

Executive Summary

The recent restoration of wolves to the greater Yellowstone ecosystem created a new degree of complexity that makes it difficult to project long-term trends in abundance for ungulates. In contrast to other areas in North America, the greater Yellowstone ecosystem already supported a diverse predator complex, with five other large predators (i.e., black bears, coyotes, grizzly bears, humans, and mountain lions). Previous studies of relatively simple faunal systems with 1-2 predator and prey species suggest that wolves can have substantial top-down control on ungulates by decreasing their abundance and altering their spatial and temporal distribution, movements, and browsing patterns. Such effects have significant implications for natural resource managers because a reduction in ungulate abundance can lead to “trophic cascade” effects such as alterations in species abundance and community composition, nutrient concentrations of plants, and the physical structure of the vegetation and the environment. A reduction in ungulate abundance also typically results in lower harvest limits for humans. Thus, it is essential that natural resource decision-makers have reliable knowledge regarding the population dynamics of ungulates and wolves, as well as any other trophic-level effects that these interactions produce in the ecosystem.

We evaluated the initial consequences of wolf recovery on the world-renown, migratory population of northern Yellowstone elk by: 1) coalescing and integrating information on their abundance, classification (i.e., age, sex), and vital rates; 2) evaluating the adequacy and reliability of these data as they are currently collected; 3) evaluating trends in abundance and vital rates over time, including pre- and post-wolf restoration periods; and 4) evaluating the relative influence of human harvest and wolf removals on their demographics.

Though our analyses are, by necessity, a simplification of the system, results suggest that elk abundance will continue to decrease in the near future until levels of harvest by humans and/or predators decrease sufficiently. This conclusion should be viewed with caution due to several oversimplifications and uncertainties about parameter values used in our analyses. Also, we anticipate that neither hunter harvest or wolf predation will remain at current levels into the future owing to a variety of biological, political, and societal processes. For example, after the completion of our analyses for this report, the Fish, Wildlife, and Parks Commission of Montana reduced the number of late season antlerless permits for northern Yellowstone elk from 2,080 during 2003 to 1,400 during 2004. Thus, actual trends in elk and wolf populations may differ substantially from predictions of our models.

We also caution against generalizing the results of our investigation regarding the consequences of wolf recovery on the dynamics of northern Yellowstone elk to other elk populations in the northern Rocky Mountains. We suspect that the effects of wolf predation on elk populations will be highly situation specific, depending on a complex of factors including elk densities, abundance of other predators, presence of alternative ungulate prey, winter severity, land ownership, human harvest, livestock depredations, and levels of human-induced wolf deaths. A coalition of natural resource professionals

and scientists representing federal and state agencies, conservation organizations and foundations, academia, and land owners are collaborating on a comparative research program involving three additional wolf-ungulate systems in the western portion of the greater Yellowstone ecosystem. These ongoing studies were initiated 3-5 years ago to gain a broader understanding of the ecological consequences of wolf recovery. Results to date indicate that the effects of wolf predation on elk population dynamics can range from substantial to quite modest.

The following paragraphs contain a brief synopsis of our findings. For a more detailed presentation, we suggest that the reader review Chapter 1 (Introduction), Chapter 2 (Integrating Demographic Data and Population Models), Chapter 5 (Age-Structured Modeling), and Chapter 7 (Management Implications). Additional supporting information for our findings and recommendations is provided in Chapter 3 (Vital Rates and Limiting Factors), Chapter 4 (Lotka-Leslie models), and Chapter 6 (Generalized Models).

Synopsis of Findings:

Mean and maximum pregnancy rates in the prime age classes (i.e., ages 3-15) of Yellowstone elk were consistent at approximately 0.90 over a wide range of elk densities (i.e., 1.5-9 elk/km²). Given the relatively high reproductive rates observed for prime-aged northern Yellowstone elk when counts were >12,000 animals, it is unlikely that a biologically significant density-dependent increase in reproductive rates will occur if elk abundance decreases owing to predation or other factors.

Survival of prime-aged female elk, as estimated using age at death data from elk harvested during the Gardiner Area Late Elk Hunt on the northern Yellowstone range of Montana, was relatively constant at 0.85 (95% CI = 0.81 to 0.87). These estimates of survival may not reflect the entire population because the majority of elk do not migrate outside the park except during the most severe winters, and there is evidence of an age segregation pattern across the winter range.

The primary method used to index recruitment for northern Yellowstone elk each year has been late winter classification surveys to obtain population composition estimates. To evaluate if these composition estimates provide reliable indices of recruitment, we compared calf:cow ratios in a given year with spike:cow ratios the following year. Calf:cow ratios during a given year were significantly and linearly correlated with spike:cow ratios the following year, suggesting that estimates of composition from late winter classification surveys provided a reasonable index of recruitment.

The number of elk migrating out of Yellowstone National Park on the northern range during winter is positively correlated with snow water equivalent (i.e., the amount of water in the snow), which is an index of snow accumulation. However, winter calf survival rates were poorly correlated with snow water equivalent, likely because there were substantial variations in density of northern Yellowstone elk. A given snow water equivalent level would likely have a greater adverse effect on calf survival when elk

density is relatively high. Moreover, there is likely a threshold effect between snow water equivalent levels and calf survival.

The Wolf Program of the Yellowstone Center for Resources aged more than 600 northern Yellowstone elk killed by wolves during the winters of 1995-2002. Calves accounted for 40 percent of the total wolf-killed elk detected during the winters of 1995-2002. In addition, wolves concentrated on female elk >14 years of age. Thus, wolf predation to date has largely affected the survival of calves and senescent age classes of female northern Yellowstone elk.

Substantial variability in the population trend of northern Yellowstone elk appears to be associated with hunter harvests outside the park. During 1996-2002, approximately 5-19 percent (mean \approx 11 percent) of the adult female population was harvested each year during the late season hunt. Annual harvests were relatively consistent at approximately 27 ± 5 percent (95% CI) of the maximum number of elk estimated to migrate north of the park. This rate of harvesting is higher than the migratory portion of the population could support in the long term because the maximum growth rate for elk populations is approximately 28 percent. Thus, there has to be some degree of mixing between elk that typically migrate outside the park and those that typically remain within the park during winter. This “mixing” likely occurs during years of increased snow accumulation.

We used simple models that incorporate only population counts and removals to obtain estimates of population trends and growth rates (λ , “lambda”) of northern Yellowstone elk. Following a moratorium on elk removals inside the park, and with small human harvests outside the park, the population grew rapidly and counts increased from 3,172 elk in 1968 to 12,607 elk by 1975 (i.e., λ equal to 1.19). During 1976 to 1988, the growth rate of the population slowed substantially (i.e., $\lambda \approx$ 1.04), but counts of northern Yellowstone elk increased from approximately 12,600 to 19,000 elk. Previous investigators suggested that the growth rate of the population slowed during 1982-1988 because the population was approaching its “carrying capacity” between 20,000 and 25,000 elk. However, increased hunting removals outside the park boundary may have contributed to the slower growth rate during this period. The population decreased at a rate of approximately three percent per year (i.e., $\lambda \approx$ 0.975) during 1988 to 2002.

Annual winter counts severely underestimate actual numbers of elk present in many years. For example, a very high hunting removal estimate of 4,515 elk occurred in 1992, which equated to 29 percent of the pre-count estimate of 15,587 elk. This high removal was followed by two years of an apparent population increase, which is simply impossible if the counts and removals are accurate because the maximum rate of increase for elk populations is approximately 28 percent per year.

Because simple count-removal trend models do not consider the dynamics of the population (i.e., birth and death rates, age structure), we also used a Lotka-Leslie model to describe the mathematical relationships between age-specific fecundity and survivorship and the rate of population growth. An estimate of the population growth rate (lambda) derived using reproductive and survival data for northern Yellowstone elk

was 1.20. This estimate agrees closely with the estimate of 1.19 during 1968-1975 (i.e., a period of virtually no removals) derived using the simple count and removal model. However, this growth rate was not realized during other periods between 1935 and 1968 owing to off-take of animals.

The age structures of human and wolf harvests of northern Yellowstone elk are quite different, with hunters during the late hunt concentrating on prime-age females and wolves focusing on calves and senescent-age females. To explore the relative effects of historic levels of these mortality sources on the trajectory of the population, we constructed a series of age-structured population models using the data described elsewhere in this report. We used age-specific fecundity and survival schedules to estimate the baseline number of animals in each age class that would die in the absence of hunting or wolf predation at each of three population levels. We then compared these estimates with model projections of the number of animals killed given varying wolf predation and hunter harvest rates.

Model projections indicated that the number of calf elk removed by wolves and hunter harvest is well below projected losses due to baseline conditions. These results suggest that there is substantial potential for both mortality factors to be compensatory, especially wolf predation. In contrast, model projections using all levels of wolf and hunter kill exceeded projected baseline levels of adult female elk dying by 3- to 12-times. Thus, nearly all off-take of adult females by wolves and hunters is likely additive owing to the very high survival rates of prime-age females at population levels well below carrying capacity and in the absence of hunting and major predators.

Initial population projections revealed that the age structure of the projected elk population could not support the age-specific structure of wolf predation as estimated from the ages of elk killed by wolves. Thus, our model did not capture an important dynamic of the system, which we speculate deals with spatial dynamics and underestimation of the size of the elk population. We hypothesize two patterns of elk movement (individual fidelity to seasonal movement patterns; age- or reproductive-specific seasonal movement patterns) that, in conjunction with the spatial segregation of predominant mortality factors (wolf predation within the park, hunting mortality outside the park), could account for these incogruities.

Projections of wolf predation demonstrate that the growth rate of the population is increasingly depressed with higher predation rates, and that the smaller the elk population the larger the effect of wolf predation on the trajectory of the elk population. In general, however, the elk population would continue to increase under nearly all predation rate-population level combinations. In contrast to the wolf predation projections, the effect of varying harvest rates is the same for all three elk population levels. The differences in the projections for wolf and hunter mortality is due to the differences we built into the model structure (i.e., the number of animals killed by wolves remaining constant in all simulations, while hunter harvest is proportional to the number of elk in the population).

While nearly all projections (17 of 18) with a single source of mortality demonstrated stable or continued growth in the elk population, combining both sources of mortality resulted in declining elk populations for the majority of the projections (20 of 27). The effect of the combined mortality sources on the trajectory of the elk population became more pronounced at lower elk populations.