0.061	1.00	0.05
16	15.5	1.000	0.038	1.00	0.05
17	16.5	1.000	0.118	1.00	1.00

Harvest

Outside Yellowstone National Park, segments of the northern elk herd are harvested in Montana hunting districts 313 and 316. Total general season harvest in district 313 ranged from a low of 27 in 1971 to a high of 766 in 1986 (Table 4). Average bull and spike (yearling male) harvests were relatively low in the 1970's ($\bar{x}$ = 83/year) and substantially increased in the 1980's ($\bar{x}$ = 230/year). Cow harvests remained relatively low ($\bar{x}$ = 33/year) through both decades except for unusually high harvests in 1986 and 1989 (305 and 400, respectively). Calf harvests were variable but were higher during the 1980's than during the 1970's.

The general season bull and spike harvests for district 316 increased slightly during the 1980's ($\bar{x}$ = 99/year) from the 1970's ($\bar{x}$ = 85/year; Table 5). The average cow and calf harvests were similar between the two decades.

In district 313, a late hunting season was initiated during the 1975–76 winter and has continued nearly every winter to present. Total harvests varied each year depending on the number of elk migrating out of Yellowstone National Park (Table 6). The bull harvest has decreased since 1975–76, primarily due to the reduction in bull and either-sex permits (Mack et al. 1990). Cow and calf harvests were quite variable, particularly during the late 1980's.

Table 4. Point estimates and adjusted values of the elk (*Cervus elaphus*) harvest during the regular hunting season in Montana hunting district 313, 1971–1990 (Chrest and Childress 1976; Chrest and Herbert 1980; Carlson 1987; T. Lemke, Montana Department of Fish, Wildlife, and Parks, Livingston, personal communication).

	Point estimate of harvest						Adjusted harvest			
Year	Bulls	Spikes	Cows	Calves	Unknown	**Total**	Bulls	Spikes	Cows	Calves
1971–72	20	0	7	0	0	27	20	0	7	0
1972–73	12	11	22	0	0	45	12	11	22	0
1973–74	66	4	24	0	4	98	68	5	25	0
1974–75	13	0	11	0	10	34	18	0	16	0
1975–76	126	18	34	5	11	194	133	20	36	5
1976–77	23	49	12	2	2	88	24	50	12	2
1977–78	85	34	22	0	8	149	90	36	23	0
1978–79	94	67	30	3	4	198	96	68	31	3
1979–80	36	56	22	2	2	118	37	57	22	2
1980–81	35	84	21	1	0	141	35	84	21	1
1981–82	140	58	21	1	0	220	140	58	21	1
1982–83	226	100	17	0	0	343	226	100	17	0
1983–84	118	120	38	28	0	304	118	120	38	28
1984–85	102	57	51	4	0	214	102	57	51	4
1985–86	146	103	53	9	0	311	146	103	53	9
1986–87	397[a]		305	64	0	766	397[a]		305	64
1987–88	99	99	76	12	0	187	99	99	76	12
1988–89	314	314	98	9	0	421	314	314	98	9
1989–90	198	198	400	44	0	642	198	198	400	44

[a] Harvest data includes bulls and spikes from 1986 to 1990.

Table 5. Point estimates and adjusted values of the elk (*Cervus elaphus*) harvest during the regular hunting season in Montana hunting district 316, 1971–1990 (Chrest and Childress 1976; Chrest and Herbert 1980; Carlson 1987; T. Lemke, Montana Department of Fish, Wildlife, and Parks, Livingston, personal communication).

	Point estimate of harvest						Adjusted harvest			
Year	Bulls	Spikes	Cows	Calves	Unknown	**Total**	Bulls	Spikes	Cows	Calves
1971–72	45	20	17	0	1	83	46	20	17	0
1972–73	68	3	33	7	0	111	68	3	33	7
1973–74	61	11	27	8	5	112	63	12	29	8
1974–75	64	18	23	0	15	120	73	21	26	0
1975–76	77	25	25	0	19	146	88	29	29	0
1976–77	72	18	34	7	0	131	72	18	34	7
1977–78	64	9	21	0	18	112	75	25	12	0
1978–79	80	13	16	4	0	113	80	13	16	4
1979–80	37	17	17	0	5	76	39	18	19	0
1980–81	60	13	19	0	10	102	66	15	21	0
1981–82	60	23	31	10	0	124	60	23	31	10
1982–83	52	25	22	4	1	104	53	25	22	4
1983–84	85	15	0	0	0	100	85	15	0	0
1984–85	107	15	24	0	0	146	107	15	24	0
1985–86	86	17	36	6	0	145	86	17	36	6
1986–87	97[a]		23	8	0	128	97[a]		23	8
1987–88	125		41	6	0	172	125		41	6
1988–89	62		4	0	0	66	62		4	0
1989–90	143		26	4	0	173	143		26	4

[a] From 1986 to 1990, total bulls and spikes.

Table 6. Number of elk (*Cervus elaphus*; calves, cows, and bulls) harvested during the Gardiner late hunting season in Montana hunting district 313, 1975–1976 to 1989–1990.

Year	Number of hunters	Calves	Cows	Bulls	Illegal kills[a] Known	Illegal kills[a] Unknown	**Total**
1975–76	1,283	140	362	705	68	—	1,207[a]
1976–77[b]	—	—	—	—	—	—	—
1977–78	—	191	241	370	38	—	803[c]
1978–79	—	2	3	30	—	—	70[d]
1979–80	643	25	157	285	—	—	487[e]
1980–81	1,109	16	42	75	7	—	133
1981–82	1,448	100	422	491	—	—	1,015[f]
1982–83	1,734	232	681	462	—	73	1,448
1983–84	1,799	396	815	396	60	46	1,653
1984–85	1,835	291	742	173	45	—	1,206
1985–86	1,681	205	728	126	33	—	1,059
1986–87	1,453	206	566	71	15	—	843
1987–88	967	56	148	11	—	—	215
1988–89	2,486	458	1,846	48	—	—	2,352
1989–90	690	58	326	39	—	—	423

[a] For elk in the known column, sex and age were recorded and included in the totals for calves, cows, and bulls; unknowns had no sex and age recorded and were only included in yearly totals.
[b] No late hunting season was held.
[c] Includes 1 legal kill of unknown sex or age.
[d] Harvest was estimated. Late hunt held in Slip and Slide and Six Mile areas. No check station data were obtained.
[e] Includes 6 females and 14 males of unknown age.
[f] Includes 2 elk of unknown age and sex.

Harvest data from districts 313 and 316 (including the late hunt) were pooled and the resulting data were entered into the POP-II model (Table 7). For the model, adult age classes were presumed to be harvested at equal rates. For the first year of simulation, the bull harvest was not included because the sex–age class percentages accounted for the observed bull/cow ratio in the population. If the first year's bull harvest had been included, a lower bull/cow ratio for the first year's simulation would have resulted.

Wounding Loss and Illegal Harvest

Wounding loss or illegal kills are expressed as a percentage of the total legal harvest and are added to the total legal harvest in the POP-II model. An estimate of illegal harvest was obtained during the Gardiner late hunt for several years (Table 8). A value of 10% for adult males and females was used in the model to account for unknown wounding loss and unreported illegal kills. Five percent wounding loss was used for calves because they are not selected for in most hunting situations, and we believe they would be wounded and illegally killed at lower rates than adults.

Table 7. Combined elk (*Cervus elaphus*) harvest from the general and late hunting seasons in Montana hunting district 313 and general season in Montana hunting district 316, 1971–1972 to 1989–1990. Values in each age–sex class have been proportionately adjusted to include harvested elk of unknown age and sex.

Year	Bulls[a]	Cows	Calves	**Total**
1971–72	86	24	0	110
1972–73	94	55	7	156
1973–74	148	54	8	210
1974–75	112	42	0	154
1975–76	975	427	145	1,547
1976–77[b]	164	46	9	219
1977–78	597	276	191	1,064
1978–79	317	53	11	381
1979–80	443	201	37	681
1980–81	275	84	17	376
1981–82	773	475	111	1,359
1982–83	890	756	249	1,895
1983–84	746	876	435	2,057
1984–85	454	817	295	1,566
1985–86	478	817	220	1,515
1986–87	565	894	278	1,737
1987–88	235	265	74	574
1988–89	424	1,948	467	2,839
1989–90	380	752	106	1,238

[a] The number of spikes (yearling males) harvested was not separated from the bulls category because of the inability to consistently determine the spike harvest each year.
[b] No late hunt conducted.

Table 8. Illegal elk (*Cervus elaphus*) harvest expressed as percent of total legal harvest for late season hunts on Montana hunting district 313, 1975–1976 to 1986–1987 (Chrest and Childress 1976, 1978; Chrest and Herbert 1981, 1983, 1984, 1985; Chrest 1986; Carlson 1987).

Year	Illegal harvest	Legal harvest	Illegal harvest as percent of legal harvest
1975–76	68	1,139	6.0
1977–78	38	765	5.0
1980–81	7	126	5.6
1982–83	73	1,375	5.3
1983–84	106	1,547	6.9
1984–85	45	1,161	3.9
1985–86	33	1,026	3.2
1986–87	15	828	1.8
Mean	—	—	4.7

Recruitment

Three different age classes contributed to reproduction in our POP-II model. Houston (1982) provided information on age class pregnancy rates (Table 9), which were considerably higher than hunter-reported pregnancy rates (Table 10). However, field checks indicated hunters missed some fetuses and hunter information should only be used as a relative pregnancy index (Chrest 1986). We used the pregnancy rates (Table 9) in Houston (1982) as a guide in establishing reproductive groups for the model. Houston (1982) showed that yearling pregnancy rates were negatively related to population size and winter severity; however, Houston (1982) indicated that winter severity may have had more of an effect on yearling pregnancy than population size.

For our models, group 1 consisted of calves and yearlings (age classes 1 and 2, respectively). Group 2 consisted of adult cows to the age of 15.5 (age classes 3–16). Group 3 consisted of cows 16.5 years old and older (age class 17). Groups 1 and 3 did not contribute to reproduction in the model because of their substantially lower pregnancy rates. Group 2 females contributed to all of the reproduction based on the classification data gathered during early winter (Table 11). Because reproduction in our

Table 9. Pregnancy rates for elk (*Cervus elaphus*) on the northern winter range in Yellowstone National Park, 1950–1967 (Houston 1982:37–39).

Year	Age class	Weighted pregnancy rate	*N*
1935–68	1.5	0.1356	357
1961–68	1.5	0.1483	313
1950–67	2.5	0.9351	247
1961–67	1.5	0.1559	221
1962–67	2.5	0.9442	217
1962–67	2.5–15.5	0.9496	1,111
1962–67	3.5–15.5	0.951	894
1962–67	16.5+	0.3516	37

Table 10. Pregnancy and lactation rates of cow elk (*Cervus elaphus*) harvested during the Gardiner late hunt in Montana hunting district 313, 1983–1984 to 1986–1987 (Chrest and Herbert 1984, 1985; Chrest 1986; Carlson 1987).

Year	Pregnant (%)	*N*	Lactating (%)	*N*
1983–84	71.0	580	35.4	810
1984–85	64.9	667	39.3	657
1985–86	56.0	689	34.6	670
1986–87	62.1	542	33.5	508

Table 11. Early winter classification of the northern Yellowstone elk (*Cervus elaphus*) herd, 1967–1968 to 1989–1990 (Houston 1982; F. J. Singer, National Park Service, Yellowstone National Park, unpublished data).

Year	Adult bulls/100 cows	Spike bulls/100 cows	Total bulls/100 cows	Calves/100 cows	*N*
1967–68	36	14	47	37	952
1968–69	39	12	51	45	1,694
1969–70	46	17	52	47	1,654
1970–71	42	15	57	44	2,267[a]
1971–72	37	13	50	35	2,795
1972–73	35	8	42	33	2,589
1973–74	33	12	46	30	4,442
1974–75	32	11	42	25	3,449
1975–76	25	5	30	29	2,352
1976–77	12	3	14	17	3,253
1977–78	18	8	26	26	2,664
1978–79	21	6	27	24	3,982
1979–80	—	—	—	—	—
1980–81	—	—	—	—	—
1981–82	—	—	—	—	—
1982–83[b]	—	6	—	41	1,030
1983–84	—	12	—	38	945
1984–85	—	7	—	34	894
1985–86	26	4	30	48	5,363
1986–87	16	7	23	33	5,574
1987–88	19	5	24	40	4,697
1988–89	15	3	19	24	2,613
1989–90	20	5	25	19	5,479

[a] All numbers are from ground classifications adjusted according to percent of adult males in aerial samples from 1971 to 1979 (Houston 1982).

[b] From 1982–83 to 1984–85, ground classifications were conducted producing biased bull ratios (Houston 1982), hence bull ratios are unreported.

models is based on early winter classification, any density-dependent factors affecting net reproduction would be reflected in the classification data.

Early winter classification data were summarized from 1967–68 to 1989–90 (Table 11). Before 1970–71 (and possibly 1 to 2 years later), bull/cow, spike/cow, and calf/cow ratios were probably inflated due to the herd reductions before 1968 (Houston 1982). In general, the bull/cow and spike/cow ratios have declined from 1975–76 levels to present ones, with the total bull ratio varying from 19 to 30/100 cows. Calf/cow ratios declined between 1969–70 and 1978–79. Calf/cow ratios increased in 1982–83 and remained relatively high until 1988–89, when the severe summer drought and the severe winter reduced calf survival. These conditions may have lowered the reproductive condition for cows, which subsequently reduced newborn calf survival the following spring of 1989 (Singer et al. 1989) and resulted in a low observed calf/cow ratio in early winter 1989–90.

Houston (1982) and Vore (1990) reported the sex ratio of newborn calves on the northern range to be 50:50. This value was used in the model.

Elk Option 2

A second elk model was developed using data beginning in 1971–72. The Elk Option 2 model is similar to Elk Option 1. The following differences are described :

1. Biological years of operation—The years of simulation for this model began in biological year 1971 (June 1971–May 1972). Model simulation ended in 1989 (June 1989–May 1990).
2. Population proportions for sex–age classes—Different sex–age class proportions were used in this model. We again entered the proportions into POP-II as in Elk Option 1. Multiplying factors were used to get the bull/cow and calf/cow ratios in Houston's (1982) survivorship table to equal the observed bull/cow and calf/cow ratios in biological year 1971. The percentage of each age class contributed to the population was entered into POP-II (Table 12).
3. Estimated beginning population—We assumed Houston's (1982) 1970–71 elk count of 7,282 tallied 75% of the total elk population, and we estimated the early winter elk population was 9,709. From elk classifications in 1970–71 (201 total elk/100 cows), the maximum number of cows able to give birth was 4,830. From the calf/cow ratio in 1971–72 (35:100), the total number of calves produced was 1,691. Total adult elk plus calves yielded an estimate of 11,400 elk for the beginning population for biological year 1971.

Mule Deer

Biological Years of Operation

Model simulation began in biological year 1975. Simulations ended in biological year 1989.

Number of Age Classes

No age data from the mule deer harvest are available. From a nearby mule deer population in the Bridger Mountains, Montana, Mackie et al. (1982) suggested few females live beyond 10 to 12 years and few males survive beyond 8 years. Using these data as a guide, 13 age classes were used in the POP-II model. For males, overwinter survival was modified so no male would survive beyond age class 11 (10.5 years).

Population Proportions for Sex–Age Classes

Life table data have not been collected for the northern range mule deer population. Therefore, we allowed POP-II to compute the percent of animals in each age class. Buck/doe and fawn/doe ratios for the first biological year of model simulation were needed for the computation. Buck/doe and fawn/doe ratios were obtained by modifying observed late winter classification (explained later in the Recruitment section). After entering these data, the user must decide on a hypothetical annual survival rate for male and female adults. Mackie et al. (1982) stated that a mule deer population in central Montana had an average annual mortality of 30–33%. We used these figures as a guide and entered an annual survival rate of 60% for males and 80% for females. The 80% female survival rate was near the range offered in Mackie et al. (1982).

Estimated Beginning Population

Population counts were not conducted in 1975. The earliest count occurred in winter 1978–79 (Foss and Taylor 1980), when 1,108 deer were

Table 12. Age class composition of the northern range elk (*Cervus elaphus*) herd for 1971–1972. Values modified from Houston's (1982) survivorship curve.

Age class		Houston's data (number)		Calculated percent composition[a]			
POP-II	Actual	Males	Females	Males (number)	Percent of total	Females (number)	Percent of total
1	0.5	1,000	1,000	1,737	9.46	1,737	9.46
2	1.5	361	677	606	3.30	677	3.69
3	2.5	339	664	570	3.11	664	3.62
4	3.5	335	662	563	3.07	662	3.61
5	4.5	330	660	554	3.02	660	3.60
6	5.5	325	656	546	2.97	656	3.57
7	6.5	309	652	519	2.83	652	3.55
8	7.5	261	643	438	2.39	643	3.50
9	8.5	197	640	331	1.80	640	3.49
10	9.5	155	637	260	1.42	637	3.47
11	10.5	114	628	192	1.05	628	3.42
12	11.5	94	621	158	0.86	621	3.38
13	12.5	63	609	106	0.58	609	3.32
14	13.5	35	596	59	0.32	596	3.25
15	14.5	23	555	39	0.21	555	3.02
16	15.5	10	521	17	0.09	521	2.84
17	16.5	0	501	0	0.00	501	2.73
Total	—	3,951	10,922	6,695	—	11,659	—

[a] Calculated values were obtained by adjusting calf/cow and bull/cow ratios from the survivorship curve to equal the ratios for biological year 1971 (June 1971–May 1972). Correction factors used were 1.68 for each male age class 1.5 years or older and 1.73 for male and female calves (POP-II age class 1). Percentages were calculated from the total adjusted elk numbers.

classified. Because no starting point was available, we set the beginning population as low as possible. After several model test runs, the starting population was set at 2,000 for the beginning of biological year 1975. The modeled population crashed when starting populations lower than 2,000 were used. This value represents the total number of bucks, does, and newborn fawns in the population.

Natural Mortality

Preseason and postseason mortality data were not collected for the northern range mule deer herd. No preseason mortality was assigned to any age–sex class in the model. Initial postseason mortality was set at zero. The oldest age class (13) automatically all died.

Initial test runs suggested some overwinter mortality was needed in the younger age classes to align the model with the observed data. Some arbitrary guesses on age class mortality were used to prevent the model from creating unrealistically high populations and high buck/doe ratios. As a general guide, we used the U-shaped mortality curve, which proposes high young mortality, low middle age mortality, and then progressively higher mortality in older age classes. Low overwinter mortality settings for fawns are most likely because the reproduction estimates were taken in middle-to-late April when most overwinter mortality had probably occurred. Fawn postseason mortality (overwinter mortality) was set at 5% for males and females because reproductive estimates were gathered after most overwinter mortality had occurred (middle-to-late April). This mortality rate is probably near the maximum because when higher male fawn mortality rates were used, too few males survived to support the observed harvest. We assigned 5% postseason mortality for age class 2 (1.5-year-old) males and 0% mortality for age class 3–8 males. We increased mortality for age classes 9 and 10 to 10% and 20%, respectively. Males, age class 11 and above, had 100% mortality. Relatively low male mortality rates for the middle age classes were needed to sustain the high male harvests observed during the 1980's.

Female age classes 1–9 were assigned postseason mortality rates of 5%. Female postseason mortality for age classes 10, 11, and 12 was 10, 20, and 30%, respectively. The higher female death rates were used to lower the unrealistically high population numbers being simulated when no mortality was encountered. Portions of the northern range may have higher female mortality rates because vehicle collisions kill a disproportionally large number of does each winter.

Mortality Severity Indices

No information is available relating mule deer mortality to winter severity indices. After several test runs, mortality severity values were used in certain years to compensate for the disparity between observed and simulated buck/doe ratios.

Harvest

Most of the legal harvest for northern range mule deer occurs in Montana hunting districts 313 and 316. The adult buck harvest in district 313 steadily increased from 86 in 1974–75, peaked to 549 in 1983–84, and then declined to 244 in 1989–90 (Table 13). The antlerless harvest remained relatively low during the late 1970's to 1981–82 and then increased during the middle to late 1980's (Table 13). In 1988–89 and 1989–90, antlerless harvests again dropped to late 1970's levels. Statistics are not compiled on the number of fawns in the antlerless harvest. We assumed the annual fawn harvest was zero. All antlerless harvests were considered adult does for the model.

Nearly all deer harvested in hunting district 316 were bucks (Table 14). The average yearly buck harvest from 1974–75 to 1989–90 was 53 (range 30–92). Except for 1974–75 and 1975–76, relatively few or no antlerless deer were harvested. The harvest statistics from districts 313 and 316 were combined (Table 15) and entered into the model.

Harvest Rates for Sex-Age Classes

No data were available on differential harvests between age classes. Therefore, all adult sex–age classes were assumed to be harvested at equal rates.

Table 13. Mule deer (*Odocoileus hemionus*) harvest for Montana hunting district 313 on Yellowstone's northern winter range, 1974–1975 to 1989–1990 (Foss 1981, 1982, 1984a, 1984b, 1986a, 1986b, 1987).

					Adjusted harvest[a]	
Year	Bucks	Anterless	Unknown	**Total**	Bucks	Anterless
1974–75	82	38	6	126	86	40
1975–76	141	60	14	215	151	64
1976–77	74	7	—	81	74	7
1977–78	139	—	—	139	139	—
1978–79	212	—	4	216	216	—
1979–80	223	26	—	249	223	26
1980–81	223	26	5	254	227	27
1981–82	450	47	7	504	456	48
1982–83	465	101	5	571	469	102
1983–84	549	197	—	746	549	197
1984–85	341	239	—	580	341	239
1985–86	242	215	—	457	242	215
1986–87	337	151	—	488	337	151
1987–88	232	121	5	358	235	123
1988–89	432	71	—	503	432	71
1989–90	244	32	—	276	244	32

[a] Deer of unknown sex were proportionally added to the buck and antlerless totals in the adjusted harvest based on the relative proportions of the known buck and antlerless harvest.

Table 14. Mule deer (*Odocoileus hemionus*) harvest for Montana hunting district 316 on Yellowstone's northern range, 1974–1975 to 1989–1990 (Foss 1981, 1982, 1984a, 1984b, 1986a, 1987; T. Lemke, Montana Department of Fish, Wildlife, and Parks, Livingston, personal communication).

					Adjusted harvest[a]	
Year	Bucks	Anterless	Unknown	**Total**	Bucks	Anterless
1974–75	35	24	4	63	37	26
1975–76	51	21	7	79	55	24
1976–77	27	—	3	30	30	—
1977–78	30	4	—	34	30	4
1978–79	57	—	—	57	57	—
1979–80	74	—	—	74	74	—
1980–81	92	—	—	92	92	—
1981–82	83	6	—	89	83	6
1982–83	47	—	—	47	47	—
1983–84	40	—	—	40	40	—
1984–85	42	—	—	42	42	—
1985–86	55	—	—	55	55	—
1986–87	44	4	—	48	44	4
1987–88	55	—	—	55	55	—
1988–89	58	—	—	58	58	—
1989–90	52	—	—	52	52	—

[a] Deer of unknown sex were proportionally added to the buck and antlerless totals in the adjusted harvest based on the relative proportions of the known buck and antlerless harvest.

Table 15. Total mule deer (*Odocoileus hemionus*) harvest for Montana hunting districts 313 and 316, 1974–75 to 1989–90. Totals include proportional adjustments for harvested mule deer of unknown sex.

Year	Bucks	Anterless	**Total**
1974–75	123	66	189
1975–76	206	88	294
1976–77	104	7	111
1977–78	169	4	173
1978–79	273	—	273
1979–80	297	26	323
1980–81	319	27	346
1981–82	539	54	593
1982–83	516	102	618
1983–84	589	197	786
1984–85	383	239	622
1985–86	297	215	512
1986–87	381	155	536
1987–88	290	123	413
1988–89	490	71	561
1989–90	296	32	328

Wounding Loss and Illegal Harvest

No data were available on illegal hunter kill or wounding loss. As with elk, we assumed a 10% loss for adult males and females.

Recruitment

Postseason buck/doe and fawn/doe ratios were collected sporadically from 1974–75 to 1989–90 (Table 16). Spring fawn/adult ratios were most consistently collected, and these data were modified to obtain the postseason buck/doe and fawn/doe ratios used in POP-II.

The number of adults in the survey was calculated from spring fawn/adult ratios. Using buck/doe ratios, the number of adult does and bucks in the population was estimated. When observed buck/doe ratios were missing, the average observed ratio ($\bar{x}$ = 14 bucks/100 does) was used. After calculating the total numbers of bucks, fawns, and does from the classification sample, we then calculated the buck/doe and fawn/doe ratios used in POP-II (Table 17). The calculated fawn/doe ratios probably represent the minimum recruitment (after overwinter survival) for a particular biological year. An assumption used in these calculations was that

Table 16. Mule deer (*Odocoileus hemionus*) classifications for Montana hunting district 313 and portions of 314 on the northern winter range north of Yellowstone National Park (Stewart 1976; Foss 1986b; Lemke and Singer 1989, 1990).

	Postseason[a]				Spring[a]		Fawn	Recruitment
Year	B/100 D	F/100 D	F/100 A	*N*	F/100 A	*N*	mortality (%)	(%)
1974–75	—	—	58	—	34	—	41	—
1975–76	—	—	—	—	14	338	—	—
1976–77[b]	—	—	—	—	—	—	—	—
1977–78	—	—	—	—	39	401	—	—
1978–79	16	42	36	157	32	1,108	11	24
1979–80	17	67	52	345	40	91	23	29
1980–81	—	—	61	286	—	—	—	—
1981–82	15	65	56	97	40	300	29	29
1982–83	—	—	55	381	48	727	13	32
1983–84	7	65	60	303	29	420	52	23
1984–85	21	88	73	159	47	508	36	32
1985–86	0	42	42	68	44	562	0	31
1986–87	—	—	—	—	47	493	—	—
1987–88[c]	—	—	—	—	45	649	—	—
1988–89[d]	—	—	—	—	14	1,796	—	—
1989–90[d]	7	41	35	745	34	1,327	3	—

[a] B/100 D = bucks/100 does; F/100 D = fawns/100 does; F/100 A = fawns/100 adults.
[b] No census was conducted.
[c] Includes helicopter and ground surveys.
[d] Includes portions of districts 313 and 314 (east and west side of the Yellowstone River).

the observed buck/doe ratios did not change significantly from postseason to early spring.

For the model, female age classes ranging from 2 to 12 (1.5–11.5 years old) contributed to reproduction. The newborn sex ratio is unknown for northern range mule deer, and we initially used a 50:50 ratio. This ratio was found inappropriate because the model estimated too few males in the population to sustain the observed buck harvests. With a 50:50 ratio, the model would not operate after 4 years of simulations. We changed the ratio to 55 males/45 females. This value sustained the harvest, and model test runs simulated buck/doe ratios similar to those observed in the field.

Moose

Biological Years of Operation

Model simulations began in biological year 1975 because this was the earliest date classification data were collected (Erickson 1978). Model simulations ended in biological year 1989.

Table 17. Data used to calculate the northern winter range mule deer (*Odocoileus hemionus*) buck/100 does and fawn/100 does ratios used in the POP-II model, 1975–1976 to 1989–1990.

Year	Spring F/100 A[a]	*N*	Adults	Average or observed B/100 D[b]	Number: Bucks	Number: Does	Number: Fawns	Calculated POP-II ratios: B/100 D	Calculated POP-II ratios: F/100 D
1975–76	14	338	296	14	36	260	42	14	16
1976–77[c]	—	—	—	—	—	—	—	14	36
1977–78	39	401	288	14	35	253	113	14	45
1978–79	32	1,108	839	16	116	723	269	16	37
1979–80	40	91	65	17	9	56	26	16	46
1980–81	36[d]	286[e]	210	14	26	184	76	14	41
1981–82	40	300	214	15	28	186	86	15	46
1982–83	48	727	491	14	60	431	236	14	55
1983–84	29	420	326	7	21	305	94	7	31
1984–85	47	508	346	21	60	286	162	21	57
1985–86	44	562	390	14	48	342	172	14	50
1986–87	47	493	335	14	41	294	158	14	54
1987–88	45	649	448	14	55	393	201	14	51
1988–89	14	1,796	1,575	14	193	1,382	221	14	16
1989–90	34	1,327	990	7	65	925	337	7	36

[a] F/100 A = fawns/100 adults; B/100 D = bucks/100 does; F/100 D = fawns/100 does.
[b] Average bucks/100 does = 14.
[c] No census done; used average bucks/100 does ratio and average spring fawns/100 adults ratio.
[d] Used average spring fawn/100 adults ratio.
[e] Used total number of animals classified after the hunting season.

Number of Age Classes

Sixteen age classes were used in this model. Postseason mortality was modified to eliminate males older than age class 12 (11.5 years old). Females were present in all age classes.

Population Proportions for Sex–Age Classes

Life table data were not collected for northern range moose. We had the POP-II program compute the proportions in each age-sex class. Beginning bull/cow and calf/cow ratios were 78 and 37, respectively. We set the hypothetical annual male survival rate at 80%. We set the female survival rate at 90%.

Estimated Beginning Population

Houston (1982) believed 200 moose was a conservative estimate for the northern range. Considering the difficulty in surveying moose in forests (Houston 1982), we doubled Houston's estimate for our model.

Natural Mortality

Preseason and postseason mortality data were not available for northern range moose. We assumed no preseason mortality occurred. We used postseason mortality rates adapted from the Jackson herd moose population model in Wyoming (Roby 1990) for our model. Postseason mortality was 20% for calves, 3% for yearlings, and 2% for adults older than 2 years. Lack of overwinter mortality data and the untested status of the hunter survey data precluded our use of mortality severity indices.

Harvest

Harvest data were compiled from five Montana hunting districts (316, 317, 318, 322, and 328) bordering the northern range. The bull moose harvest was relatively stable most years ($\bar{x}$ = 20/year; Table 18). The most bulls were harvested in 1983 (27) and the fewest in 1988 (14). Cow harvests were more variable and ranged from 3 to 14 individuals ($\bar{x}$ = 8/year). Calves were harvested 9 of 15 years. Total calf harvest was low, ranging from one to four individuals per year.

Harvest Rates for Sex–Age Classes

Age class harvest data were not available for moose. Therefore, we assumed all adult age–sex classes were harvested at equal rates in the model.

Wounding Loss and Illegal Harvest

Wounding loss and illegal harvest data were unavailable for moose on the northern range. Rates used in the elk models were used in the moose model: 5% for calves, 10% for bulls and cows.

Recruitment

The Montana Department of Fish, Wildlife, and Parks collected moose hunter survey reports from 1975–76 to 1989–90. In these reports, hunters

Table 18. Total moose (*Alces alces*) harvest from Montana hunting districts (316, 317, 318, 322, and 328) associated with Yellowstone's northern range, 1975–1989 (Erickson 1980; Mack et al. 1990; T. Lemke, Montana Department of Fish, Wildlife, and Parks, Livingston, personal communication).

	Hunting district[a]																	
	316			317			318			322			328			**Total**		
Year	B	C	Ca	B	C	Ca	B	C	Ca	B	C	Ca	B	C	Ca	B	C	Ca
1975	5	3	—	5	—	—	5	1	—	8	4	—	—	—	—	23	8	—
1976	6	—	—	3	—	—	3	1	—	6	2	—	—	—	—	18	3	—
1977	3	2	—	1	—	—	7	—	—	4	3	—	—	—	—	15	5	—
1978	2	5	—	4	—	—	3	4	—	8	2	—	—	—	—	17	11	—
1979	3	3	—	5	—	—	1	4	1	7	3	—	—	—	—	18[b]	12	1
1980	3	2	—	3	—	—	7	1	—	3	1	1	—	—	—	17[c]	4	1
1981	5	1	—	5	—	—	4	2	—	9	2	—	—	—	—	23	5	—
1982	5	3	—	5	—	—	5	2	2	11	—	2	—	—	—	26	5	4
1983	5	—	—	3	—	—	6	2	1	13	1	1	—	—	—	27	3	2
1984	5	—	—	3	—	—	3	3	1	8	3	1	1	—	1	20	6	3
1985	4	1	—	4	—	—	3	1	2	9	3	—	1	—	1	21	5	3
1986	4	3	—	2	3	—	3	3	—	8	5	—	2	—	—	19	14	—
1987	3	3	—	2	2	—	3	4	1	11	3	—	—	—	—	19	12	1
1988	3	—	—	1	4	1	5	2	2	5	3	1	—	—	—	14	9	4
1989	4	3	—	3	3	1	3	4	—	10	4	—	2	—	—	23[c]	14	1

[a] B = bulls; C = cows; Ca = calves.
[b] Includes four unclassified moose, two each arbitrarily assigned to the bull and cow harvest.
[c] Includes one unclassified moose, arbitrarily included in the bull harvest.

recorded the number of bulls, cows, and calves they observed in an area. We used reports tallying the maximum number of bulls, cows, and calves observed within an area; we used observations we believed were unduplicated. Counts not specifying the sex of individuals or having unknowns were not used. The modified counts were then summed for all areas within a hunting district, and the values from the five hunting districts were summed to obtain yearly classification indices for the northern range (Table 19). The hunter classification data may underestimate production (Swenson 1982). If production estimates were low, our model probably calculated minimum population estimates.

In Montana, Schladweiler and Stevens (1973) reported 31.8% of yearling moose were pregnant compared to 86.3% for adults. In British Columbia, no yearlings were pregnant (Edwards and Ritcey 1958). Considering the lower yearling pregnancy rate, only cows 2.5 years (age class 3) or older contributed to reproduction in our model. Schladweiler and Stevens (1973) found an equal calf sex ratio in the harvest; thus, a 50:50 reproductive sex ratio was used in the model.

Table 19. Maximum number of unduplicated moose (*Alces alces*) sightings obtained from Montana moose hunter survey reports (Montana hunting districts 316, 317, 318, 322, and 328), 1975–1989 (Erickson 1978, 1979, 1980, 1981; Swenson 1982, 1984a, 1984b, 1985; Swenson and Foss 1986; T. Lemke, Montana Department of Fish, Wildlife, and Parks, Livingston, personal communication).

	Number				Bulls/100	Calves/100
Year	Bulls	Cows	Calves	*N*	cows	cows
1975–76	38	49	18	105	78	37
1976–77	26	41	15	82	63	37
1977–78	23	40	9	72	58	23
1978–79	31	39	16	86	79	41
1979–80	39	73	21	133	53	29
1980–81	34	63	14	111	54	22
1981–82	19	17	7	43	112	41
1982–83	38	61	11	110	62	18
1983–84	40	45	9	94	89	20
1984–85	45	83	18	146	54	22
1985–86	27	56	18	101	48	32
1986–87[a]	2	9	2	13	22	22
1987–88[a]	7	10	3	20	70	30
1988–89[a]	15	32	12	59	47	38
1989–90	67	80	20	167	84	25

[a] From 1986–87 to 1988–89, hunter survey results were unavailable, and moose horseback survey results from the U.S. Forest Service were used (Alt and Foss 1987).

Results

Elk Option 1

We performed several test runs of the model to create a final model predicting conditions similar to those observed in the field. The bull/cow and calf/cow ratios were used as guides for obtaining a final model. After several runs, we modified the reproductive output to obtain nearly exact simulated and observed calf/cow ratios (Fig. 1). The simulated bull/cow ratios were reasonable until 1983 (Fig. 2). After 1982–83, bulls must have had higher overwinter mortality than during previous years. To lower the simulated bull/cow ratios, we applied winter mortality severity index values to a series of years (1983–87). Although the final simulated values do not exactly equal the observed bull/cow ratios (Fig. 3), they approximate the observed trend. The final population estimates reasonably follow the observed trends (Fig. 4).

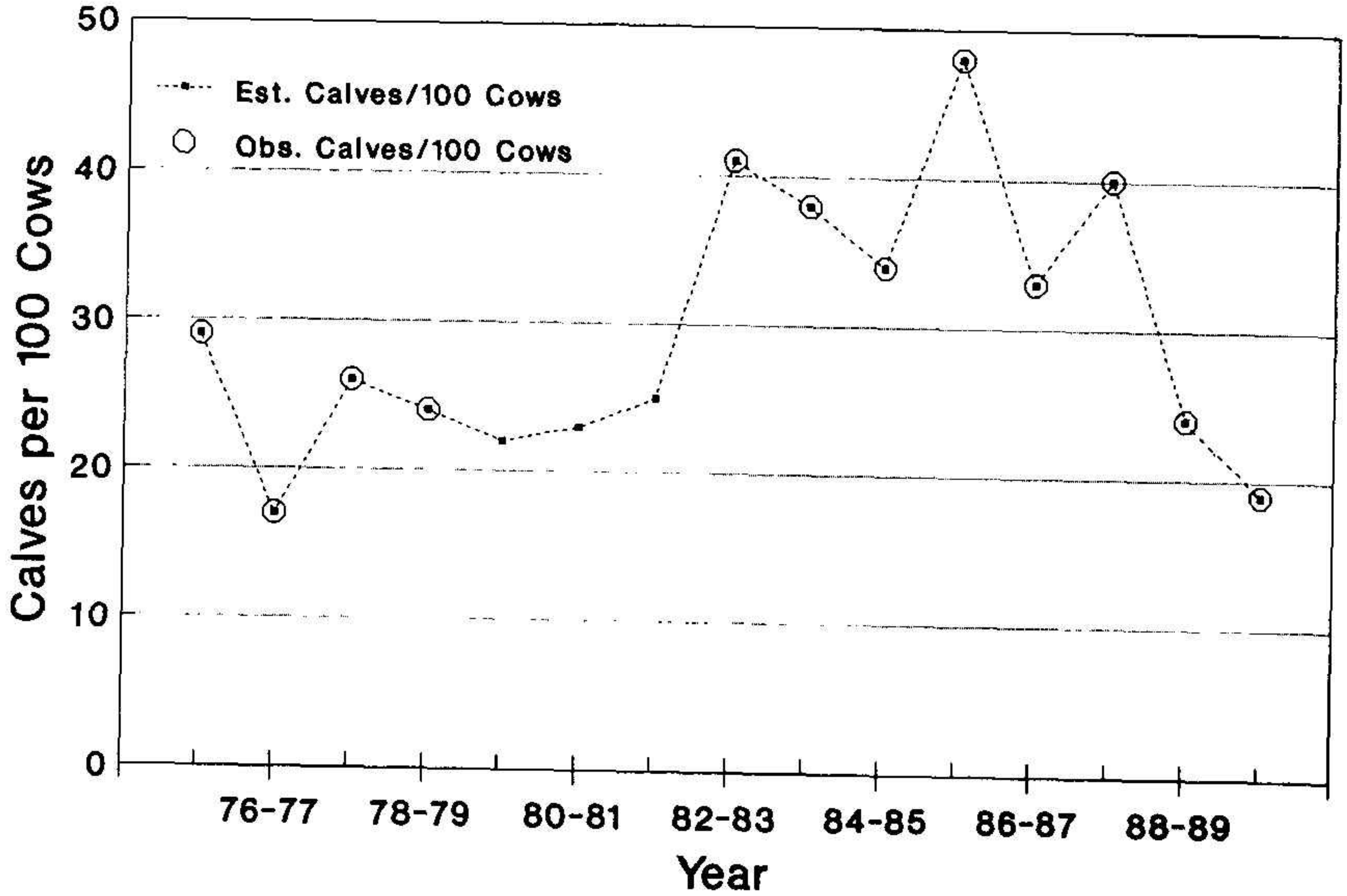

Fig. 1. Observed (*Obs.*) and the POP-II estimated (*Est.*) calf/cow ratios for the Elk Option 1 model.

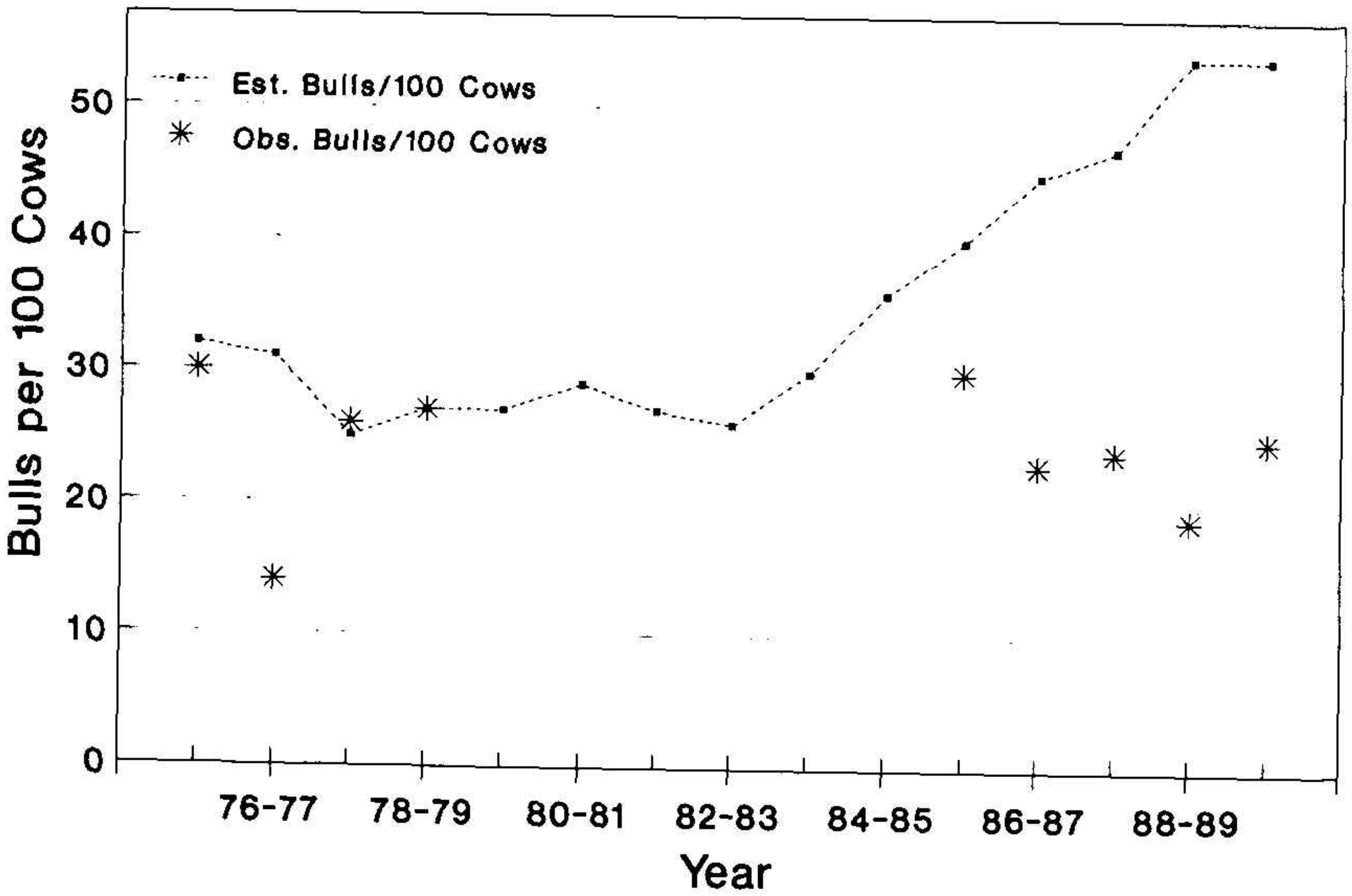

Fig. 2. Observed (*Obs.*) and the POP-II estimated (*Est.*) bull/cow ratios for the Elk Option 1 model before applying increased bull mortality rates.

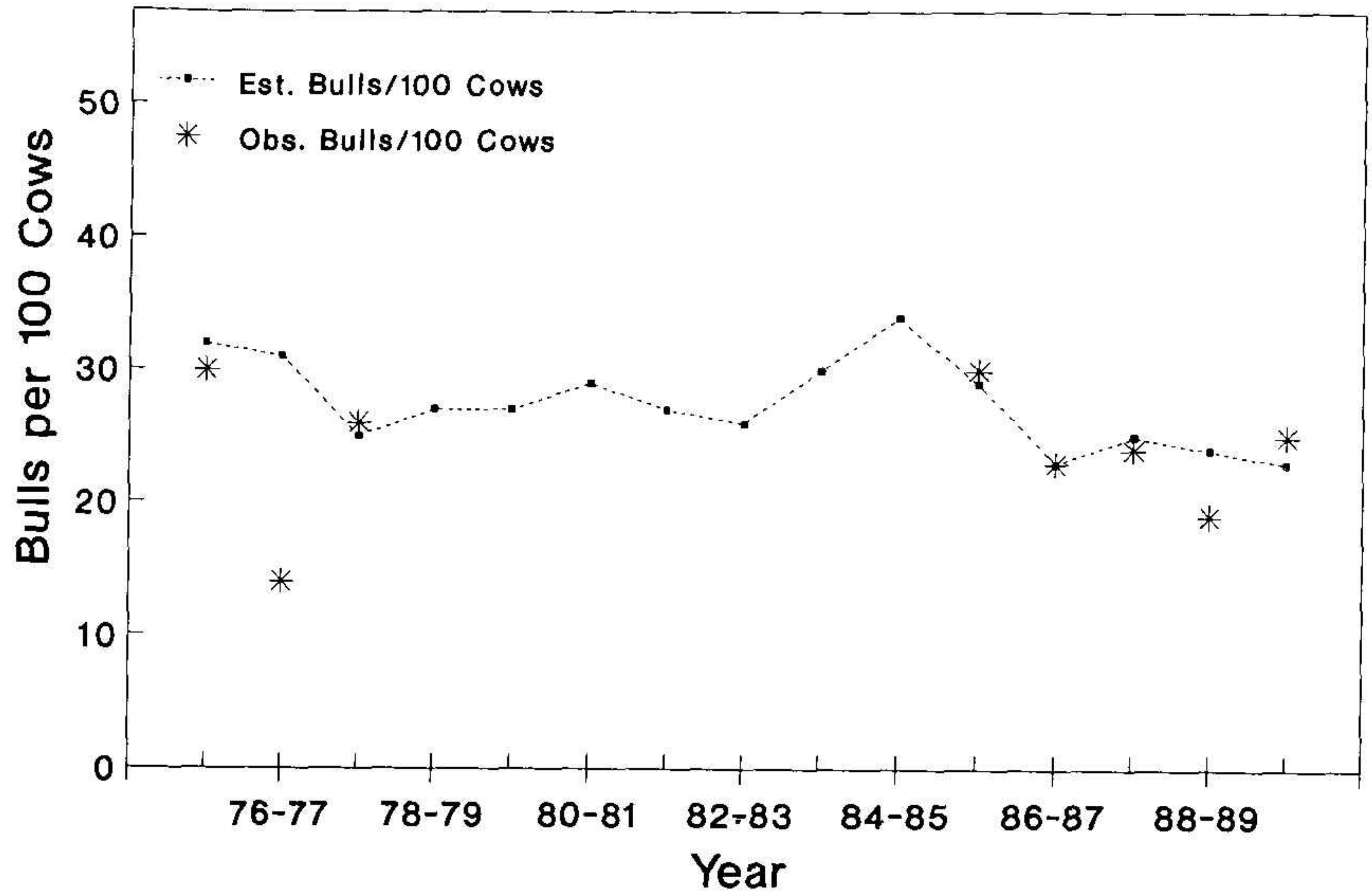

Fig. 3. Observed (*Obs.*) and the POP-II estimated (*Est.*) bull/cow ratios for the Elk Option 1 model after higher winter mortality rates were applied.

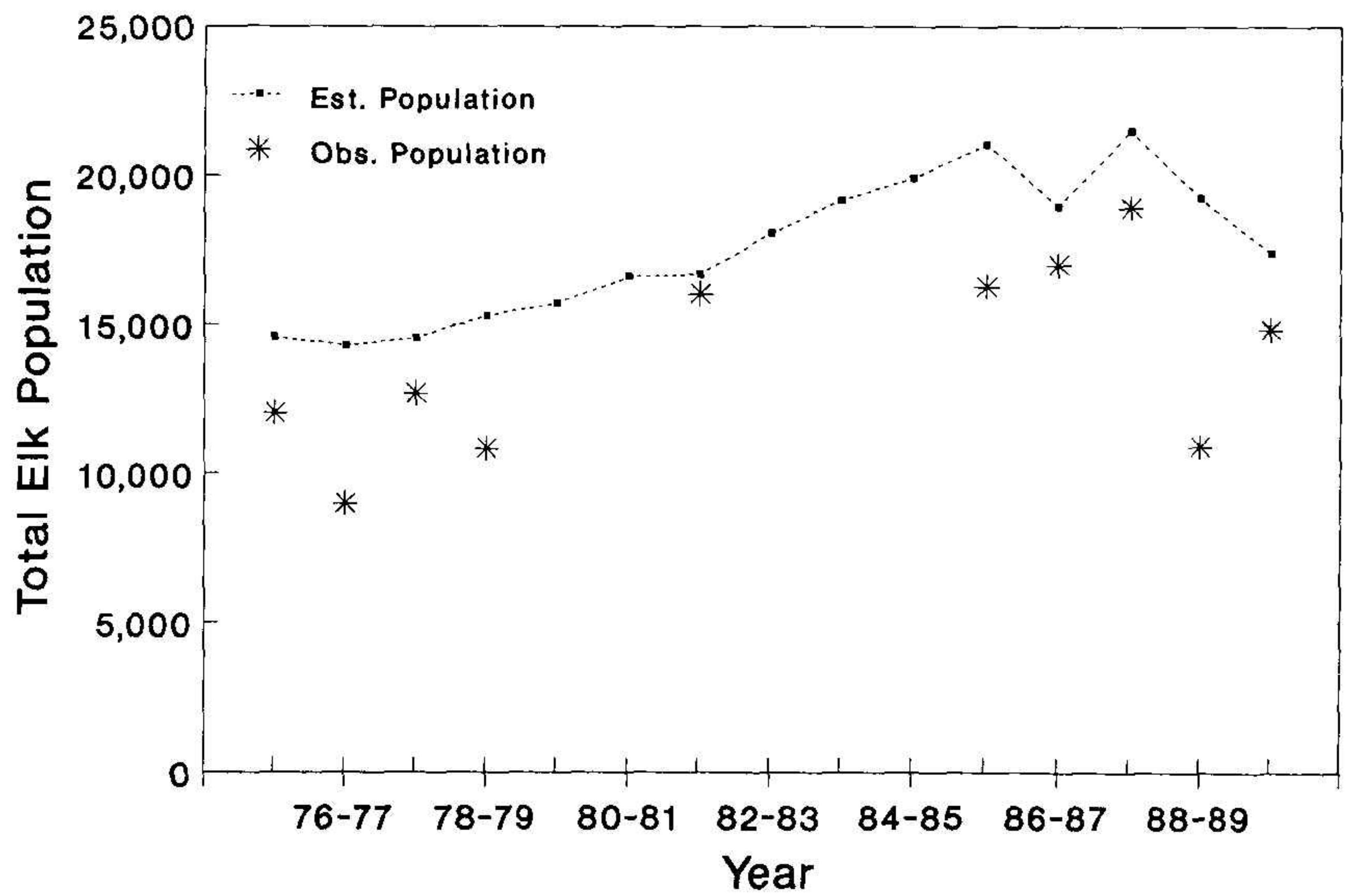

Fig. 4. Observed (*Obs.*) elk counts and the POP-II estimated (*Est.*) elk population for the Elk Option 1 model.

Elk Option 2

Calf ratios were aligned as stated previously (Fig. 5). The bull/cow ratios followed observed trends until 1984 when mortality severity indices were again used to closely align the observed and simulated values (Fig. 6). The population estimates produced values slightly higher than observed total elk counts (Fig. 7).

Before 1984, the Elk Option 1 model averaged 1,187 more elk than Elk Option 2 (Table 2). After 1984, both options produced similar results (Elk Option 1 averaged 213 more elk than Elk Option 2).

Mule Deer

We considered the final model complete when the simulated fawn/doe and buck/doe ratios were similar to observed values and trends. We modified the reproductive output and obtained similar observed and simulated values (Fig. 8).

The initial death rates used in the model produced reasonable buck/doe ratios until 1985. After this date, modeled buck ratios were higher than observed ratios, and the modeled ratios did not follow observed trends (Fig. 9). We used mortality severity indices during specific years (1984–87) to create more reasonable buck/doe ratios. These indices brought the

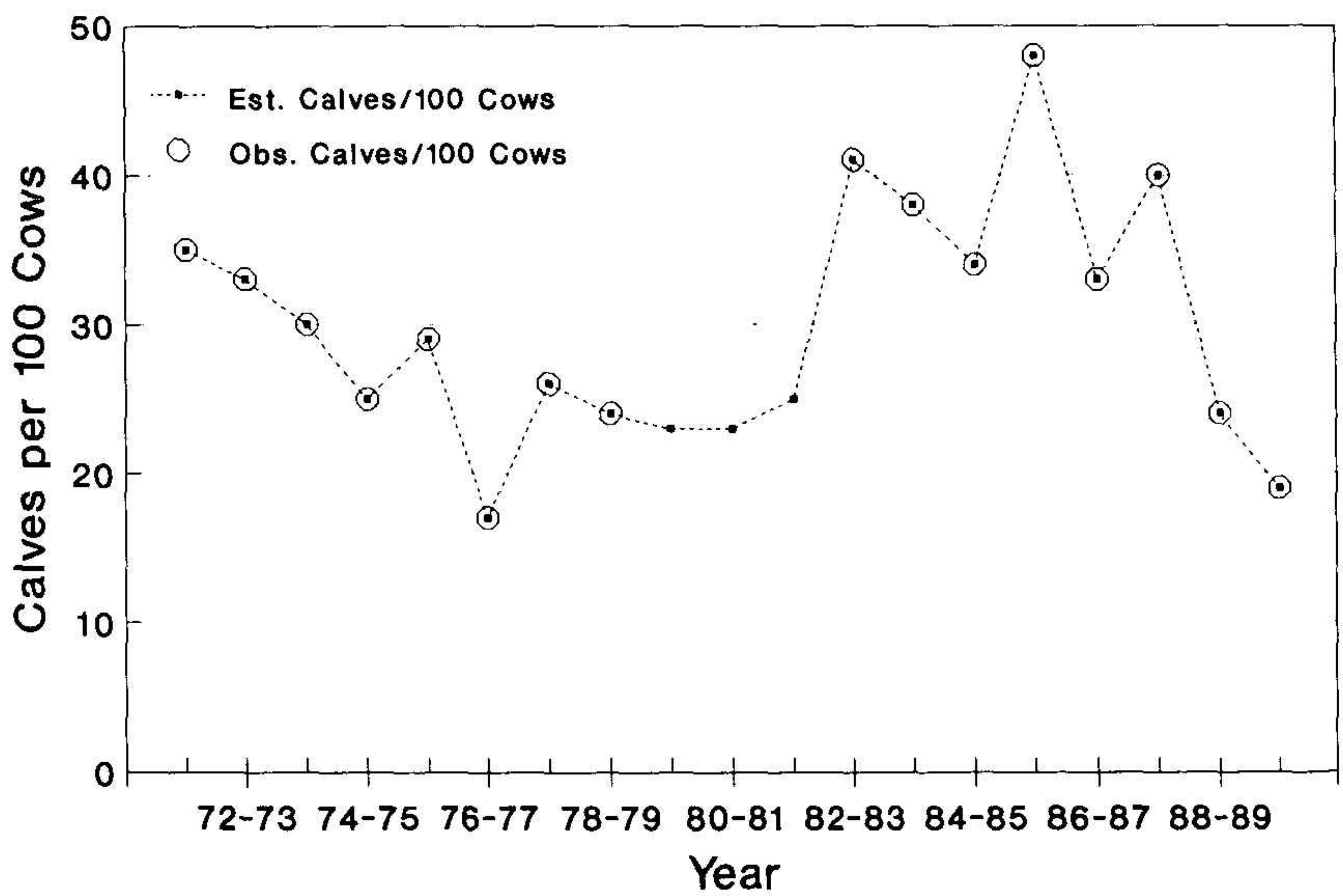

Fig. 5. Observed (*Obs.*) and the POP-II estimated (*Est.*) calf/cow ratios for the Elk Option 2 model.

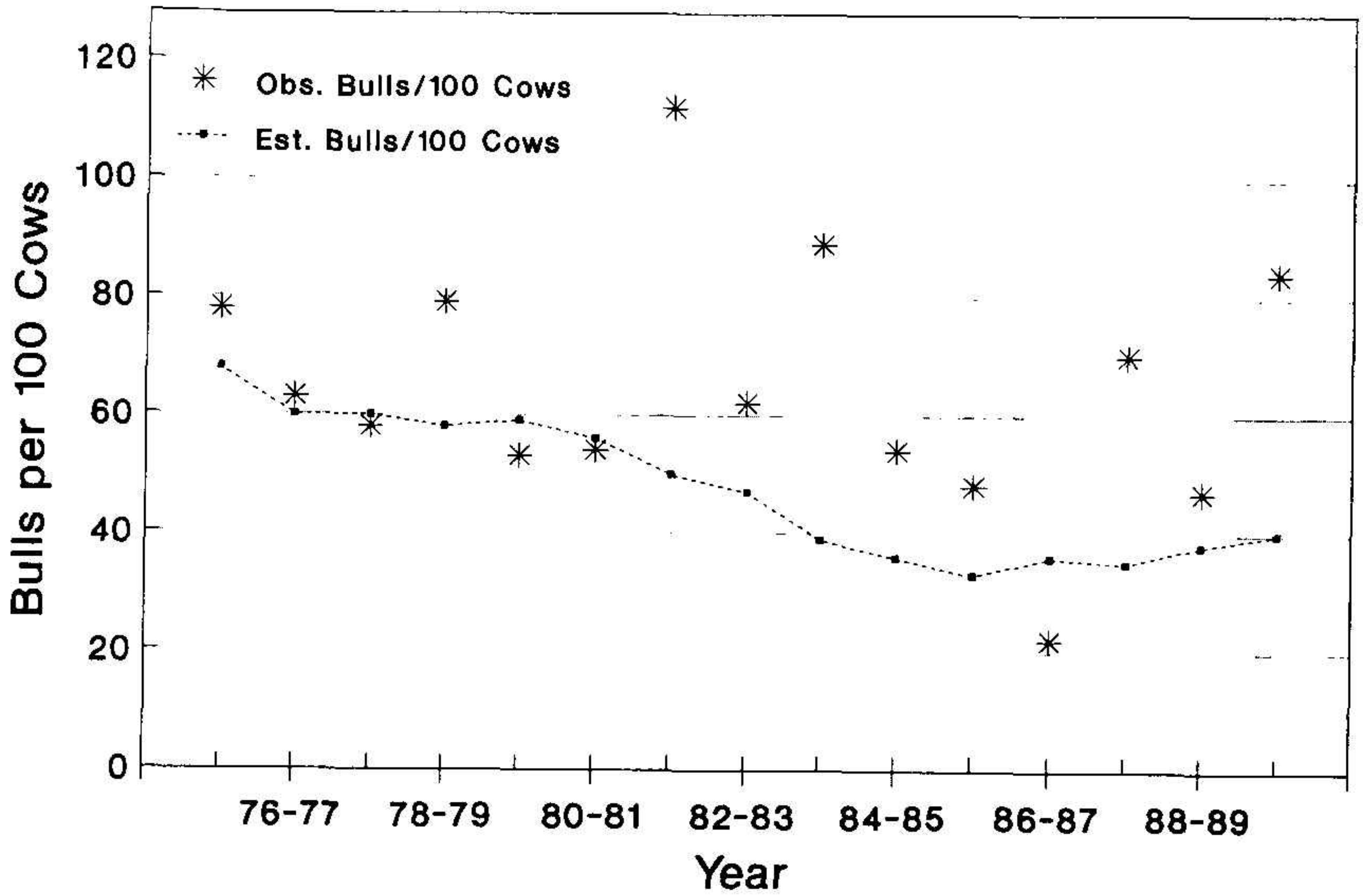

Fig. 6. Observed (*Obs.*) and the POP-II estimated (*Est.*) bull/cow ratios for the Elk Option 2 model.

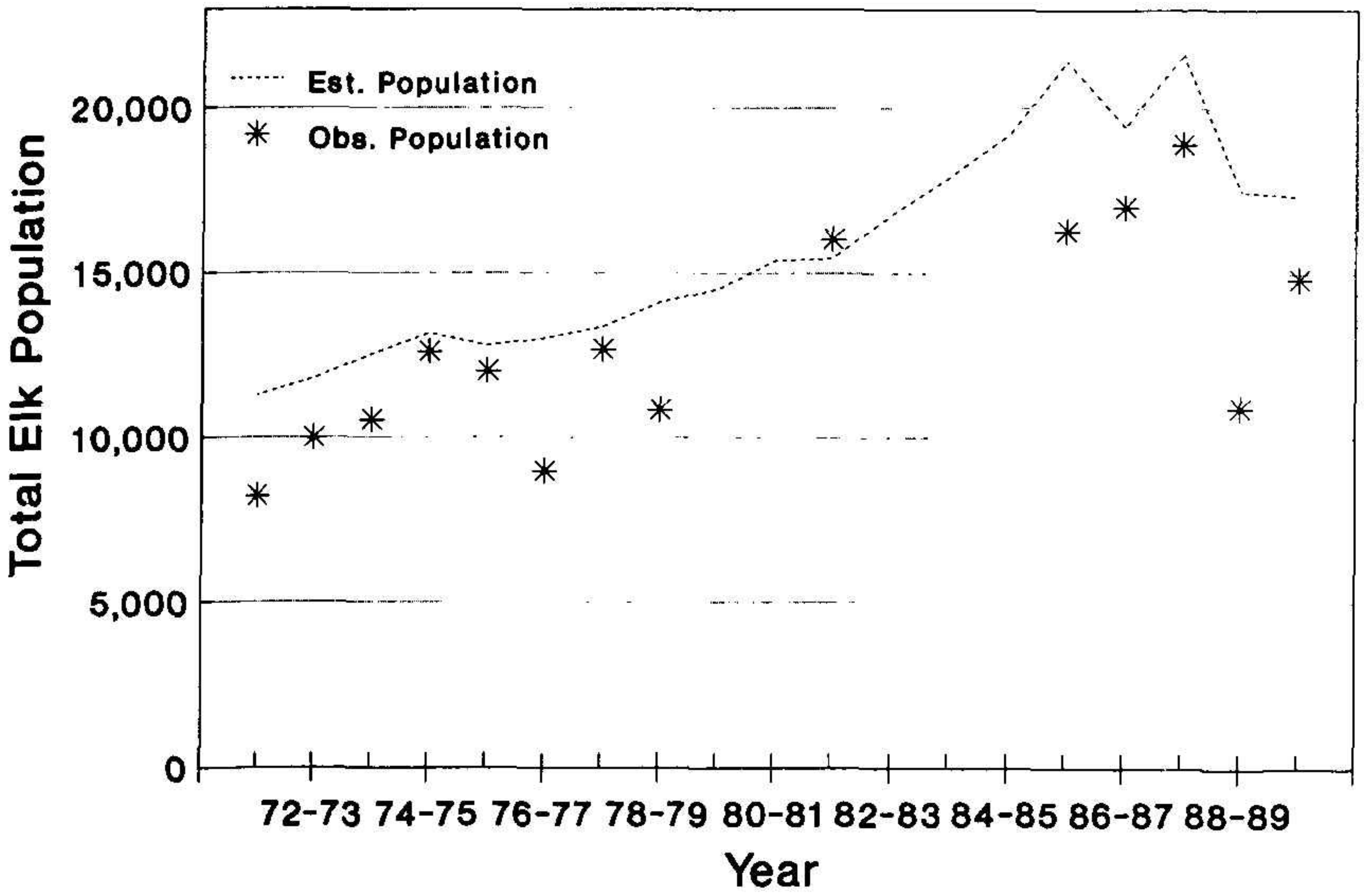

Fig. 7. Observed (*Obs.*) elk counts and the POP-II estimated (*Est.*) elk population for the Elk Option 2 model.

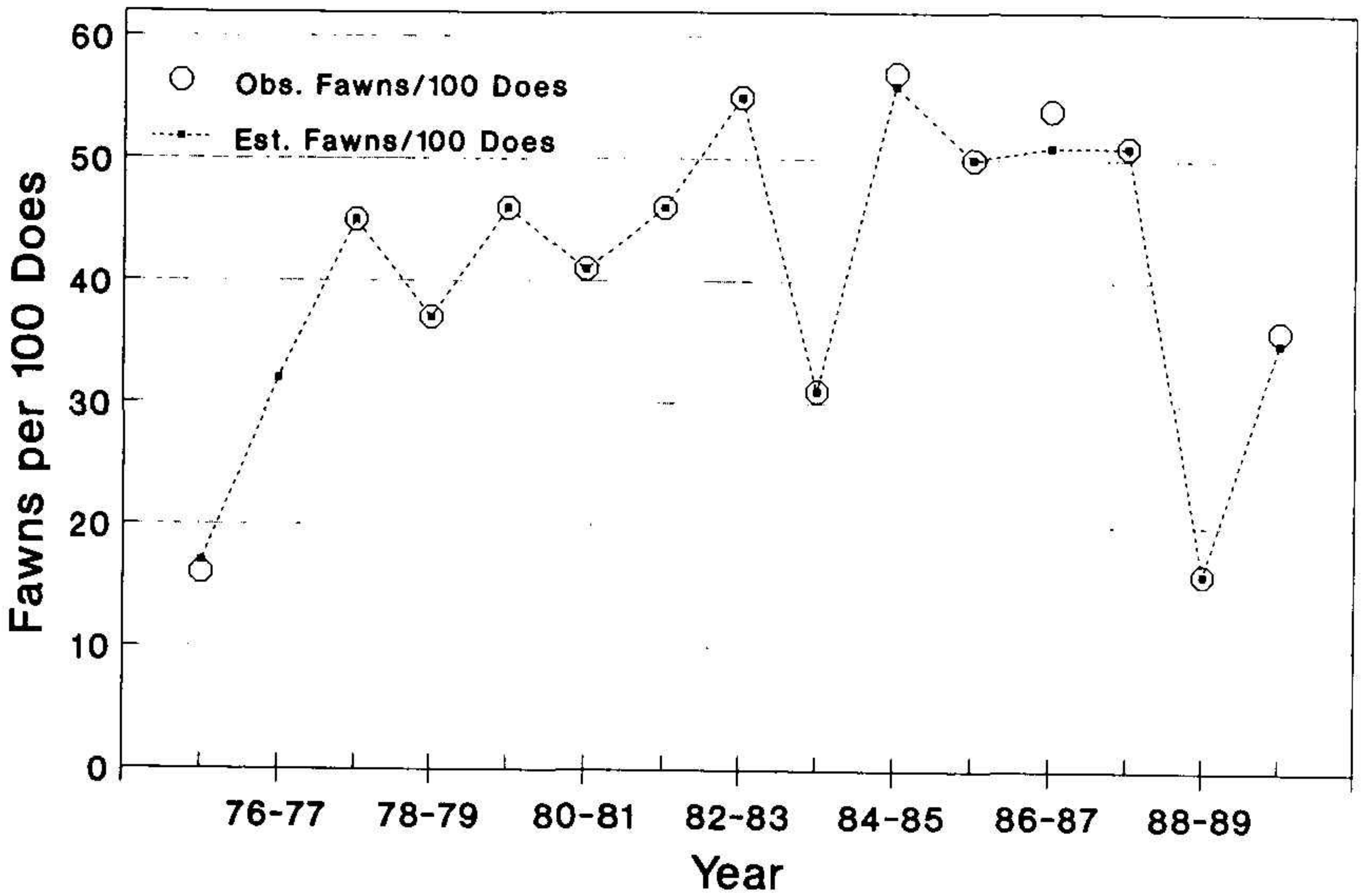

Fig. 8. Observed (*Obs.*) and estimated (*Est.*) fawn/doe ratios for the POP-II mule deer model.

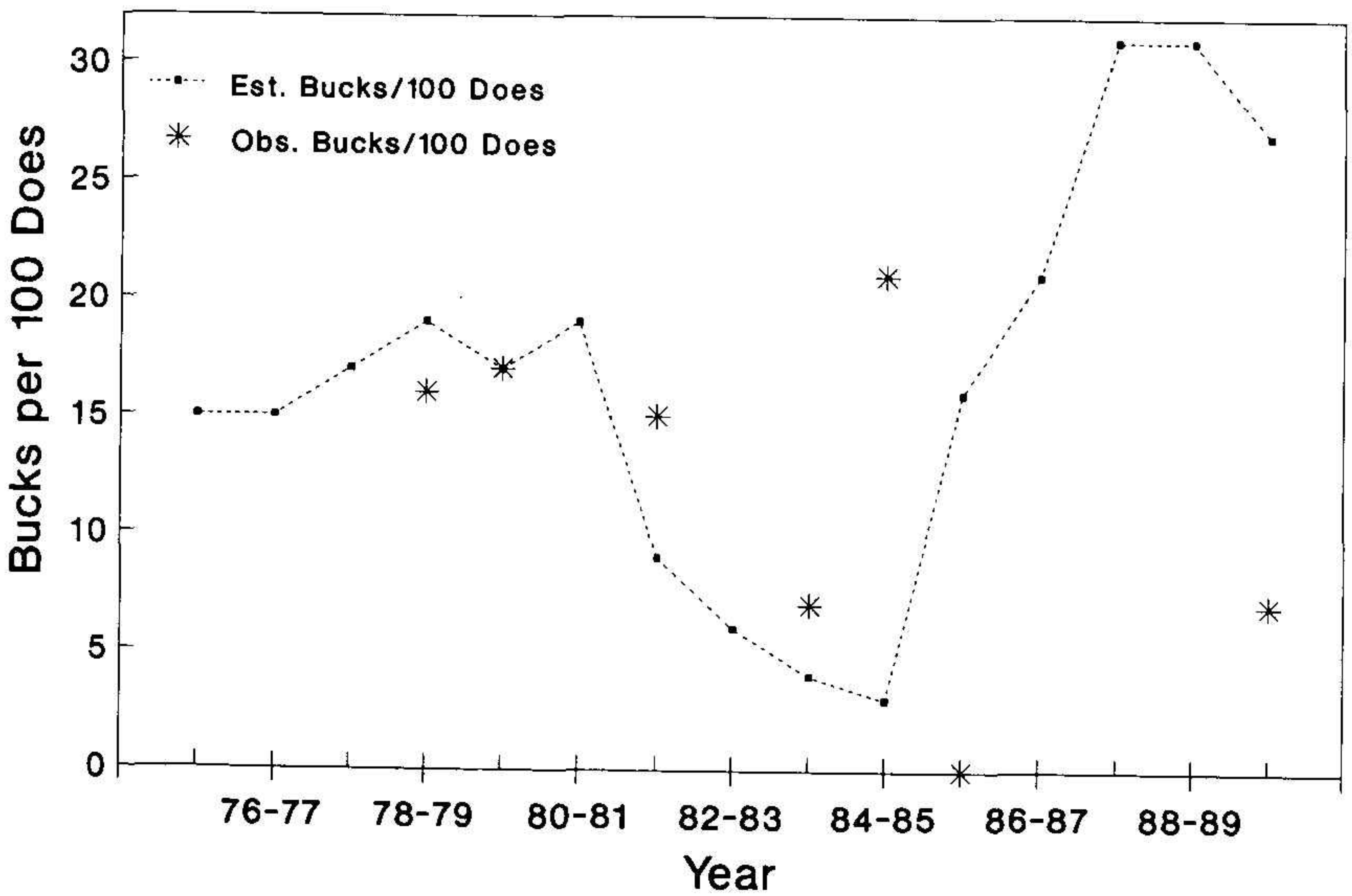

Fig. 9. Observed (*Obs.*) and the POP-II estimated (*Est.*) buck/doe ratios before applying increased buck mortality rates to the mule deer model.

buck/doe ratio trend under control but a low harvest during 1987–88 increased the buck/doe ratios. We therefore artificially increased the 1987–88 buck harvest by 100 and produced more reasonable estimated buck/doe ratios (Fig. 10). The final population estimates are higher than the observed trend counts (Fig. 11).

Moose

We aligned the observed and simulated reproductive rates to obtain identical values (Fig. 12). No effort was made to alter the simulated bull ratios. The simulated values agree with the lower limits of the hunter observed trends (Fig. 13). This disparity suggests hunters see a larger number of bulls than cows. The resulting population estimates show a stable to slightly increasing moose population (Fig. 14).

Discussion

Elk Populations

Each elk population model option (Elk Option 1 and Elk Option 2) has advantages over the other in estimating northern range elk populations. The advantage of Elk Option 1 is it begins 1 year before elk resumed extensive migrations outside Yellowstone National Park (1975–76). Before 1984, the higher population estimates of Elk Option 1 probably more

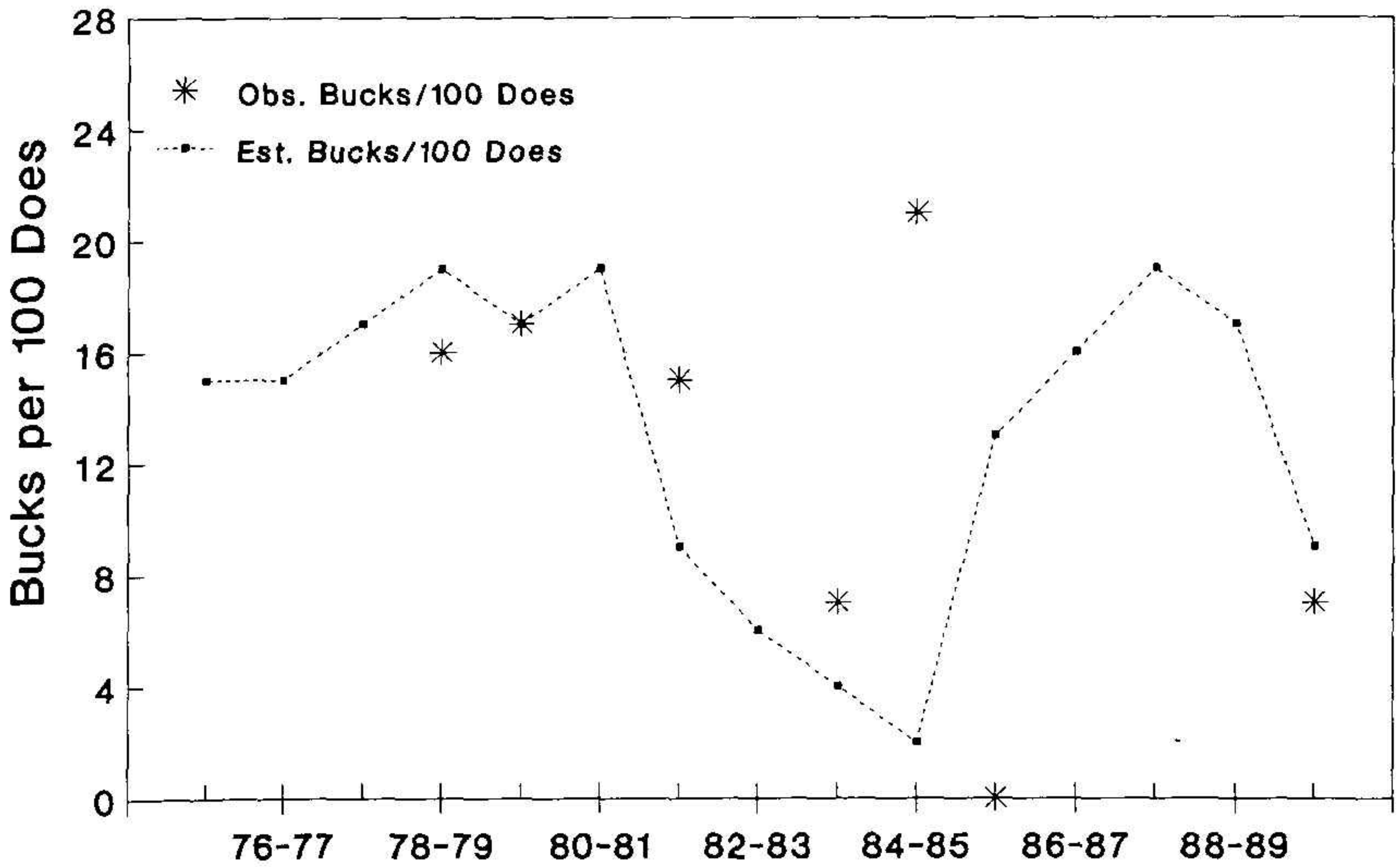

Fig. 10. Observed (*Obs.*) and POP-II estimated (*Est.*) buck/doe ratios after applying increased buck mortality rates to the mule deer model.

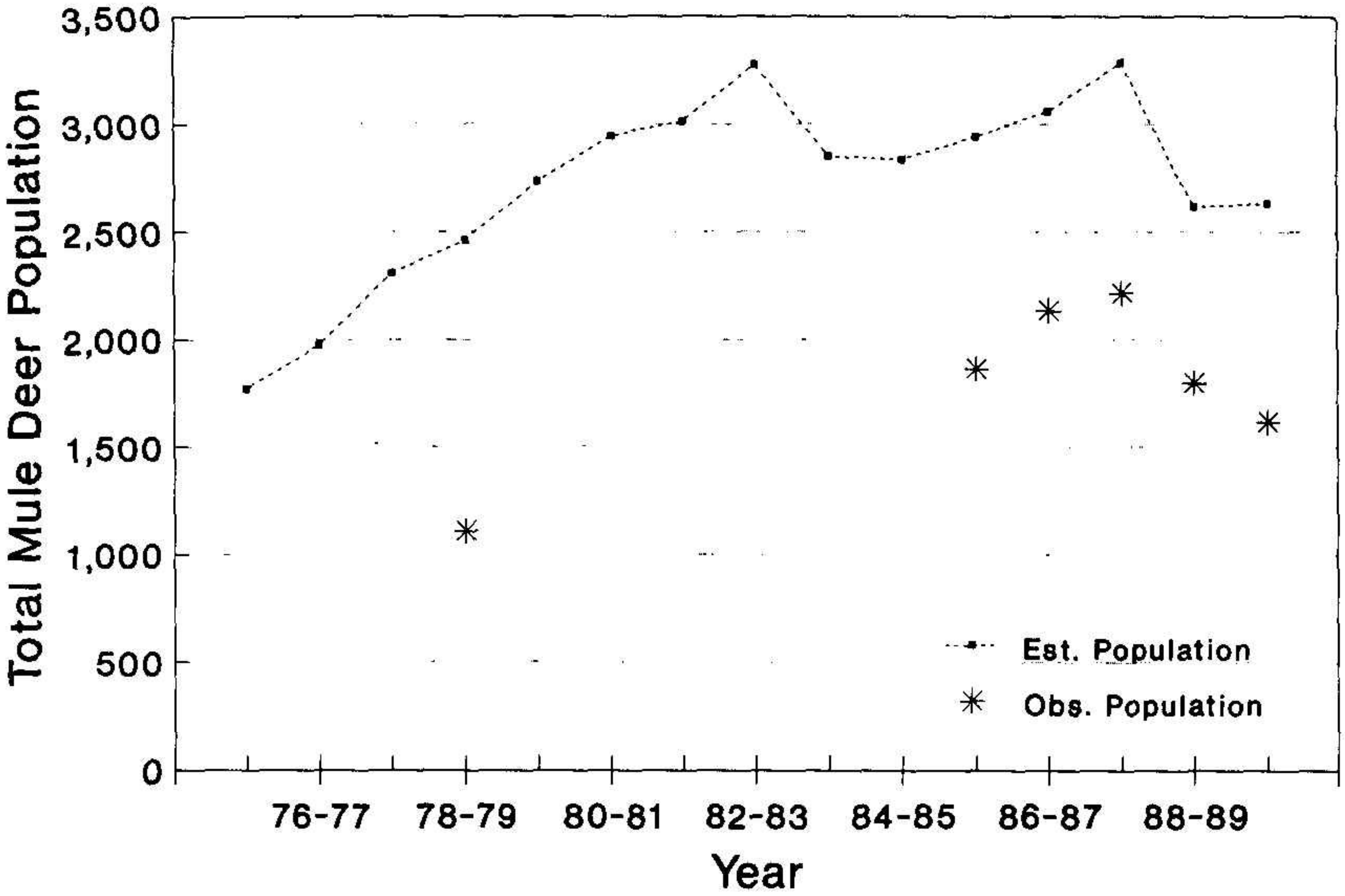

Fig. 11. Observed (*Obs.*) mule deer counts and the POP-II estimated (*Est.*) mule deer population.

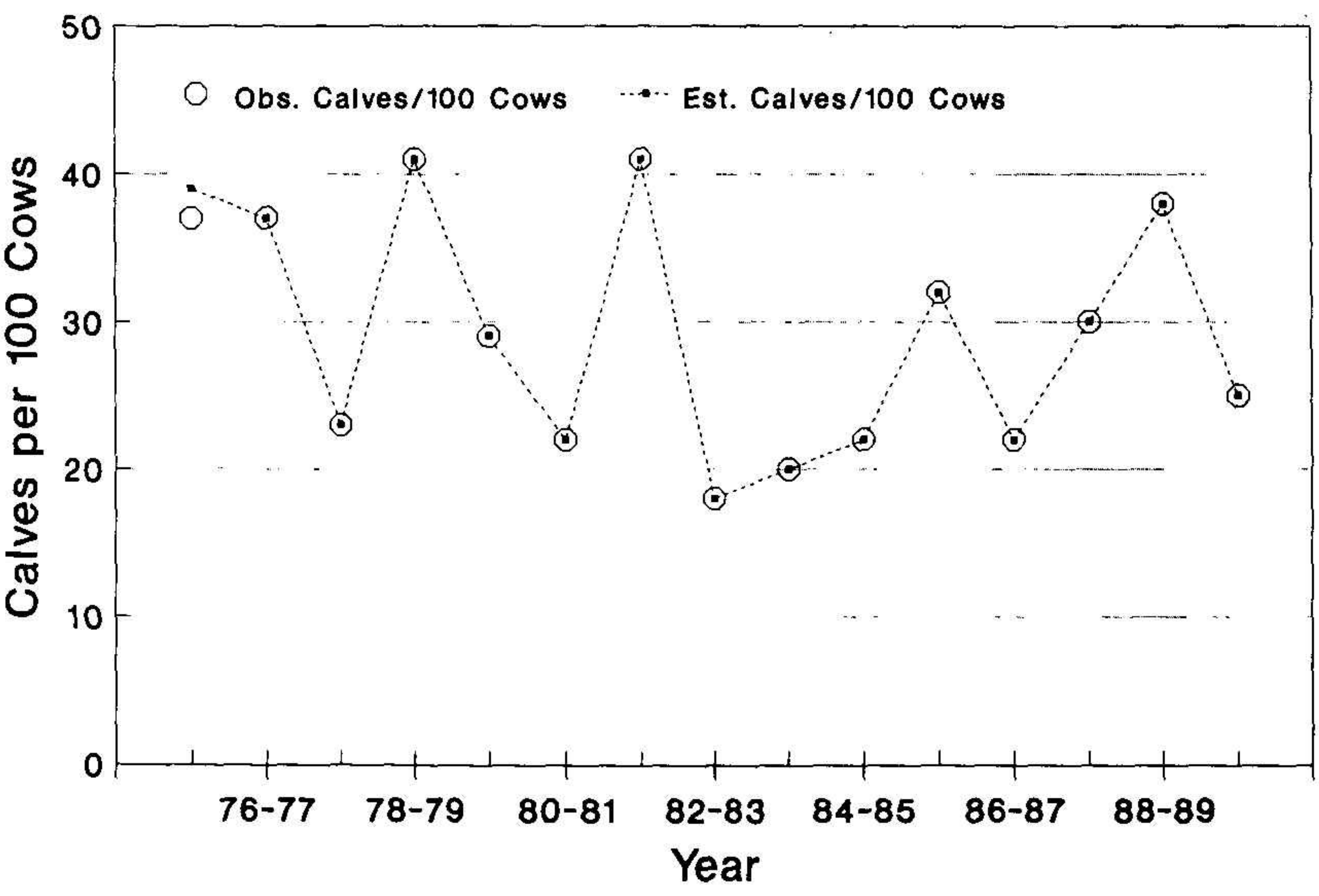

Fig. 12. Observed (*Obs.*) and estimated (*Est.*) calf/cow ratios for the POP-II moose model.

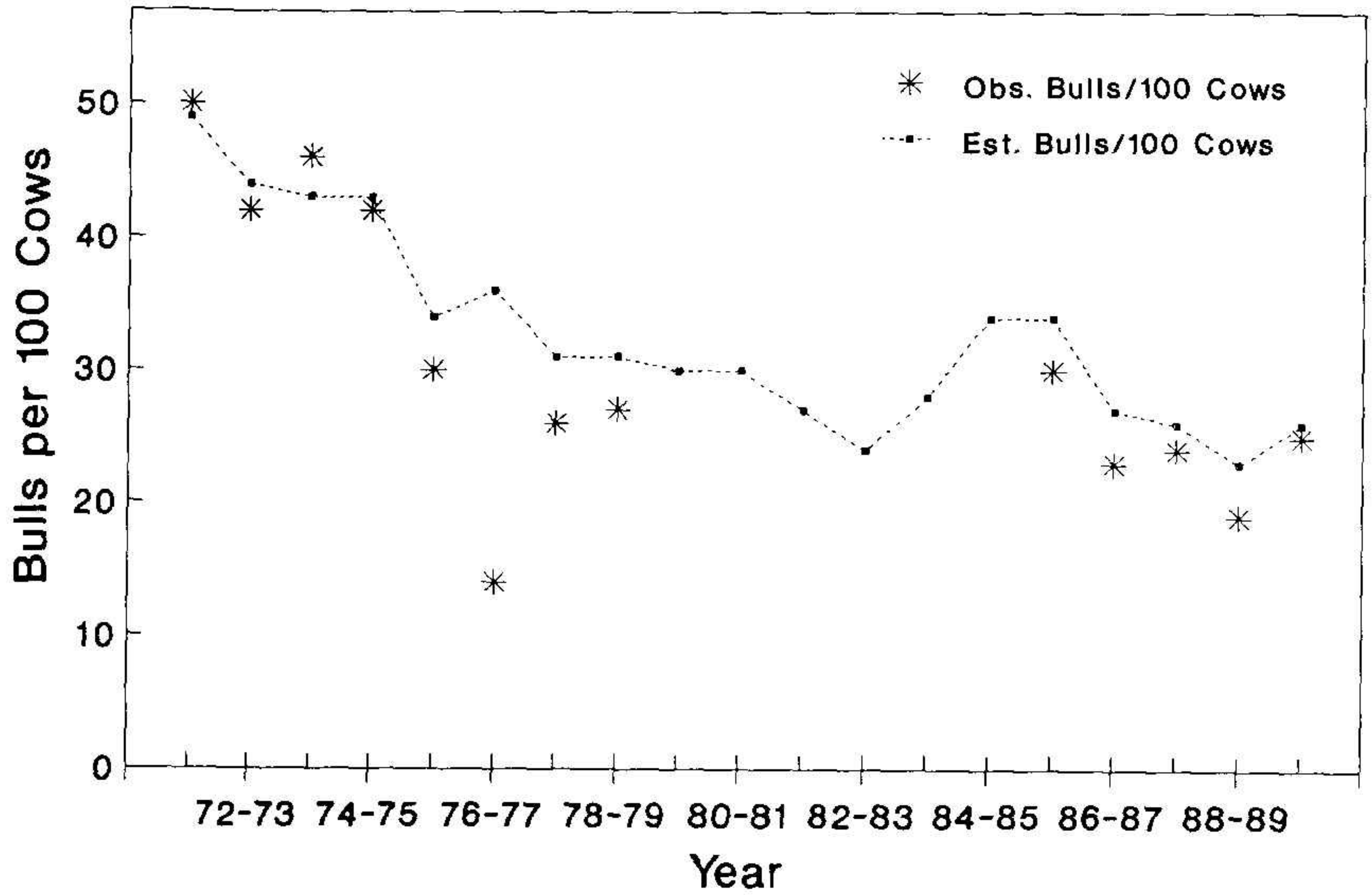

Fig. 13. Observed (*Obs.*) and estimated (*Est.*) bull/cow ratios for the POP-II moose model.

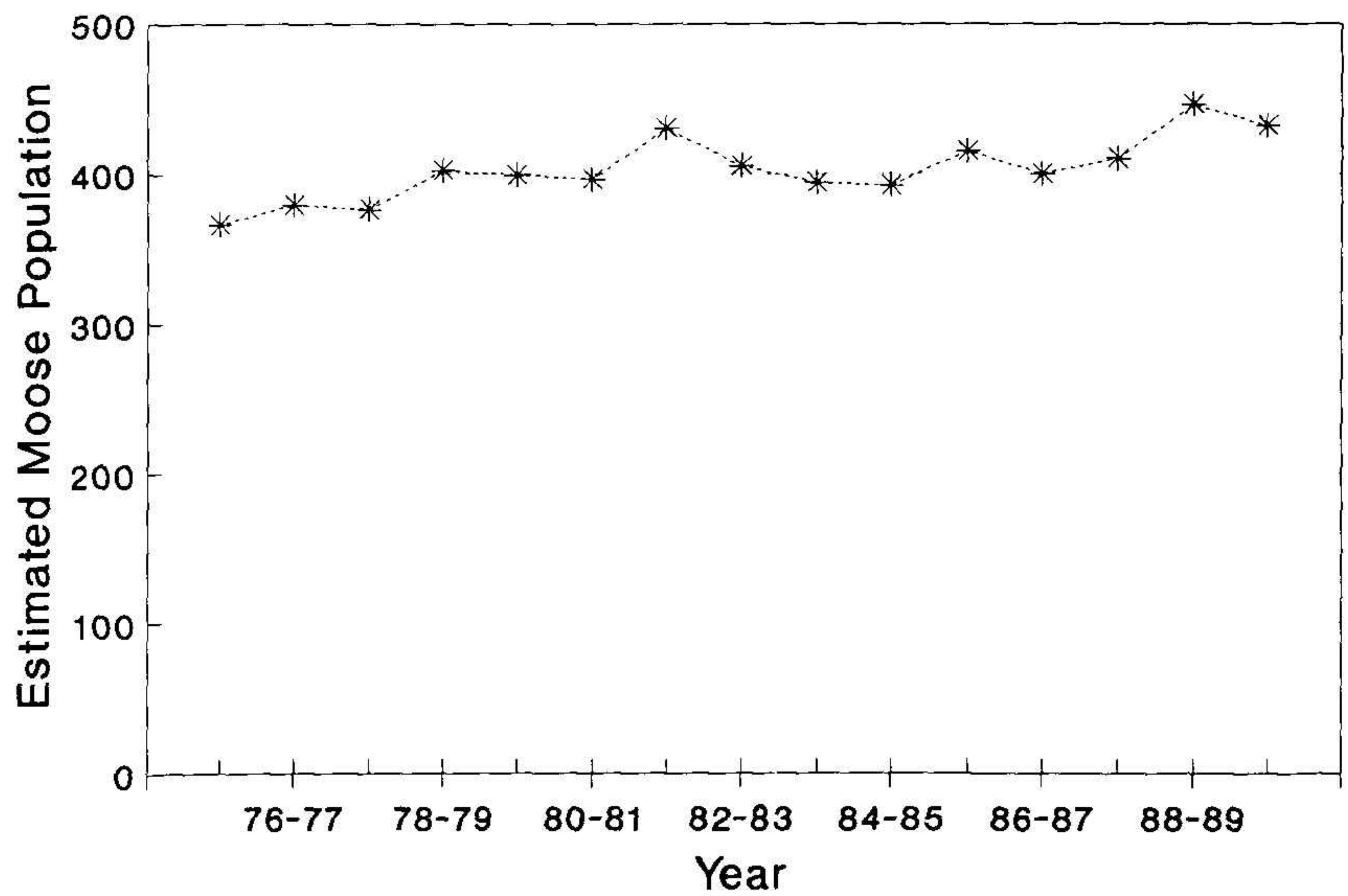

Fig. 14. Estimated moose numbers in Yellowstone's northern range using the POP-II moose model.

closely reflect the increased carrying capacity resulting from migrations into previously unused northern winter range habitat. The Elk Option 2 model has two main advantages. First, a longer period of population and harvest data were included in the model. Second, this model required fewer overwinter mortality adjustments than Option 1 and produced lower bull/cow ratios (implying higher bull mortality) that more closely followed observed trends.

Before 1984, we prefer the population estimates produced from Elk Option 1. After 1984, negligible differences in population estimates exist between the two models, and we have no preference for either.

Using the Elk Option 1 population estimates, an average of 4,115 more elk (range 1,680–9,711) were in the population than were actually tallied. These differences suggest elk count sightability averaged 0.77 (Table 19).

We compared our elk population estimates with provisional elk sightability population estimates (Samuel et al. 1987; Singer et al. 1988). Both estimates use independent data sources, thus the presumed accuracy of each can be cross-checked. Elk Option 1 population estimates averaged 2% higher than sightability model estimates. The largest difference between the two estimates occurred during the 1988–89 winter when the POP-II estimate was 2,486 elk higher than the sightability model estimate. During the winter of 1988–89, elk were dispersed into conifer forests due to deep snows. The poor estimated sightability conditions (0.60; Singer 1990:2–24) and the associated sightability model likely provided an inaccurately low elk population estimate (E. O. Garton, University of Idaho, Moscow, personal communication).

Both our elk models suggest that substantially higher adult bull mortality occurred during the winters of 1986–89. High bull mortality occurred during the severe 1988–89 winter (Singer et al. 1989). Apparently, the elk population approached carrying capacity during the late 1980's (Merrill and Boyce 1991) and higher bull mortality might be expected (Anderson 1958; Clutton-Brock et al. 1982).

Mule Deer

Our estimates suggest the mule deer population increased from about 1,750 in 1975 to about 3,300 in early spring 1988. We estimate the population then declined to about 2,600 deer in early spring 1990. Comparing our population estimates with aerial counts suggests mule deer sightability averaged 0.63 (range 0.45–0.69). Ackerman (1988) found average sightability of radio-collared mule deer in southeastern Idaho was 0.54. Mule deer sightability in the Bridger Mountains, Montana, was approximately 0.66 (Mackie et al. 1980).

The initial mule deer model predicted too few males were in the population to support observed harvests, particularly during the early 1980's. To compensate for the apparent lack of bucks, we modified the reproductive sex ratio of subadults to favor males even though no evidence exists suggesting the fawn male/female ratio deviates from 50:50. This model adjustment compensated for the high buck harvests in the early 1980's, but after 1986 the model predicted more bucks were in the population than what were observed. Several factors may have contributed to these unusual predictions. The possibility exists that during the mid-1970's, when the mule deer population was expanding, more male fawns survived. As the population increased, male fawn survival may have declined, thus fewer adult bucks would be recruited into the population in later years. The POP-II program does not allow changes in age class mortality between years. The estimated male mortality rates may have been too low during the late 1980's. Another possibility is that bucks from other adjacent populations may migrate into the northern range area where they are then harvested. A third possibility is that our population estimates for the northern range mule deer herd are too low or that the observed buck/doe ratios are underestimated. Compared to female deer, buck mule deer prefer higher elevations and ridgetops (Miller 1970; Robinette et al. 1977; Geist 1981). If this buck preference occurs on the northern winter range, the helicopter classifications may miss some bucks occupying higher-elevation forested slopes and mountain tops.

Moose

The moose population model is primarily based on untested hunter harvest survey information. This provisional model suggested moose on the northern range slowly increased from a postharvest estimate of 366 moose in 1975 to about 432 moose in 1989. With this model, we are able to present some preliminary conclusions. First, the northern range moose population likely exceeds the best aerial counts 5-fold (highest aerial count, 80 animals). Second, our model suggests the moose population had to be double Houston's (1982) estimate of 200 moose to support the actual harvests.

Recommendations

POP-II ungulate population models provide a potentially valuable tool for wildlife managers of the Yellowstone area. The elk population model can be enhanced by incorporating more accurate estimates of overwinter mortality on sex and age groups into the model. We recommend early winter helicopter classifications and late winter elk counts be added to the current program of early winter counts and late winter classifications. We also recommend accurate aging (cementum annuli) of hunter-harvested elk.

The mule deer population model lacked complete census information covering the entire northern winter range. The model consistently estimated fewer bucks than were observed, suggesting that the total population size is much larger than predicted in the model; bucks are underestimated in surveys; or bucks from adjacent areas immigrate to the northern range area. More information is needed on the distributions, seasonal movements, and immigration and emigration for the northern Yellowstone mule deer herd. Age-class mortality and overwinter mortality (particularly between age-sex classes) data are also needed for this herd.

We consider our POP-II moose model a provisional population model for the northern range moose herd. More information and better understanding is needed on all aspects of moose population biology on the northern range. Before more modeling can be done, more information must be gathered on sex and age ratios, accurate ages of harvested animals, age class mortality, and moose population size. The validity of the hunter survey data needs to be tested, particularly if the survey data underestimates calf ratios.

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Effects of Restoring Wolves on Yellowstone Area Big Game and Grizzly Bears: Opinions of Scientists

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Abstract. Fifteen North American wolf (*Canis* spp.) and wolf–prey researchers noted for their expertise concerning interrelations among wolves, grizzly bears (*Ursus arctos*), and prey species were selected by their peers for participation in a modified Delphi study. Opinions were obtained regarding potential effects of wolf reintroduction in Yellowstone National Park on (1) their likely prey in the park, (2) the recovery of Yellowstone area grizzly bears, and (3) big game hunting by humans in areas surrounding the park. The study, conducted during fall 1989, called for questions to be answered by a panel of experts, followed by a collation of responses by project coordinators. Panelists completed two questionnaires asking both general and specific questions about the issues. Following each

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successive contact, opinions were compiled and new or more probing questions were asked. The following are the major findings: (1) the core wolf population would be centered in Yellowstone National Park, but because wolves do not recognize political boundaries, the park might not sustain recovery levels; (2) a wolf population of about 12 packs that spend most of their time in the park seems realistic after the population has stabilized (within 20 years of reintroduction); (3) extinction of any prey species in the Yellowstone area is thought to be extremely unlikely; (4) there will be relatively minor changes in prey species' behavior and distribution if wolves are reintroduced in the park; (5) elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) will be the primary prey for wolves—elk throughout the year, mule deer in summer; (6) wolves and grizzly bears can coexist, but panelists had differing opinions about the specific effects of wolf reintroduction on grizzly bears; (7) reduced hunting effort by humans in areas surrounding the park should be effected only when necessary and only in conjunction with wolf control measures and other prey management strategies; and (8) research is needed to better understand the interrelations among wolves, grizzly bears, and prey species in the park and surrounding areas and the added effect of big game hunting by humans in the surrounding areas.

The Endangered Species Act of 1973 directs the U.S. Fish and Wildlife Service, as well as all other federal land and resource management agencies, to protect and restore species listed by the Fish and Wildlife Service as endangered or threatened. The gray wolf (*Canis lupus*) is listed as endangered in most of the contiguous 48 states and is listed as threatened in Minnesota. Much discussion has been generated concerning the potential for reintroducing gray wolves in Yellowstone National Park. To explore such an action, a Northern Rocky Mountain Wolf Recovery Plan was approved in 1987 (U.S. Fish and Wildlife Service 1987). The plan offers a framework for recovery action and proposes reintroduction of wolves to several northern Rocky Mountain recovery areas, including Yellowstone National Park. That proposal, however, raised numerous questions and concerns about the potential effects of wolf restoration.

We addressed two primary questions: How may a reintroduced population of wolves affect the prey base in Yellowstone National Park and the big game hunting by humans in areas surrounding the park? and Would a reintroduced population of wolves harm or benefit grizzly bears (*Ursus arctos*) in the vicinity of the park?

The U.S. Fish and Wildlife Service and the National Park Service selected several approaches to assess the potential effects of reintroducing wolves to the Greater Yellowstone area (Yellowstone National Park et al. 1990). One approach was to seek and synthesize the opinions and best judgments of experts who have thought scientifically and intuitively about the interactions among wolves, grizzly bears, and prey species (Koth et al. 1990).

We examined the opinions and best judgments of 15 North American gray wolf and wolf–prey scientists and researchers known for their studies of the interrelations among wolves, grizzly bears, and prey species. Topics explored include the potential effects of a reintroduced population of wolves on (1) their potential prey in Yellowstone National Park, (2) the recovery of Yellowstone area grizzly bears, and (3) big game hunting by humans in areas surrounding the park.

Methodology

The Delphi Process

Several techniques have been developed to collect and analyze the conventional wisdom maintained by experts in a discipline while limiting some of the negative effects of group dynamics. We used the Delphi technique in our study. We modified the Delphi process to first identify individuals who are most knowledgeable about the interactions between wolves, grizzly bears, and prey species and were subsequently able to make predictions about the future of wolves in Yellowstone National Park based on the collective opinions of the participants.

The Delphi technique is appropriate where individual judgments must be tapped and then pooled—especially when characteristics of the task include uncertainty, inadequate data, incomplete theory, a high order of complexity, multiple objectives, and the need for intuitive and synthetic reasoning. Variations of the process have been used successfully in numerous natural resource applications (Shafer et al. 1974; Gunderman 1978; Baughman and Ellefson 1983; Schuster et al. 1985; Miller and Cuff 1986; Phillips et al. 1986; Gregersen et al. 1989; Schneider 1992).

The basic Delphi technique uses a series of written questions distributed to a panel of geographically dispersed participants who are knowledgeable of the issues under study (Delbecq et al. 1975; Ewert 1981). Questions are answered by these experts and returned to project coordinators for collation and synthesis. Results are returned to panel members for clarification, follow-up questions, and possible voting.

Most Delphi studies follow this basic approach and are usually modified to meet specific study objectives and needs. While the Delphi process often leads to consensus or agreement among panelists, no ideas introduced into the process are lost, and minority opinions are retained as a source of ideas for further study, discussion, and analysis.

Study Methods

The Delphi inquiry began in August 1989 and was completed by late December 1989. A process of peer referrals was used to identify an expert panel. A list of 25 North American wolf and prey researchers was provided by personnel of Yellowstone National Park and the Fish and

Wildlife Service as an initial starting point. These individuals were contacted and asked to present a list of experts most qualified to render an opinion on wolf–prey relations. From the 50 experts named, 12 of the most frequently mentioned scientists (persons mentioned at least 3 times) were selected as study participants. This process eliminated bias in panel selection and assured representation of the most qualified professionals in the field. Because an original goal of the study envisioned 15 panel members, we made a decision, in conjunction with the Yellowstone National Park staff and the Fish and Wildlife Service, to add three additional experts. Each added scientist was well known throughout the wolf and prey research community and was mentioned at least two times during the initial peer referral process. All 15 agreed to participate (panel members are listed in the Appendix).

Panel members received two questionnaires[1] preceded by a briefing packet that included a Yellowstone map and information on predator–prey relations (Weaver 1978; Greater Yellowstone Coordinating Committee 1987; U.S. Fish and Wildlife Service 1987; Knight et al. 1989; Singer 1989). The first mailing was in October 1987. The first questionnaire asked experts to use their experience and background information provided to answer several open-ended questions based in part on a report by Singer (1989) that was included in the briefing packet. Each question required short answers or numerical responses. The wolf–prey issues addressed included, but were not limited to, wolf movements, ungulate distribution and demography, prey preferences, grizzly population trends, sport hunting effort, boundary concerns, and changes over time.

The second questionnaire, mailed in November 1989, was based on responses from the first round of questions. Respondents were asked for probabilities of occurrence and levels of agreement or disagreement with the potential effects of wolves suggested by panel members in the first round. For example, each panelist provided an estimate in the first questionnaire of the number of wolf packs that would spend most of their time within the park and commented on the potential territories of these wolf packs. Project coordinators compiled the results and identified potential wolf pack levels and potential wolf territories. In the second questionnaire, panelists estimated the probability that these potential pack levels would occur in the park. At the same time, panelists were asked if they agreed or disagreed with the several potential locations of wolf territories. For example, panelists were asked if they agreed, disagreed as written, or were not sure about the following statement: "Wolf pack boundaries will occur on major river systems, elk calving areas, and other major geographic features."

[1] Copies of background information sent to panelists, each questionnaire, summary statements for each question addressed, and individual panelist's answers and verbatim remarks (anonymously summarized) are available from the authors on request.

Panelists were sent a report in December 1989 that summarized the individual and aggregate study results to confirm and clarify responses to the second questionnaire. Project coordinators considered panelists' comments in the preparation of the final report (Koth et al. 1990) to the National Park Service.

Turnaround time for each mailing was about 2 weeks followed by a period of compilation and analysis and development of new questions. Panelist adherence to the response deadlines generally was excellent, and 100% participation was achieved throughout the study. Every panelist, however, may not have answered every question.

Analysis Methods

A majority of the results we present are reported as the number or percentage of panelists that responded in a certain way to selected questions. *Panelist consensus* or *consensus among panelists* refers to items where 60% or more of the responding panelists provided the same answer. Topics lacking central convergence or having a high degree of uncertainty also were reported.

Panelists specified ranges of responses in the first questionnaire to estimate potential numbers of wolf packs and total numbers of individual wolves that would spend time in Yellowstone National Park. The midpoint of each estimate was used to calculate a mean response for all panelists that responded to these questions. In the second questionnaire, panelists estimated the probability that certain specified pack levels (determined from the first round) would occur in the park.

A map of the park (along with reference maps of topography, average snow depth, and ungulate densities) was distributed to each panelist in the first questionnaire to facilitate identification of potential areas for colonization by reintroduced wolves to Yellowstone National Park. Participants were to mark areas of probable wolf habitation on the maps. These individual maps were then compiled into a single map representing the percentage of respondents indicating probable areas of wolf colonization. Panelists reviewed this information for geographic accuracy in the second questionnaire. At the same time, panelists were asked to describe their opinions on summer versus winter movements of wolves throughout these park locations.

In the first questionnaire—to determine the most important factors that influence prey population levels in Yellowstone—each panelist was instructed to list one (or more) factor. In the second questionnaire, panelists ranked each of the factors generated by the group. Final factor rankings were determined by identifying the top 10 factors using the highest number of responses (total frequency) per factor; then the mean of the panelist rankings for those factors was used to create a rank from most important—1—to least important—10.

Results

Results are organized around the following issues: (1) wolf numbers, (2) wolf movements, (3) overall effects of wolf reintroduction on ungulates, (4) specific effects of wolf reintroduction on prey species, (5) effects of wolf reintroduction on grizzly bears, (6) sport hunting issues, (7) sport hunting and wolf predation, and (8) sport hunting and wolf control.

Wolf Numbers

Panelists estimated the number of wolf packs that will spend a majority of their time within Yellowstone National Park after the wolf population has stabilized. The 15 responses ranged from 3 to 35 with a mean of 13. Eleven (73%) predicted that from 6 to 15 packs would spend at least 6 months within the park.

Panelists then estimated the probability that certain specified pack levels would occur in the park. No consensus (29–54%) was reached concerning pack levels of 30 and below. Panelists reached consensus (69%) that higher pack levels (31–35) were unlikely.

Panelists also provided a parallel estimate of the number of individual wolves that would spend at least 6 months of the year within the park. Although a total range of 24–300 wolves and a mean of 150 wolves was indicated in the responses, 8 panelists (53%) predicted that between 51 and 150 wolves would spend at least 6 months within park boundaries.

Mean pack size was calculated to range from 7 to 22 individuals when pack numbers and total population estimates made by panelists were compared. However, 64% were in the 7–10 category.

Eight of 12 panelists (67%) indicated that from 5 to 10 additional packs might have territories located primarily outside of the park. The most frequent response was 5 packs (6 panelists), with a range of 3–20+ packs indicated by all responding panelists.

Wolf Movements

One of our goals was to determine potential areas for colonization by reintroduced wolves. Although several panelists thought it would be difficult to predict potential wolf locations accurately without on-site inspections, most generally felt that wolves have the potential to locate nearly anywhere within the park (Figure). Panelists expect wolves to be found throughout the park during summer. In winter, however, wolves most likely would be found in the north-central portion of the park. Panelist's comments regarding the colonization map suggest that the southeastern portion of the park, while suitable for wolf habitation, would not have as large a concentration of wolves as the north-central and northwestern portions, where larger areas of suitable habitat would be found.

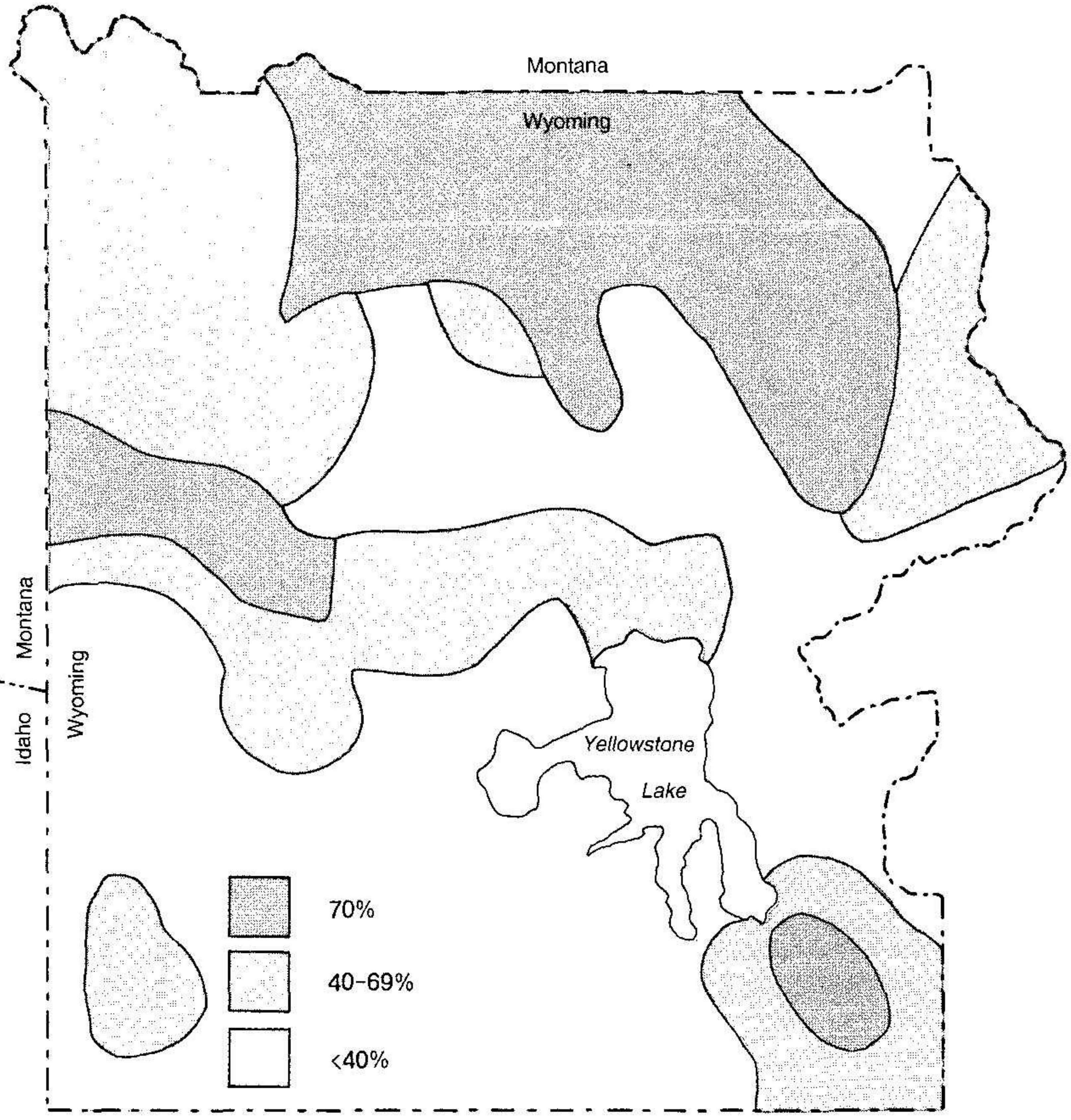

Figure. Potential wolf habitat in Yellowstone National Park based on response from 11 panelists. Percent of panelist agreement is represented by *shaded areas.*

Panelists thought it would take up to 20 years to develop a stable mosaic of wolf pack territories because wolves would be colonizing a new area. Territories would change in response to changing prey distribution, prey abundance, and pack size and dominance. If major declines in primary prey populations were sustained, there would be fewer wolves, but the remaining packs would have larger territories. The opposite might hold if there were sustained major increases in the primary prey population. In addition, the experts thought that some individual pack territory boundaries might correspond to major geographic features such as river systems, roads, or watershed divides.

Panelists thought that, in winter, wolf packs would hunt mainly in areas of low elevation where ungulates, particularly elk (*Cervus elaphus*) congregate. Packs would roam freely throughout their territory with little or no use of the homesite (dens, rendezvous sites). According to the panelists, effects of snow depth on wolf movements will vary depending on snow density, crust, and trail or road systems. Panelists emphasized that snow depth affects ungulate movements directly and wolf movements indirectly. Accordingly, wolf movements would fluctuate year to year as a function of winter severity and of the related major prey distribution.

Panelist opinions were divergent concerning when packs might leave their winter range, how often packs would visit major prey areas within their territories during winter, and whether wolves commonly would hunt in winter as a pack or periodically as a subunit of the pack.

Panelists thought that, in summer, most wolves would be within park boundaries and that spatial organization of wolves would be fairly rigid, with each pack defending a home territory when rearing pups. Wolves would be most active around their homesites, making daily hunting forays from their dens and rendezvous sites, usually within the pack's territory. These forays would involve mainly subunits of the pack (one to three individuals) hunting independently and returning to the rendezvous sites to feed pups and to socialize with other pack members. Panelists confirmed that it is difficult to predict the potential location of denning sites beyond general geographic areas.

Occasional forays into neighboring pack territories have been observed elsewhere. Panelists expected that such forays also would occur within the Yellowstone wolf system, but panelists held varying opinions regarding their frequency. Consensus among panelists suggests that the frequency of extraterritorial forays would increase if food shortages occur and that packs with territories having an annually variable prey base would have the greatest tendency to make extraterritorial forays in winter.

No consensus was reached about how many or when reintroduced wolves might disperse by permanently leaving the original pack. The consensus of the panelists was that the chance of survival and successful colonization of dispersed wolves in a new area is uncertain. Mortality would be related to human-induced deaths, prey abundance, and wolf hostility. Panelists did not reach a consensus regarding the likelihood that some wolves may attempt homing when released.

Overall Effects of Wolf Reintroduction on Ungulates

Primary Prey Species

Panelists expected elk to be the primary prey for wolves in all seasons. Mule deer (*Odocoileus hemionus*) might be primary prey during summer but secondary prey throughout the rest of the year. Moose (*Alces alces*) were considered a potential prey, although panelists felt there was insufficient data to formulate an opinion on the importance of moose as prey for wolves in Yellowstone. Bison (*Bison bison*) have the potential to be important prey depending on a variety of factors including type and source of wolf introduced, development of hunting skills, and changing relations of prey over time. Pronghorn (*Antilocapra americana*), mountain goats (*Oreamnos americanus*), and bighorn sheep (*Ovis canadensis*) would be available prey species but would not likely be important sources of food for wolves.

Vulnerability

Panelists indicated that elk would be the most vulnerable prey except in summer when mule deer would be the most vulnerable. Mule deer were ranked second in vulnerability in all other seasons. Moose, bison, pronghorn, bighorn sheep, and mountain goats were ranked progressively less vulnerable. Caution is necessary in interpreting these findings, however, because panelists stressed that many factors influence the degree of vulnerability (i.e., number of individuals in prey species, relative prey availability, condition of individual prey, age and sex of prey, and carrying capacity of prey habitat).

Winter was thought to be the most vulnerable time for all prey species—with the possible exception of mule deer and pronghorn, which tend to winter in areas of high human activity. Other vulnerable times frequently mentioned were calving and rutting seasons and following heavy snows in fall.

Demographic Changes

According to the panelists, overall prey population conditions would benefit from wolf predation because wolves prey primarily on weak and inferior individuals. Panelists expected that wolves would select younger animals, resulting in low recruitment of young into the adult segment of the prey populations. Aged animals also would be vulnerable to predation. Panelists thought that wolf predation on the ungulates would render them less subject to density dependent mortality and epizootics because of dampened oscillations in prey population. Specific changes in the average ages of prey populations, male/female ratios, and pregnancy rates could not be agreed on by a consensus of responding panelists.

The consensus was that weather-related effects could depress prey populations following severe winters. Panelists agreed that wolf predation would reduce pulses in prey mortality now caused at intervals by severe winters and resulting die-offs. No clear consensus could be reached, however, on the compensatory effects of wolf predation on prey populations close to the nutrient–climate ceiling (i.e., whose numbers are being regulated by available forage and severe winter weather).

According to a consensus of panelists, most distributional changes of prey populations would be relatively local, implying few geographical consequences. The prey most likely would stay in better escape terrain, assume more defensive behaviors, and be more alert, skittish, and nervous.

Wolf Predation and Prey Populations

Panelists were asked to identify and rank factors that influence prey population levels in Yellowstone National Park. Rankings were made for the elk (primary prey), mule deer, and the remaining ungulate species

(Table 1). Wolf predation ranked third in importance as a factor influencing elk population levels, second for mule deer, and fifth for other ungulate prey species. Panelists believed that effects on ungulates would vary over time depending on the dynamic relations established between wolves and prey.

Over time, predation by wolves (under a 10- or 20-pack level) would not threaten any prey species with extinction in the Yellowstone area according to 92% of the panelists; answers generally show a 0–1% probability of occurrence for extinction—with one dissenting panelist. Even at a 30-pack level, deemed improbable by a consensus among panelists, more than 60% of the responses were still a 0% probability.

Specific Effects of Wolf Reintroduction on Prey Species

Elk

Nine of 14 responding panelists (66%) indicated there would be little or moderate change in behavior and distribution of elk in Yellowstone if wolves were reintroduced. No consensus, however, was reached on specific changes in elk distribution following reintroduction of wolves, with the exception that calving areas may be relocated to safer places like slough bends, river islands, and higher elevations if these were in close proximity to previously used sites. Ideas that were examined included occurrence of cohesive groups, smaller aggregations, greater dispersal of individual elk, sexual segregation, migration, and relocation near human-made facilities.

Because many elk populations in the park are currently at high densities and show signs of nutritional stress related to competition for quality food, their potential for numerical growth is limited. Therefore, panelists thought that wolf predation would induce an initial decline in elk numbers, which in turn would reduce nutritional stress and improve reproduction. A consensus among panelists suggested that young elk likely would be preyed on more often than adult elk in all seasons except, perhaps, winter.

Ten years after wolf reintroduction—assuming a stable wolf population of 10 packs of 10 wolves each—85% of the responding panelists expected that elk numbers would be reduced by less than 20%. The range of potential reductions was between 4 and 30%; the most frequent response was a reduction of 10% (4 panelists). In a second scenario with 20 packs of 10 wolves each, the elk population would be reduced from 6 to 40%, according to panelists.

Mule Deer

Overall, 77% of the responding panelists indicated there would be moderate or little change in behavior and distribution of mule deer as the result of wolf reintroduction. As with elk, however, panelists provided a broad range of opinions on how specific mule deer behavior and distribu-

Table 1. Importance of factors influencing prey population levels in Yellowstone National Park, according to panelists.

Factor	Elk			Mule deer			Other ungulates		
	Rank[a]	Total freq	Mean score	Rank	Total freq	Mean score	Rank	Total freq	Mean score
Winter severity (snow depth, temperature, snow conditions)	1	11	2.4	1	11	2.2	2	10	2.3
Distribution and abundance of suitable forage	2	7	2.7	3	5	3.0	4	7	3.0
Wolf predation	3	9	2.8	2	10	2.4	5	5	3.2
Habitat quality and quantity	4	7	2.9	5	8	3.6	3	9	3.0
General weather–vegetation interaction	5	9	3.1	4	7	3.4	1	4	1.8
Summer rainfall/drought	6	6	4.3	7	5	4.2	7	3	4.3
Sport hunting	7	8	4.9	6	7	4.0	6	4	3.8
Wildfire suppression	8	6	6.2	9	6	7.2	—	—	—
Mountain lion predation	9	7	7.9	8	7	5.6	—	—	—
Competition with livestock outside park and grazing management practices	10	6	8.0	10	5	9.0	—	—	—
Topography and drainage patterns	—[b]	—	—	—	—	—	8	3	4.7
Bear predation	—	—	—	—	—	—	9	3	6.7
Land uses outside park that alter native habitat	—	—	—	—	—	—	10	5	7.2

[a] Rank was determined by a 2-step process: (1) The 10 factors were identified by the highest number of responses (total frequency) per factor; 13 panelists answered the question; (2) Mean panelist rankings for each factor was used to create a rank from most important (1) to least important (10).

[b] Not an important factor.

tion might change related to wolf reintroduction. Panelists held a wide variety of opinions on the following:

1. the amount of carrion available at any time,
2. the relocation to water escape routes,
3. the selection of hiding cover,
4. the prey using territorial boundaries of wolf packs or higher elevations as places of refuge, and
5. the females and fawns moving closer to human habitation.

As mentioned, mule deer were ranked as the second most vulnerable prey species to wolf predation in fall, winter, and spring and most vulnerable in summer. Some panelists, however, thought that the importance of mule deer in winter was overrated because mule deer on the northern range reportedly leave the park in winter and seek human-made facilities in the residential valleys nearby (e.g., Gardiner, Montana).

Consensus among panelists suggests that young mule deer would more likely be preyed on than adult deer in summer and fall. The opposite would hold true during winter. In spring, wolves would prey on young and adult mule deer in approximately equal numbers.

Assuming a stable wolf population of 10 packs of 10 wolves each, two-thirds of the responding panelists predicted a reduction in the mule deer population of between 15 and 30% 10 years after wolf reintroduction. The range of potential reductions was between 0 and 30%, with the most frequent response being a reduction of 20% (3 panelists). In a second scenario with 20 packs of 10 wolves each, three panelists predicted that reductions in mule deer numbers would vary widely (5–50%). The most frequent response was a reduction of 10% (3 panelists).

Bison

Overall, 71% of the responding panelists indicated there would be little or no change in the behavior and distribution of bison due to wolf reintroduction. On the other hand, panelists held widely varying opinions about the potential nature and extent of wolf predation on bison. Of 15 respondents, 4 predicted that wolves in Yellowstone would prey on bison only occasionally. Another five panelists indicated a strong potential for wolves to develop hunting skills over time and utilize the bison as a primary prey, resulting in more wolves wintering within park boundaries. Three panelists indicated that bison utilization by wolves is dependent on the type of wolf introduced to the park (i.e., whether or not the wolves had previous experience hunting bison).

Assuming a stable wolf population of 10 packs of 10 wolves each, all panelists responding expected a reduction of less than 20% in the park's bison population 10 years after wolf reintroduction. The most frequent response was a reduction of 10% (6 panelists). With 20 packs, 69% of the responding panelists felt the bison population would be reduced by 15% or less. Responses ranged from 0 to 30%, and the most frequent responses were 10, 15, and 20% (3 panelists each).

Moose

Overall, 67% of the responding panelists indicated there would be moderate or little change in the behavior and distribution of moose due to wolf reintroduction. A consensus of the panelists was that moose may select water escape areas (rivers, islands, lakeshores, peninsulas) for calving, avoid areas of high wolf activity, and may locate near human activity. Four panelists felt moose (with the exception of cows with calves) would not change their habits because of wolves.

A consensus of panelists suggested that moose are not highly vulnerable to wolf predation when compared with elk and mule deer. Several panelists, however, indicated that more information was needed on moose densities, locations, and behaviors within the Greater Yellowstone area before reliable predictions can be made.

Assuming a stable wolf population of 10 packs of 10 wolves each, 72% of the responding panelists expected a reduction of 15% or less in the moose population 10 years after wolf reintroduction. Responses ranged from 0 to 30%, and the most frequent response was a reduction of 10% (5 panelists). Under a 20-pack system, a reduction of 20% or less was expected by 77% of the panelists. Responses ranged from 4 to 50%, and the most frequent response was a reduction of 10% (4 panelists).

Pronghorn

Ninety-two percent of the responding panelists felt that pronghorn would be the least affected species being considered. Eighty-six percent (13 panelists) expected little or no change in the behavior or distribution of pronghorn related to wolf reintroduction in Yellowstone.

Reductions in the pronghorn population under a 10-pack system 10 years after reintroduction are expected to be less than 10% according to all panelists. Assuming a 20-pack system, 92% of the responding panelists predicted a reduction of 10% or less for pronghorn populations in the park. Estimated reductions under a 20-pack system ranged between 0 and 50%, with the most frequent answers being a reduction of 0 or 10% (5 panelists each).

Bighorn Sheep and Mountain Goats

Moderate or little change in the behavior or distribution of bighorn sheep and mountain goats was anticipated by 80% of the responding panelists. Panelists anticipated that bighorn sheep and mountain goats would remain in alpine areas and spend more time near cliffy escape cover.

Reductions in mountain goat and bighorn sheep populations under a 10-pack system of reintroduced wolves were not expected to exceed 5%.

Under a 20-pack system, a reduction of 10% or less was expected for bighorn sheep and less than 1% for mountain goats.

Beaver

Several panelists noted the importance of rodents, other small mammals, and birds in wolf diet, focusing in particular on the beaver (*Castor canadensis*). Generally, panelists describe beaver as an important food source when ungulates are less available. Four panelists cited the scarcity of beaver within the park and felt that beaver would not be heavily affected by wolves. Another four respondents thought the effect would be somewhat more significant, but they failed to elaborate specifically on what the increased effects would be.

Coyote

All panelists stated that the coyote (*Canis latrans*) population would be reduced with restoration of wolves to the Yellowstone ecosystem because of competition for food. They indicated coyote populations would shift to marginal wolf areas and peripheral areas of wolf territory. The ecological niche of the wolf and coyote differ—coyotes can subsist on a wider variety of prey size, including small mammals.

Effects of Wolf Reintroduction on Grizzly Bears

The consensus among panelists was that in other locations, including the Yukon, Alaska, and Glacier National Park, wolves and grizzlies generally do well together. No consensus about the specific effects of wolf reintroduction on grizzly bears was reached, however, because panelists were divided about whether wolf predations would provide bears with more protein and a more consistent carrion supply (from wolf-killed carcasses) for a greater period of the year.

Four respondents described the overall effect of wolf reintroduction on grizzly bears as slightly beneficial, four participants termed the effect neutral, and six panelists thought the result would be slightly negative. While there was no consensus about the direction of the effect, panelists did think the magnitude of change would be slight rather than significant.

Of the six panelists who believed wolves would provide more protein for bears, four identified the overall effect on grizzlies as slightly beneficial. The six panelists who thought wolves would not provide more protein called the effect neutral or slightly negative. The two remaining participants, who were not sure whether wolves would provide more protein, described the overall effect as slightly negative.

Eleven of 14 respondents indicated that wolves would provide some kills on which bears might directly feed. Bears and wolves would compete for carcasses, and occasional bear–wolf conflicts would occur at kill sites. Deaths of both bears and wolves could occur during these uncommon conflicts, but direct interspecies killing would be insignificant. Panelist consensus suggests that grizzly bears often would dominate at kill sites and should be able to drive wolves from kills. In general, grizzlies would scavenge more from wolves than vice versa.

Overall, the consensus among panelists was that although some predation of wolves on bear cubs and adults (females with cubs) would occur, the level would be insignificant. Little consensus occurred concerning specific aspects of wolf predation on bears. For example, there was much uncertainty about whether wolves would occasionally dig up hibernating cubs.

Panelists did not expect wolves to affect grizzly bears in other ways. For example, the activities of grizzly bears were not expected to be restricted by the presence of wolves, even for bears that hunt ungulates in traditional calving and rutting areas. Occasional and infrequent harassment of bears by wolf packs would not likely reduce current bear predation opportunities. Wolves were not expected to make ungulates more vulnerable to grizzly bears by increasing mobility of ungulates and making them more conspicuous. Some panelists were uncertain concerning harassment (5) and increased vulnerability (6).

Panelists agreed that further research is needed on two issues. Responding to an inquiry about whether wolf kills would provide approximately 3% of grizzly ungulate foods, panelists often noted a low percentage or less than 5% in their comments—they were not willing to make an actual prediction. Also, there was no consensus on whether certain segments of the bear population, mostly breeding females with cubs, would become more alert and excitable on a regular basis due to the presence of wolves.

Sport Hunting Issues

None of the responding panelists thought that wolf distribution should be limited to Yellowstone National Park. Eleven of 14 responding panelists disagreed or strongly disagreed with that position (the others were unsure). In general, panelists argued that although the core wolf population would be centered in the park, the imposition of artificial or political boundaries to wolf distribution may not allow wolves to sustain recovery levels. Wolves could be expected to move seasonally outside the park or to establish territories that straddle park boundaries. Because wolves may establish territories exterior to the park boundaries, the potential conflict between wolves and sport hunting was considered.

Overall, the panel was almost evenly divided over whether or not reduced sport hunting levels would be a necessary concession associated with wolf reintroduction. Six respondents agreed that reduced sport hunting would be necessary but mentioned that only certain species might be affected or that reductions in sport hunting might take place in future years rather than immediately. Seven panelists disagreed, indicating that actual hunting policies would depend on the number of wolves, wolf management outside the park boundaries, and the relation of hunted prey populations to a nutrient and climate ceiling imposed on the prey populations.

Panelists were then asked if they agreed that harvest levels should be reduced for specific prey species after wolf reintroduction. No consensus was evident (Table 2) regarding the need to reduce sport hunting-related kills of elk, mule deer, bison, or moose, but more panelists agreed than disagreed that sport hunting for these species should be reduced. A consensus of panelists was that sport harvest levels for pronghorn, bighorn sheep, and mountain goats would be unaffected.

Panelists raised related issues including timing considerations (reductions in ungulate harvest may not be needed at first but may be necessary later); the need for research, monitoring, and clear objectives before setting a sport-hunting policy; and the complexity of factors that influence such a decision concerning potential changes in sport harvest levels. A common remark was that sport hunting reductions could be made when and where appropriate, but blanket generalizations were not now possible. Panelists held varying opinions about the level of sport hunting reductions that might be necessary.

Elk

Eight of 14 panelists disagreed that most elk herds are hunted near maximum sustained yield and mentioned that it varies by herd. Most herds were thought to be harvested near or below maximum sustained yield—some lightly exploited populations are increasing. Because of high current elk densities in and near the park, thinning of the elk herd was described as desirable. Ten panelists (67%) agreed that the sustainable elk harvest would decline with wolf predation on elk, but the same number thought that even at a 20-pack level, sport hunting for elk would still be possible. No consensus was reached on the level of annual elk harvest by sport hunters or if male-only harvesting should be recommended with wolf reintroduction.

Table 2. Number of panelists responding by category to the statement "Hunting levels should be reduced after wolf reintroduction . . . ."

Species[a]	Strongly agree	Agree	Not sure	Disagree	Strongly disagree
Elk	2	5	4	3	0
Mule deer	3	3	5	2	1
Bison	1	3	7	4	0
Moose	2	4	4	3	1
Pronghorn	1	0	0	9	4
Bighorn sheep	1	2	0	9	2
Mountain goat	2	0	4	7	1

[a] Elk = (*Cervus elaphus*); mule deer = (*Odocoileus hemionus*); bison = (*Bison bison*); moose = (*Alces alces*); pronghorn = (*Antilocapra americana*); bighorn sheep = (*Ovis canadensis*); mountain goat = (*Oreamnos americanus*).

Mule Deer

Panelists reached consensus (10 of 14) that where mule deer sport harvest levels currently exceed 20%, the effect of wolf predation could be severe. Six panelists felt sport hunting would be possible, however, even with a population of 100 wolves. Five experts were not sure. Consensus was not reached concerning mule deer sport harvest levels or male-only hunting.

Bison

The sport hunting harvest of bison generally has been low, except during the winter of 1988–89, when bison moved outside the park and hunters harvested 568 animals. The potential exists for significant effects of the reintroduction on bison if bison are subjected to both high levels of predation and sport harvest. Ten of 14 responding panelists agreed that the effect of sport harvest plus wolf predation would depend on whether bison were preferred by wolves but that neither the movement of bison from the park nor the pattern of bison utilization by wolves could be predicted. In this uncertain situation, panelists generally agreed (with two dissentions) that changes in current bison harvest levels would not be needed following wolf reintroduction. Sport harvest could be quickly eliminated if the population were severely affected.

Moose

Ten of 14 panelists said they were not sure if most moose are year-round residents of the park. At high moose sport harvest levels of between 10 and 20%, a consensus among panelists suggested that wolf predation could have a severe effect on moose populations.

Sport Hunting and Wolf Predation

All 13 responding panelists agreed (5 strongly agreed) that it could not be assumed that a reduction in sport hunting would simply make up for wolf kills in an additive manner. This concept is key to managing a system where sport hunting is a factor, because hunters and predators generally do not kill the same ages and sexes of animals. Both mortality factors, however, are highly selective and density dependent.

Some of the ungulate species populations could decline with wolf predation if human harvesting were high, especially if high human harvesting coincided with a consecutive series of severe winters (8 of 14 panelists agreed). The mortality rate for the various ungulate species due to wolf predation would be difficult to determine.

Sport Hunting and Wolf Control

Interaction in a multiple-prey system is made more complex by the inclusion of sport hunting. Panelists were unanimous in their opinion that sport hunting and control of wolves by humans must be addressed together.

They rejected the position that effects on ungulate populations could be managed by efforts outside the park that either reduced predation by lowering wolf numbers or by reduced sport hunting (but not both). However, beyond consensus that problem wolves that kill livestock must be removed, there was no consensus about the combination of management strategies that would best meet multiple objectives.

A consensus among panelists suggested that authorities control wolves by means other than eradication whenever possible. Those that disagreed generally perceived population control as a periodic solution and supported a broad spectrum of management rather than a simple reduction in wolf numbers. Respondents did not reach consensus about when wolf control should begin. Finally, the panelists did not accept establishing a minimum population size for each prey species and initiating wolf control measures only if these population levels are reached. Evaluation of the holistic system involving wolves and ungulates on a continuous basis and devising management strategies accordingly was deemed better than reacting to a crisis of low prey populations.

Conclusions

The views offered by the 15 North American wolf and wolf-prey scientists indicated both diversity of opinions and consensus regarding the potential effects of wolf reintroduction in Yellowstone National Park. Panelists were in general agreement about a variety of concerns and topics related to reintroduction. They saw wolves as part of the original ecosystem of the park. Their collective judgment suggests that wolves can be successfully reintroduced in Yellowstone with relatively minor changes to both prey species and grizzly bears. Panelists generally thought that some modifications in sport hunting outside the park might be necessary, but the complexity of factors that influence such decisions was beyond generalizations. The reader is reminded that the Delphi technique generally leads to a consensus among participants and that while the panel members were knowledgeable about wolves, most were not intimately acquainted with the Yellowstone ecosystem.

Below are highlighted the most salient expert opinions resulting from panelists' deliberations:

- The core wolf population would be centered in Yellowstone National Park, but areas outside the park may be essential to maintain population levels necessary to sustain recovery.
- A viable wolf population of about 12 packs that spend a majority of their time within the park seemed realistic after the population had stabilized (within 20 years after reintroduction).
- If wolves were reintroduced, extinction of any prey species (moose, elk, mule deer, pronghorn, bison, mountain goat, or bighorn sheep) in the Yellowstone area would be extremely unlikely.

- Overall, there would be relatively minor changes in prey species' behavior and distribution if wolves were reintroduced in the park. However, for several species (moose, elk, mule deer, bison), there would be some decline in populations over a 10-year period after reintroduction.
- Elk and mule deer would be the primary prey for wolves—elk throughout the year and mule deer in summer. Other prey species would be relatively minor sources of food.
- Panelists agreed unanimously that wolves and grizzly bears could coexist. Opinions differed, however, about specific effects of wolf reintroduction on grizzly bears—would wolf predation provide bears with more protein from wolf-killed carcasses and a more consistent carrion supply? All panelists called the overall effect slight or neutral.
- Reducing mortality from sport hunting for various ungulate species in areas surrounding the park would not be an associated requirement if wolves were restored to the Yellowstone ecosystem. Mixed opinion occurred, however, concerning whether reduced sport harvest of elk would be necessary to facilitate wolf reintroduction. Reduced sport hunting levels should be implemented only when necessary, and then only in conjunction with wolf control measures and other prey population management tools.
- More research is needed to better understand the interrelations among wolves, grizzly bears, prey species, and sport hunting for big game in areas surrounding the park.

Opinions varied considerably about the reintroduction of wolves into the Yellowstone ecosystem when specific topics and questions about effects were addressed. This reflects the complexity of issues and relations that could affect reintroduction. Further, even with the background information on Yellowstone National Park provided the panelists, their degrees of familiarity with this ecosystem could influence their opinions (or their willingness to express certain conclusions) about the potential influence of specific factors on wolf reintroduction. It is understandable, then, that scientists would differ in their responses to the more site-specific and situation-specific topics and questions. Nevertheless, panelists offered their judgments as well as reservations on most questions and topics examined. Collectively, their views represent valuable information and a range of ideas worthy of further study, discussion, and analysis. We hope the insights of these experts will be combined with the results of other studies associated with wolf reintroduction in Yellowstone to further the dialogue concerning this important and far-reaching topic.

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As the nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

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