

Review

Yellowstone's ungulates after wolves – expectations, realizations, and predictions

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Abstract

We evaluated the initial implications of wolf (*Canis lupus*) recovery on ungulates in Yellowstone National Park and compared expectations prior to wolf restoration with observed impacts since restoration. The numerical and functional responses of colonizing wolves in Yellowstone's prey-rich environment were higher than expected and close to the maximum rates predicted prior to wolf restoration. Counts of northern Yellowstone elk (*Cervus elaphus*) decreased more (50%) than predicted (5–30%), and will likely continue to decrease given the strong preference of wolves for elk and continued high kill rates despite this substantial reduction in elk abundance. Contrary to expectations, human harvests were not reduced appreciably concurrent with wolf restoration, but instead remained similar to pre-wolf restoration years. However, antler-less permits were gradually reduced by 51% during 2000–2004 and additional reductions may be necessary while wolf densities remain high. There have been no substantial effects of wolf recovery on other ungulate species (bighorn sheep (*Ovis canadensis*), bison (*Bison bison*), moose (*Alces alces*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*)). However, wolf recovery may eventually contribute to increased bison and pronghorn abundance by decreasing elk and coyote abundance, respectively. Wolf recovery may also contribute to more-pronounced spatial structuring of sex/age classes of northern Yellowstone elk through changes in their distribution, migration, and age structure. The initial consequences of wolf recovery support the premise that wolves may naturally achieve densities above their threshold for ecological effectiveness and contribute to significant changes in ecosystems, including the amelioration of ungulate-caused landscape simplification.

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1. Introduction

Soule et al. (2003) predicted that the restoration of wolves (*Canis lupus*) to the greater Yellowstone area would lead to significant modifications of the structure or composition of the ecosystem, including changes in the abundance, distribution, and behavior of ungulates. Such effects would 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 (e.g., Singer et al., 1994). A reduction in ungulate abundance also typically results in lower human harvest limits.

Previous studies of relatively simple faunal systems with 1–2 predator and prey species suggest predation by wolves on ungulates may be more effective in locales where other large carnivores and alternate prey are present (Crete and Manseau, 1996). The greater Yellowstone area already supported a diverse faunal complex prior to wolf restoration, with five other large predators (i.e., black bears *Ursus americanus*, coyotes *Canis latrans*, grizzly bears *Ursus arctos*, humans, and mountain lions *Puma concolor*) and eight ungulate species (i.e., bighorn sheep *Ovis canadensis*, bison *Bison bison*, elk *Cervus elaphus*, moose *Alces alces*, mountain goats *Oreamnos americanus*, mule deer *Odocoileus hemionus*, pronghorn *Antilocapra americana*, white-tailed deer *Odocoileus virginianus*). Thus, wolf restoration created a new degree of complexity that makes it difficult to project long-term trends in abundance for ungulates.

Prior to wolf restoration, there was a concerted effort to predict the ecological effects of wolves on ungulates in and near Yellowstone National Park (Yellowstone). Our goal is to retrospectively evaluate if reality met expectations, and offer predictions on potential faunal shifts that can be evaluated in the future. We focused our assessment on northern Yellowstone elk because most of the pre-wolf restoration predictions focused on this world-renowned population.

2. Wolf abundance, predation rates, and off-take

The ecological effects of wolf restoration on ungulates in Yellowstone will largely depend on the realized numerical and functional responses of wolves. Between 50 and 130 wolves were predicted to reside in Yellowstone following restoration, with wolf abundance generally tracking elk abundance over time (e.g., Boyce, 1993; Mack and Singer, 1993). However, the numerical response of colonizing wolves in Yellowstone’s prey-rich environment has initially exceeded predictions by 20–30%. The rate of increase for the 31 wolves restored to

Yellowstone in 1995–1996 approximated the biological maximum for the species (Eberhardt et al., 2003), and by 1997 there was evidence that wolves had attained densities that could lead to changes in the abundance, distribution, and behavior of Yellowstone’s ungulates and, in turn, the biomass, productivity, or composition of other species (Ripple and Larsen, 2000; Soule et al., 2003). By 2004, there were at least 159 wolves residing in 14 packs within Yellowstone, representing a density of >50 wolves per 1000 km² (Smith et al., 2003, 2004a). The predicted decrease of wolves with decreases in elk counts from ≈17,000 to 8300 during 1995–2004 has not been observed. In fact, wolf numbers continued to increase at a relatively high rate despite the ≈50% decrease in elk numbers.

It is uncertain if this numerical response represents an irruptive pattern, in which wolves overshoot equilibrium levels, or a density that can be supported given the current abundance of ungulate prey. The wolf-to-elk ratio in Yellowstone during 2002 was approximately one wolf per 155 elk, which was similar to the average ratio of one wolf per 166 elk expected after wolf recovery (Boyce, 1993). However, wolf abundance on the winter range of northern Yellowstone elk increased again from ≈84 to 106 wolves by December 2003, which equates to a ratio of approximately one wolf per 100 elk. Eberhardt et al. (2003) suggested that the wolf–elk system on the northern winter range of Yellowstone could eventually remain at a level roughly equivalent to one wolf per 40 elk, which is a substantially higher ratio than the prediction by Boyce (1993). This glaring disparity in predictions of the eventual equilibrium point highlights the major remaining uncertainty regarding the long-term effects of wolf restoration on Yellowstone elk. The increase in wolf abundance during 2003 occurred in an area where virtually all wolf habitat was occupied to some extent and wolf densities were already the highest recorded in the scientific literature (Smith et al., 2003). Wolf territories have been quite labile and further subdivision and increases in density seem likely given the relatively high abundance of ungulate prey (Smith et al., 2003). Given that no significant decreases in wolf functional or numerical responses have been detected despite a 50% decrease in elk abundance, we anticipate that the ratio of wolves to elk will continue to increase in the near future. At some point, however, disease, food limitation, or social strife will limit wolf population growth by initially decreasing pup survival and reproductive rates. Thus, whether wolves can sustain high densities as elk numbers decrease (Eberhardt et al., 2003), or have overshoot their equilibrium levels (Boyce, 1993), will only be answered through continued monitoring.

Realized kill rates by wolves in Yellowstone during winter have been higher than the expected 2–4 ungulates per 100 wolf days (i.e., 7–15 ungulates/wolf/year; Mack and Singer, 1992, 1993) and closer to the maximum rate

of 7 ungulates per 100 wolf days (i.e., 25 ungulates/wolf/year) envisioned by Boyce and Gaillard (1992) and Boyce (1993). Following wolf restoration, estimated kill rates during winter averaged 6 ungulates per 100 wolf days (range = 3–8) on the northern range (Smith et al., 2004b) and 8 ungulates per 100 wolf days (range = 5–15) in the west-central portion of Yellowstone (Jaffe, 2001; R. Garrott, Montana State University, unpublished data). These relatively high kill rates during winter may reflect the response of colonizing wolves in Yellowstone's prey-rich environment. Summer kill rates of wolves in Yellowstone are unknown, but likely lower than the winter rates for adult ungulates (Messier, 1994). If wolves kill substantial numbers of neonatal elk during summer, however, then the overall kill rate might actually be higher because more calves would be killed to obtain the same relative amount of biomass. An ongoing study of neonatal survival will provide insights on neonatal elk selection by wolves.

It is uncertain how the kill rates of wolves in Yellowstone will change in response to decreasing elk densities. Predation rates can vary with changes in both predator and prey density, but there is no agreement on how kill rates of wolves change with prey or wolf density (e.g., Eberhardt, 2000). Also, there has been insufficient time since the restoration of wolves in Yellowstone to measure predation over a wide range of prey densities. The functional response of wolves is often modeled using a formulation in which kill rate decreases as prey density decreases. However, a compilation of published empirical data from several wolf-ungulate systems suggests a nearly constant killing rate per wolf over a wide range of prey densities (Eberhardt et al., 2003; Fig. 1). Thus, it is possible that wolves in Yellowstone may maintain a relatively high and constant kill rate until ungulates reach low densities (<1 elk/km²). Smith et al. (2004b) found no evidence of lower kill rates as elk densities decreased in Yellowstone during 1995–2000; thereby providing some support for this concept.

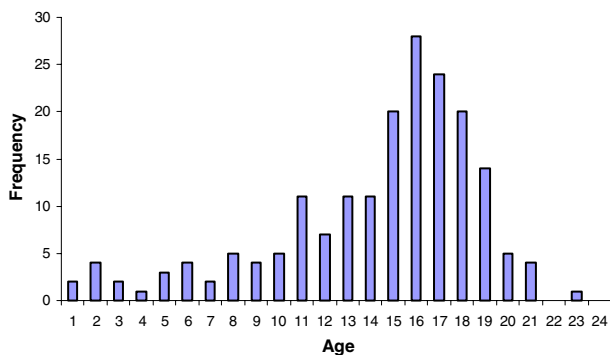


Fig. 1. Age-frequency distribution of adult female northern Yellowstone elk killed by wolves on the northern range of Yellowstone National Park during 1995–2002.

Estimated off-take by wolves in Yellowstone during 2003 was substantially higher than the expected maximum of 1500 wild ungulates per year by a recovered wolf population of 100 wolves in 10 packs (Mack and Singer, 1992, 1993). White et al. (2003) estimated a kill rate of 25 kills/wolf/year based on a moderate kill rate of ≈ 0.075 kills/wolf/day during winter (October–May; Smith et al., 2004b), and summer (June–September) kill rates 70% of the winter rate (Messier, 1994). For 100 wolves, the estimated annual off-take would be 2,500 ungulates, approximating the situation on the northern range during winter 2004 when more than 100 wolves resided there. However, at least 159 wolves lived throughout Yellowstone during winter 2004 (Smith et al., 2004a) and the total off-take of ungulates likely approximated 4000 animals, or 2.7 times the prediction.

3. Wolf impacts on elk

As predicted prior to wolf restoration (Boyce and Gaillard, 1992; Boyce, 1993; Mack and Singer, 1992, 1993), elk are the primary year-round prey for wolves in the park, representing 92% of kills during winters of 1995–2000 (Smith et al., 2004b). Wolf predation has been highly selective, with the age/sex of wolf-killed elk approximating 43% calves, 28% adult females, and 21% adult males (Smith et al., 2004b). Adult female elk killed by wolves on the northern range have been relatively old, with a median age of 16 years (Wright, 2003).

The abundance of northern Yellowstone elk was expected to decrease 5–30% following wolf restoration, with the extent of decrease contingent on levels of hunter harvest outside the park (Boyce and Gaillard, 1992; Boyce, 1993; Mack and Singer, 1992, 1993). However, Mack and Singer (1992, 1993) suggested that a population of 100 wolves killing 15 ungulates per wolf per year could contribute to a rapid decrease in elk abundance. Likewise, Messier et al. (1995) forecast that the abundance of Yellowstone elk would decrease substantially more than 5–30% owing to the diverse and abundant predator complex, occasional severe winter-kills, and moderate to liberal human harvests.

Trend counts indicate that northern Yellowstone elk have decreased by ≈ 6 –8% per year since wolves were reintroduced (White et al., 2003; Vucetich et al., 2004). White et al. (2003) concluded that predation by wolves and moderate to liberal human harvests of prime-aged females were the primary factors contributing to this decreasing trend. They concluded that nearly all off-take of adult female elk by wolves and hunters was likely additive owing to the very high survival rates of prime-aged females in the absence of hunting and major predators, and at population levels well below carrying capacity. Similarly, Varley and Boyce (in press)

identified wolf predation, human harvest, and stochastic perturbations caused by winter severity and forage production as significant variables influencing the trend in abundance of northern Yellowstone elk. However, they concluded that wolf predation had a stabilizing effect on elk abundance owing to the selection of primarily calves and “old cows” (i.e., >9 years of age). In contrast, Vucetich et al. (2004) concluded that the observed decrease in elk abundance during 1995–2004 was explained by climate and a “super-additive” harvest rate, with wolf predation being almost entirely compensatory. They largely based this conclusion regarding wolf predation on the tendency for wolves to select elk calves and old females (Smith et al., 2004b).

These differences in interpretation likely arise, in part, from differing opinions regarding what age classes should be considered prime-aged female elk, with relatively high and constant survival and reproductive rates, and at what age senescence in these rates occurs. Predation or harvest of senescent elk has a higher potential to be compensatory because these elk have lower reproductive value. Varley and Boyce (in press) and Vucetich et al. (2004) considered adult female elk older than 9 years to have high rates of mortality. However, the best available evidence for northern Yellowstone elk strongly indicates that adult females between 3 and 16 years of age have relatively high and constant reproductive and survival rates, a pattern which is indicative of “prime-age” and typical of other elk populations in Montana and elsewhere (White et al., 2003; Cook et al., 2004). Sixty-one per cent of adult female elk killed by wolves on the northern range during 1995–2002 ($n = 188$) were 3–16 years old, compared to 11% of the kills being elk 3–9 years old (Fig. 1; Wright, 2003). If 28% of the total wolf kills of elk during winter 1995–2000 were adult females (Smith et al., 2004), then prime-aged females 3–16 years old likely comprised $\approx 17\%$ of the wolf kills of northern Yellowstone elk during 1995–2004. It is hard to rationalize that predation on these elk was largely compensatory given their typically high survival rates at population levels well below carrying capacity and in the absence of hunting and major predators.

Boyce and Gaillard (1992) suggested the recovered wolf population would not have irreversible effects on wild ungulate populations because there were no simulated management scenarios that led to the development of a predator “pit” where low prey densities were sustained by wolf predation. These predictions were based on high prey density and assumptions regarding social limitation of wolf densities. However, substantial decreases in deer, moose, and caribou populations have occurred in other areas (e.g., Alaska, Yukon) where abundant predators, harvest of ungulates, and severe winters combined in an additive fashion (Ballard et al., 1991; Gasaway et al., 1992; Hayes et al., 2003). These limiting factors also strongly influence the population

trend of northern Yellowstone elk, which has been decreasing at a relatively high rate since 2000 (White et al., 2003). Given the lag times for surviving calves to reach prime breeding age, and the lack of any apparent numerical or functional response by wolves to an approximate 50% decrease in elk abundance, we anticipate that elk numbers will continue to decrease until levels of harvest by humans and/or predators decrease sufficiently and there is sufficient time for recruitment of calves to prime breeding age and the numerical response of wolves to decreased elk abundance. We also suspect that the abundance of elk may remain at low densities owing, in part, to predation; even if the human harvest is curtailed.

The abundance of northern Yellowstone elk was predicted to continue to fluctuate in response to winter severity, habitat condition, hunter harvest, predation, and other environmental factors following wolf recovery, but with less variation owing to potential stabilizing effects of predation and harvest (Boyce and Gaillard, 1992; Boyce, 1993). The primary factors affecting the abundance of northern Yellowstone elk during 1976–1997 were moderate to liberal harvests (mean = 1579 elk/year) of elk migrating outside the park and substantial winter-kills during 1989 and 1997 (Table 1; White et al., 2003). The population was resilient during this period and experienced relatively high growth rates following weather- and human-induced decreases in abundance. In the absence of wolves, early-winter counts of northern Yellowstone elk decreased from $\approx 19,000$ to 10,500 elk following a large winter-kill and harvest of >2000 antler-less elk during winter 1989. By 1994, however, counts had increased to $\approx 19,000$ elk. Similarly, during the early years of wolf restoration, counts decreased from $\approx 17,000$ to 12,000 elk following the large winter-kill and harvest of >2000 antler-less elk during winter 1997. By 2000, however, counts had increased to $\approx 14,500$ elk.

There has been insufficient time since the restoration of wolves in Yellowstone to evaluate if the northern Yellowstone elk population will retain this resiliency. Varley and Boyce (in press) felt that an inherent resiliency would remain in the population owing to low variation in numbers of adult females, prey switching and differential selection of prey classes by wolves, and density dependent harvests. In contrast, Messier et al. (1995) predicted that wolf predation could keep this population at low densities following a population decrease owing to stochastic weather events (e.g., winter-kill), even if the human harvest was curtailed. We believe that the resiliency of the northern Yellowstone elk population following decreases in abundance owing to predation, hunter harvest, and winter-kill will depend largely on the nature and strength of density-related responses in survival and reproduction, functional and numerical response of wolves, and use of alternate prey by wolves.

Table 1

Annual variations in estimates of elk recruitment (i.e., calves per 100 adult females), spring carcass counts, winter climate covariate (i.e., snow water equivalent), and counts of northern Yellowstone bison, elk, and wolves during winter, 1986–2004

Winter	Bison	Elk	Wolves ^a	SWE ^b	Carcasses ^c	Calves: 100 adult females
1984	482	–	0	709	–	38
1985	588	–	0	1201	–	34
1986	647	15,387	0	1117	–	30
1987	708	16,162	0	601	–	22
1988	712	18,913	0	335	–	23
1989	868	10,265 ^d	0	1039	244	6
1990	461	14,829	0	946	12	19
1991	541	9465 ^d	0	513	23	–
1992	741	12,859	0	1416	69	44
1993	570	17,585	0	1063	–	–
1994	673	19,045	0	659	15	–
1995	770	16,791	0	1187	93	33
1996	771	–	21	646	39	28
1997	877	–	24	1845	599	–
1998	518	11,736	32	721	7	22
1999	534	11,742	48	1066	9	34
2000	634	14,539	44	1109	4	23
2001	–	13,400	72	467	8	29
2002	985	11,969	77	656	7	14
2003	1044	9215	84	537	4	12
2004	1460	8335	106	901	–	12

^a Wolf abundance was estimated at the end of each calendar year during September–December. We advanced each count by one year to reflect abundance during the following year, similar to the annual elk counts. Thus, the count of 106 wolves during December 2003 was used to reflect wolf abundance during the winter and summer of 2004 (i.e., October 2003–September 2004).

^b Cumulative daily snow water equivalent from October through April (Garrott et al., 2003) estimated from temperature and precipitation records at Tower Falls CLIM station. Annual average from 1949 to 2002 was 1020 cm (minimum 335 cm, maximum 2320 cm).

^c The number of deer and elk carcasses observed during spring helicopter surveys in the low-elevation, Gardiner basin portion of the winter range for northern Yellowstone elk.

^d Count is likely a substantial under-estimate due to poor survey conditions.

Density-related decreases in reproduction, recruitment, and survival were reported for northern Yellowstone elk as abundance increased from ≈ 4000 elk in 1968 to near the estimated carrying capacity of 20,000 elk by 1988 (Coughenour and Singer, 1996; Taper and Gogan, 2002). These findings suggest that predation and other limiting factors (e.g., human harvest, climate) could indirectly contribute to higher reproductive and survival rates for elk by decreasing elk density. Thus, most models of this elk population incorporate relatively strong density-related functions for recruitment and survival (e.g., Boyce and Gaillard, 1992; Boyce, 1993; Coughenour and Singer, 1996; Taper and Gogan, 2002) that, in turn, result in predictions of higher resiliency and average abundance of elk over time.

In contrast, White et al. (2003) did not include density-related formulations in their short-term (5–10 year) projection model for northern Yellowstone elk because current abundance (i.e., 9000–12,000 elk) is well below the estimated carrying capacity of 20,000–25,000 elk. Ungulate populations tend to grow at or near their biological maximum for long periods of time, with density-dependent mechanisms only operating to slow growth when the population is close to carrying capacity (Eberhardt, 2002). White et al. (2003) did not detect higher pregnancy, survival, or recruitment rates after the sub-

stantial decrease in abundance of northern Yellowstone elk during 1994–2004. Rather, estimated survival of adult females was relatively low (0.85) compared to the survival rate of 0.99 during 1969–1975, when human harvest removals were quite low and wolves were not present (Eberhardt, 2002). Also, pregnancy rates in the prime age classes (i.e., ages 3–16) during 2000–2003 were relatively high (0.90; Cook et al., 2004) and similar to those observed over a wide range of elk densities (i.e., 1.5–9 elk/km²) prior to wolf restoration (White et al., 2003). Thus, it is unlikely that a biologically significant density-dependent increase in reproductive rates will occur due to the recent decrease in elk abundance. In addition, it is unlikely that there will be a substantial increase in the number of calves produced by the yearling age class as elk density decreases in the near future. There has been low recruitment (i.e., 12–14 calves per 100 females) for northern Yellowstone elk during 2002–2004, compared to estimates of 22–44 (mean = 29) calves per 100 females during 1990–2001. Wolves selectively prey on elk calves (Smith et al., 2004b) and, as a result, it is likely that the low recruitment observed during the past several years will continue while wolves maintain high densities.

Since the 1960s, scientists have reported spatial structuring of elk sex/age classes across the winter range for

northern Yellowstone elk, with males and older females occupying the more easterly, higher elevation areas within the park and adult females with calves and yearlings tending to migrate to lower elevation areas inside and outside the park (Houston, 1982; Coughenour and Singer, 1996; Barmore, 2003; Cook et al., 2004). The causes of this apparent spatial structuring of the population are not understood, but may include individual fidelity to seasonal movement patterns and/or age- or reproductive-specific seasonal movement patterns (White et al., 2003). Regardless, the predominant mortality forces are dramatically different for elk occupying higher-elevation winter range within the park, where wolf densities are the highest, compared to elk occupying lower-elevation winter range within and outside the park (Wright, 2003). Elk within the middle- to higher-elevation winter ranges of the park experience no measurable hunter-induced mortality, but are subject to strong predation pressure on calves and older age classes of adult female elk (i.e., median age = 16 years). In contrast, wolf densities on those areas of the northern range at lower elevations within and outside the park are modest, reducing potential for predator mortality. However, elk occupying the area outside the park during the winter have been subject to intense hunting mortality, which primarily removes prime-aged females (i.e., mean age = 8 years; Lemke, 2003; Wright, 2003).

We anticipate differences in the distribution of elk, and selection of various sex/age classes by hunters and wolves, will alter the age structure of the northern Yellowstone elk population and result in more pronounced spatial structuring of sex/age classes across their winter range. Hunting will reduce survival for all age classes of female elk and result in a relatively younger age distribution in the portion of the population that typically winters outside the park. This effect will decrease as antler-less harvests are reduced. In contrast, the portion of the population that typically winters at higher elevations inside the park, where it is not exposed to hunting, likely had considerably higher survival prior to wolf restoration. Thus, this portion of the population likely developed an older age structure, with a larger proportion of animals in the senescent age classes that are more susceptible to predation. We expect that selective predation by high densities of wolves on senescent elk and calves will eventually concentrate the age structure of the portion of the population that remains within the park in the middle age classes.

We do not expect wolves to change their strong preference for elk calves during winter (Smith et al., 2004b). Thus, predation pressure on calves will remain high on higher-elevation winter range within the park, where wolf densities are the highest. Conversely, calf survival may increase somewhat outside park, where wolf densities are relatively low. This differential survival and recruitment of calves among areas of the winter range

could eventually result in higher survival for calves wintering at lower elevations where wolf density is relatively low, and little recruitment of calves wintering at higher elevations where wolf densities are relatively high. If calves demonstrate fidelity to their winter range, and higher calf survival at lower elevations is sustained over time, then the proportion of the northern Yellowstone elk population that typically migrates to lower elevations inside or outside of the park during winter will increase.

4. Wolf impacts on other ungulates

Wolves were not expected to have substantial effects on ungulates other than elk (Boyce and Gaillard, 1992; Boyce, 1993; Mack and Singer, 1992, 1993). To date, this prediction has been realized with elk comprising $\approx 92\%$ of wolf diets in Yellowstone. Bighorn sheep comprised $<0.5\%$ of total wolf kills in Yellowstone during 1995–2003 (Smith et al., 2004a) and numbers have varied within 10–20% of the count observed when wolves were reintroduced (Northern Yellowstone Cooperative Wildlife Working Group, 2003). Moose represent $<4\%$ of wolf diets in winter and only 26 instances of wolf predation on moose were recorded in Yellowstone during 1995–2003 (Smith et al., 2003). Only two mountain goat kills have been recorded since wolf restoration (Smith et al., 2003) and the relative abundance and distribution of mountain goats has continued to increase (Lemke, 2004).

Boyce (1993) predicted a decrease in abundance of at least 10–15% for mule deer following wolf restoration. However, Mack and Singer (1992, 1993) predicted that the abundance of mule deer on the northern range of Yellowstone could increase up to 36% in the presence of wolf predation, if the antler-less deer harvest were eliminated. Since wolf restoration, there has been no apparent trend in mule deer numbers on their winter range in the Gardiner basin inside and outside Yellowstone. Spring counts of this population varied between 1600 and 2500 deer during 1995–2003, and the 2003 count of 2023 deer was similar to the 17-year average of 2014 deer (Northern Yellowstone Cooperative Wildlife Working Group, 2003). Mule deer migrate out of the park during winter to areas where wolf density and use are relatively low. Thus, deer likely escape some of the most intense wolf predation during winter. The extent of predation on deer by wolves during summer is unknown.

Wolves were expected to reduce the abundance of Yellowstone bison by $<15\%$ (Boyce and Gaillard, 1992; Boyce, 1993). Approximately 3400 bison were counted during the winters of 1996 and 1997, at the onset of wolf restoration. The count decreased to ≈ 2100 bison during the winter of 1998 following the removal

of 1084 bison during the previous winter, but then increased to more than 4000 animals during 2003. Thus, the growth rate of the bison population during 1998 through 2004 averaged $\approx 15\%$ per year after accounting for removals.

Bison comprised $<1\%$ of wolf kills on the northern range and 4% park-wide during 1995–2000 (Smith et al., 2004b). Wolves have begun to exploit the abundant bison population in some interior portions of park, however, even though bison are more formidable, risky prey for wolves than elk. One wolf pack in Pelican Valley utilizes bison in late winter when they are vulnerable and migratory elk are unavailable (Smith et al., 2000). Also, bison comprised $\approx 20\%$ of the total wolf kills in the west-central portion of Yellowstone during three of five years, 1999–2003 (Robert Garrott, Montana State University, unpublished data). Thus, wolves could potentially increase their selection of bison over time or in other areas (e.g., northern range), especially if elk densities decrease substantially. Significant wolf use of bison could alter the effects of predation on elk and have substantial effects on predator–prey interactions and trajectories of the prey populations. For example, a change in preference from elk to bison by wolves could lead to stability and persistence of both bison and elk populations, with elk abundance at some level below that documented when wolves were absent from the system. However, if wolves maintain a strong preference for elk when they are at low densities, but exploit abundant bison as alternate prey, then the elk population could be driven towards very low densities (Robert Garrott and Steven Kalinowski, Montana State University, unpublished data).

Another possible scenario is that wolf restoration could actually contribute to increased bison abundance on the northern range of Yellowstone by decreasing elk abundance. During 1966–1988, which was a period of infrequent and relatively small removals, the abundance of bison in the northern and central populations increased exponentially from <100 and 230 animals, respectively, to ≈ 700 and 2400 animals. The rate of increase for the northern population was lower than the central population, despite similar amounts of bison habitat (e.g., sedge meadows, grasslands) among areas. This suggests that the northern range could apparently support higher bison densities. During 1989–1995, the central bison population continued to increase exponentially to ≈ 3400 animals, whereas the northern population varied between 400 and 900 animals owing to substantial winterkills and regular removals of bison attempting to migrate outside the park during winter. We speculate that the lower densities and increased dispersal attempts by bison on the northern range were due, in part, to inter-specific competition with elk, which increased in abundance from ≈ 4000 to 20,000 animals during 1968–1988 (Coughenour and Singer, 1996; Taper

and Gogan, 2002). There were ≈ 33 elk per bison wintering on the northern range during 1986–1988 (Singer and Norland, 1994), compared to ≈ 0.2 elk per bison wintering in the west-central portion of the park (Robert Garrott, Montana State University, unpublished data). There is substantial dietary and habitat overlap between bison and elk on the northern winter range, with $>80\%$ of both herbivores diets comprised of grasses and sedges (Singer and Norland, 1994). Thus, we anticipate that bison densities will increase on the northern range as elk densities are reduced; unless wolves begin to significantly exploit the bison population and/or substantial removal efforts occur along the park boundary.

Wolf predation on pronghorn appears to be insignificant, comprising $<0.5\%$ of total wolf kills in Yellowstone during 1995–2003 (Smith et al., 2004a). However, coyotes are a significant limiting factor for Yellowstone pronghorn, contributing to substantial fawn mortality and decreased recruitment (J. Byers, University of Idaho, unpublished data). Coyote densities were relatively high (i.e., 0.6 per square kilometer) in areas utilized by pronghorn prior to the mid-1990s; particularly in summer range areas (e.g., Lamar Valley). However, wolves kill coyotes through inter-specific aggression, and have purportedly reduced the resident coyote population by approximately one-half (i.e., 0.3 per square kilometer) in some areas of the pronghorn range (Crabtree and Sheldon, 1999). This decline should be placed in the context of pre-wolf coyote density which increased 32% (i.e., mean pack size went from 4.6 to 6.8 coyotes) prior to wolf reintroduction (Gese et al., 1996a,b). Thus, the decrease in coyote numbers (i.e., mean pack size went from 6 to 4 coyotes) documented by Crabtree and Sheldon (1999) occurred after a large increase in coyote numbers. In contrast, coyote numbers increased in northwestern Montana as wolf recovery occurred, with coyote social organization changing from singles and pairs to pairs and small packs (Arjo and Pletscher, 1999). Thus, the restoration of wolves could possibly contribute to higher recruitment of Yellowstone pronghorn if total coyote densities (residents and transients) are substantially reduced in fawning and neonatal areas. However, coyotes have the ability to compensate for high mortality rates via higher reproduction and recruitment via reduced dispersal as more pups remain philopatric with reduced intraspecific competition and increased carcass availability (Knowlton, 1972; Davison, 1980; Gese et al., 1996a,b; Knowlton et al., 1999). Coyote populations are generally regulated by environmental conditions (e.g., food supply) even when 40–50% of the coyotes are killed annually (Connolly, 1978; Knowlton et al., 1999). Thus, intensive and persistent reductions would be needed to reduce coyote numbers and predation significantly and coyote populations can recover quickly from heavy exploitation (Connolly, 1978; Knowlton et al., 1999).

It is uncertain whether wolf-induced mortality of coyotes has been high enough to reduce coyote densities to levels where predation on pronghorn fawns would be significantly reduced.

During 1999–2003, $\approx 65\%$ of Yellowstone pronghorn left the Gardiner basin winter range in spring and migrated to higher elevations within the park to summer, where wolf densities were relatively high and, as a result, coyote densities have purportedly decreased. The remaining Yellowstone pronghorn were non-migratory and fawned in the Gardiner basin where wolf densities were lower and coyote densities were believed to be higher. During 1999–2001, there appeared to be differential survival of pronghorn fawns among areas, with relatively higher survival in fawning areas used by migratory pronghorn compared to non-migratory pronghorn (Boccadori, 2002; J. Byers, University of Idaho, unpublished data). This corresponds to a trend for higher fawn survival in areas where wolf densities are relatively high and coyote densities are believed to be relatively low. If this differential mortality between fawning areas is sustained over time, then it could eventually result in a reduction in the non-migratory portion of the population if migratory animals demonstrate fidelity to their summer range. A study of the ecological interactions among wolves, coyotes, and pronghorn was recently initiated in Yellowstone to investigate this issue in more detail.

5. Wolf impacts on elk harvests

Northern Yellowstone elk that migrate out of the park may be legally harvested during four hunts managed by the Montana Department of Fish, Wildlife, and Parks. The archery, early season backcountry rifle, and general autumn rifle hunts occur during September through November and are focused primarily on bulls. Few adult females are harvested because these hunts typically occur prior to the winter migration of northern Yellowstone elk. The late season rifle hunt has occurred during December/January (1976–1991) or January/February (1992–2004), and is highly biased towards harvesting females because its primary objective is to help regulate the number of elk that winter north of Yellowstone at levels that will sustain winter habitat (Lemke, 2003).

One of the major concerns regarding wolf recovery in Yellowstone was that predation would substantially reduce the abundance of hunted ungulates, especially elk. Boyce and Gaillard (1992) projected up to a 10% decrease in hunter harvests in the greater Yellowstone area, but did not expect significant consequences of wolf recovery to the harvest of northern Yellowstone elk in Montana given the continued issuance of ≈ 700 annual permits for the late season hunt. Mack and Singer

(1992) assumed that the harvest of northern Yellowstone elk would be reduced by about 27% for antler-less elk (i.e., from an average of 994–714 per year) after the wolf population reached the recovery level (i.e., 100 wolves in 10 packs).

Harvests were not initially reduced in a density dependent manner following wolf restoration to compensate for additional off-take by wolves. Rather, the number of antler-less permits during the late season hunt was maintained between 2660 permits in 1995 and 2882 permits in 2000, when wolves reached their biological recovery level in Yellowstone (U.S. Fish and Wildlife Service, 2004). Thus, antler-less elk harvests removed an increasing proportion of elk as total elk numbers (inside and outside the park) decreased during 1990–2002. This harvest regime significantly decreased the survival rates of prime-aged females with high reproductive value and, in turn, the growth rate of the population. Snow pack strongly influenced elk vulnerability to hunting through its effects on the number of animals migrating outside the park and hunter success (National Research Council, 2002; White et al., 2003). The number of elk migrating outside the park was directly proportional to snow water equivalent and harvests were directly proportional to the number of elk wintering outside the park. Hunter success exceeded 95% during years with high levels of snow water equivalent prior to and during the late hunt, compared to a mean hunter success of 64% during 1976–2004 (Lemke, 2003).

White et al. (2003) concluded that the continuation of hunting levels set under an abundance of elk (e.g., $\approx 17,000$ elk prior to wolf restoration), in combination with severe winters, recovery of wolf numbers, and off-take by multiple predators, contributed to a 6% per year decrease in the northern Yellowstone elk population during 1995–2004. Similarly, Vucetich et al. (2004) concluded that the harvest was “super-additive”, with elk population growth decreasing by more than 1% for each 1% increase in harvest rate. Thus, White et al. (2003) concluded that the current abundance of northern Yellowstone elk (9000–12,000 elk in winter 2004) could not support moderate or liberal human harvests of prime-aged adult females, even if wolf off-take was relatively low (i.e., ≈ 1000 elk per winter). In contrast, Varley and Boyce (in press) projected that the mean annual elk harvest would decrease by 12% following wolf recovery, but hunter kill could be sustained over time at an average of ≈ 1000 elk per year. They also suggested that permitting a larger bull harvest would allow overall harvest to increase.

The disagreement over whether sizeable harvests can be sustained on the northern range may depend on how the hunt is administered. Varley and Boyce (in press) assumed that harvests were density dependent, with proportionately fewer elk being harvested at lower elk densities. Due to the strong influence of snow pack on

migration and hunter success, however, harvests of elk migrating north of the park were essentially frequency dependent during 1990–2002, with a relatively high and constant proportion ($27 \pm 5\%$) being harvested regardless of density (White et al., 2003). If this pattern continues, then harvests could accelerate the decrease in elk abundance. However, the Montana Department of Fish, Wildlife, and Parks gradually reduced antler-less permits for the late season hunt from 2882 permits in 2000 to 1400 permits in 2004 owing to decreasing abundance and low recruitment (Lemke, 2003). The 2004 permit level for the late season hunt resulted in a legal harvest of 702 elk, or 6% of the estimated population. This annual harvest was close to the predicted level of 714 northern Yellowstone elk harvested per year after the wolf population surpassed 100 animals (Mack and Singer, 1992). In addition, the Montana Department of Fish, Wildlife, and Parks has indicated that future harvest levels may be substantially reduced in a density dependent manner to partially offset elk losses due to predation, while still attempting to meet population- and habitat-related objectives on winter ranges north of Yellowstone (Lemke, 2003).

6. Long-term effects on ecological relationships and ecosystem function

Northern Yellowstone elk have inspired one of this century's most productive, if sometimes bitter, dialogues on the management of a wild-land ecosystem. For more than 50 years prior to wolf restoration, this debate focused on whether there were too many elk and the effects of grazing by these elk on vegetation communities, especially deciduous woody species. For example, willow (*Salix* spp.) communities on Yellowstone's northern ungulate winter range decreased 60% during the 80 years prior to wolf restoration and $\approx 47\%$ of the willow patches existed in a height-suppressed form (≤ 80 cm tall) due, in part, to heavy browsing by ungulates (Singer et al., 1994). Other factors involved in the willow decrease may include periods of arid climates that have occurred this century, beaver declines, and stream channel changes (National Research Council, 2002). Critics of the park's ungulate management policies, however, attributed the decrease of aspen (*Populus tremuloides*), cottonwoods (*Populus* spp.), and willows primarily to high densities of elk resulting from the park's natural regulation policy for ungulates (e.g., Kay, 1990; Beschta, 2003).

Since the restoration of wolves in Yellowstone, biologists have speculated that wolves could contribute to a "trophic cascade" of ecological changes such as alterations in species abundance or composition, nutrient concentrations of plants, and the physical structure of the vegetation and environment. Smith et al. (2003) pre-

dicted that these indirect effects of wolf recovery would be substantial and reverberate through the ecosystem. Trophic cascades occur when shifts in the biomass or abundance of species positioned at a high level in a food web exert effects on the biomass, productivity, or composition of species more than one level below. There are two primary mechanisms by which the effects of wolves could be indirectly transmitted to woody vegetation (e.g., aspen, willow) and other species in Yellowstone. First, wolf predation could result in decreased abundance of elk and, in turn, a reduction in the intensity of herbivory. Second, elk could respond to the increased risk of predation by wolves with anti-predator behaviors that alter their spatial and temporal distribution, group sizes, movements, and browsing patterns. For example, if the risks posed by predation cause elk to alter their patterns of habitat selection, then trophic effects may be manifest in shifts in the location of herbivore effects. At a finer scale, predation risk may compel elk to feed on different plants or plant parts to minimize time spent foraging and exposure to wolves and other predators. These behavioral shifts would intensify herbivory effects on some plant communities or patches and attenuate effects on others.

There are some indications that elk–wolf interactions in Yellowstone are contributing to a "release" of woody vegetation on the northern range from the effects of herbivory. The proportion of aspen, cottonwood, and willow leaders browsed in stands on the northern range decreased substantially in some areas after wolves were restored. There were also significant increases in cottonwood and willow heights, suggesting that at least some stands experienced release from herbivory (Ripple and Larsen, 2000; Ripple and Beschta, 2003; Francis Singer, U.S. Geological Survey, unpublished data). There were substantial spatial and temporal heterogeneity in these measurements, however, with apparently strong effects in some locations and weak or no effects in others. Also, there was an apparent increase in the diameters of twigs browsed, even though a large proportion of the twigs on a plant remained unbrowsed (Tom Hobbs, Natural Resource Ecology Laboratory, unpublished data).

Though it is enticing to credit wolf restoration for these apparent trophic cascade effects, we caution against leaping to absolute conclusions at this time. The circumstantial observations of woody vegetation release on some areas of the northern range of Yellowstone do not substantiate any effect of wolves because no cause and effect relationships have been demonstrated. Numerical effects (i.e., decreased elk abundance and herbivory) take time to develop because of lags in effects of predation on elk population dynamics. Thus, the extent of the observed release of woody vegetation may be greater than can be explained solely on the basis of numerical responses of the elk population to predation; especially given the relatively brief interval (i.e.,

2000–2004) since the abundance of wolves reached a level where they are contributing substantially to decreased elk abundance. Anti-predator effects can manifest relatively quickly in heterogeneous landscapes such as Yellowstone that enable elk to express a high degree of selectivity in their behaviors. Monitoring to date suggests that wolves are altering the vigilance, movements, spatial and temporal distribution, and group sizes of elk (Mao, 2003; Ripple and Larsen, 2000; Ripple et al., 2001; Bergman, 2003; Childress and Lung, 2003; Ripple and Beschta, 2003, 2004; Creel and Winnie, *in press*; Gude, 2004; Fortin et al., *in press*). These anti-predator responses likely entail costs (e.g., increased energy expenditure, reduced foraging efficiency) that could decrease fecundity and survival and have complex effects on population dynamics, depending on the effectiveness with which behavioral responses reduce predation rates. However, no one has quantified these costs or convincingly explained how changes in elk movements following wolf restoration have caused the observed distribution of woody vegetation release across the entire spatial extent of the northern range. Also, no one knows if wolf effects on elk movements will be consistently maintained over time. If wolves change their activity patterns over the landscape in response to the redistribution of prey, then the observed increases in woody vegetation biomass may be ephemeral (Fortin et al., *in press*). Continued research is needed to address the interactive effects of climate, hydrology, wolf predation/avoidance, and herbivory on the growth and persistence of woody species in Yellowstone. In addition to predation risk and the costs of anti-predator behaviors, these analyses should consider variables such as weather, water table levels, snow pack and its effects on ungulate distribution and abundance, effects of decreased moose abundance and browsing, and changes in the proportion of elk migrating to lower elevations outside the park since 1989 (White et al., 2003).

7. Conclusion

The initial consequences of wolf recovery in Yellowstone support the premise of Soule et al. (2003) that wolves are a highly interactive species that may naturally achieve densities that contribute to significant changes in ecosystems. The functional and numerical responses of wolves, as well as their estimated off-take, exceeded pre-wolf restoration predictions by a substantial margin. Thus, restored wolves rapidly attained and exceeded predicted population densities in Yellowstone which, in turn, contributed to rapid changes in the demographics and population dynamics of elk, their highly preferred prey. Counts of northern Yellowstone elk have decreased more than predicted, and counts will likely continue to decrease in the near future given the

strong preference of wolves for elk and the high kill rates.

The Yellowstone system will likely adjust for decades following wolf restoration. Thus, it is uncertain if the initial functional and numerical responses of restored wolves represent an irruptive pattern, in which wolves overshoot equilibrium levels, or a density that can be supported given the current abundance of ungulate prey. If elk abundance on the northern range of Yellowstone continues to decrease during the near future, however, then the change to the system will almost certainly lead to the amelioration of any ungulate-caused landscape simplification such as the decreased riparian habitat, beaver wetlands, and aspen recruitment (Singer et al., 1994; Ripple and Larsen, 2000; Maschinski, 2001; Ripple et al., 2001; Beschta, 2003). It is also likely that wolf recovery will eventually contribute to persistent changes in the relative abundance, distribution, and behavior of other ungulate species (e.g., bison) that can be ecologically dominant and have particularly strong, ramifying interactions in the Yellowstone system (i.e., “foundations species” per Soule et al., 2003:1239).

The long-term preservation of Yellowstone requires scientific information about populations and the ecological processes upon which sustainable ecosystems depend. Predictions of the consequences of wolves on northern Yellowstone elk based on data collected to date range from the effects of wolves on elk being almost entirely compensatory (Vucetich et al., 2004) to substantially additive (White et al., 2003). Likewise, predictions of trends in elk abundance following wolf recovery range from elk being maintained at low densities (i.e., <6000–7000 elk; Messier et al., 1995) owing, in part, to predation to elk numbers fluctuating around a mean of $\approx 10,000$ elk with long-term oscillations (Varley and Boyce, *in press*). There is also disagreement on the relative influence of human harvests on elk population dynamics, with some authors suggesting that harvests have accelerated the decrease in elk abundance and calling for further reductions in permits (White et al., 2003; Vucetich et al., 2004), while other authors suggest that harvests averaging ≈ 1000 elk per year can be sustained over time if harvest regulations are implemented in a density-dependent manner (Varley and Boyce, *in press*). The relative importance of, and interactions between various factors (e.g., climate, harvest, predation) that may limit or regulate the abundance of northern Yellowstone elk may become more apparent over time as the functional and numerical responses of wolves change in response to elk density, the harvest is further reduced, the current 7-year drought ends, and severe winters periodically occur. Thus, it is imperative that monitoring and research regarding the ecological implications of wolf recovery on Yellowstone’s ungulates continue uninterrupted to elucidate the long-term effects of this relatively unique, systems-level restoration.

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