Chapter 5

Interactions Between Wolves and Elk in the Yellowstone Ecosystem

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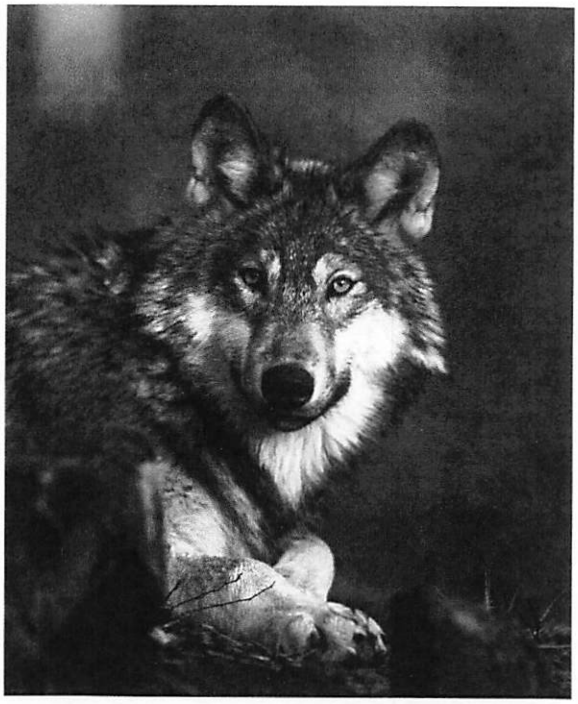
Yellowstone National Park is unique in the lower 48 states of America for two main reasons. First is its geology, which has always been unusual. Second, it holds the entire suite of large carnivores that were present at the end of the Pleistocene (11,000 years ago) together with healthy populations of large prey such as elk and bison.



▲ PHOTO 5.1 The reintroduction of the Grey Wolf to the Yellowstone ecosystem has been remarkably successful. Between 400 to 450 wolves currently occupy the Greater Yellowstone Ecosystem. This mature wolf may tip the scales at 40 Kg and live as long as 8-10 years. (U.S. Fish and Wildlife Service).

Yellowstone was not originally unusual in this regard, but increasing numbers of people and their increasing levels of consumption have rapidly and effectively squeezed wildlife off of most of the American landscape. Worldwide, when human populations expand, wildlife populations inevitably contract. For two main reasons, one ecological and one sociological, large carnivores like the wolf or the African wild dog are typically among the first to go. Ecologically, large carnivores require large areas with intact prey populations, which in turn require suitable habitat. The range of a wolf pack can easily be several hundred square kilometers, and a viable population requires many packs.

Sociologically, large carnivores often face active persecution, due to potential conflicts with people and their livestock. Despite its status as the world's first legally gazetted national park, Yellowstone has not been immune to the second process. As part of a national program of eradication, the last known wolves in Yellowstone were killed in 1924, and with them, the wolf was effectively extinct in the US portion of the Rocky Mountains. Following an absence of seven decades, 14 wolves in three packs were released inside Yellowstone in 1995, together with a release of 15 wolves in central Idaho. The following year, 16 more wolves were released in Yellowstone. Wolf recovery, and the slower but overlapping recovery of Grizzly bears over recent decades, has restored the Greater Yellowstone Ecosystem to a condition that is rather unusual for ecosystems in developed nations, with ecologically functional populations of all of the extant large carnivores native to the region at the end of the last ice age.

In addition to its intrinsic value to Yellowstone wilderness, recolonization of the wolf creates an unusual opportunity to understand the function of a terrestrial ecosystem subject to 'top-down' effects that are initiated at the apex of the food web. This statement should not be read to imply that wildlife populations in Yellowstone are regulated solely by natural processes outside of the activities of humans; humans have strong effects on the ecological processes of Yellowstone (as with virtually all modern ecosystems) and the policy of allowing 'natural regulation' of wildlife populations within the park was only adopted in recent decades - not long in ecological terms. Additionally, processes outside the park inevi[tably] have influences inside the park. For example, most elk migrate out of the park and are exposed to harvest during the hunting season. Bison are trapped and killed in large numbers, with more than half of the population slaughtered in the winter of 2007 - 2008 (as part of a poorly conceived response to the presence of *Brucella* in several species, including the far more abundant and wide-ranging elk). Humans remain the most common cause of death for wolves and bears, but my focus here is on the strong and complex interactions between wolves and elk, where each has dominant limiting effects on the other.

Wolf and Elk Recovery in Yellowstone

As with most reintroductions of large carnivores, wolf reintroduction was controversial. Attention was focused on evaluation of its probable consequences. Since the reintroduction, considerable effort has gone into research to directly measure ecological responses. Prior to the reintroduction, three concerns were commonly expressed. First was the fear of attacks on humans. No such attacks have occurred, which is not surprising, given the long record of human-wolf interactions elsewhere. For example, there are more than 3,900 wolves in Minnesota, Wisconsin and the upper peninsula of Michigan, which is more than triple the size of the Rocky Mountain population (as of December 2006), and these wolves have occupied the Great lakes region for decades with no attacks on humans.

Second was concern about predation on livestock, particularly sheep and cows. As expected, wolf packs that establish ranges outside of wilderness areas have come into conflict with animal agriculture. Predation on sheep is patchy, but local losses can be substantial, particularly when sheep graze high-elevation pastures on public land, with little human presence to dissuade wolves from occupying the area. Predation on cattle is also patchy, but is most common in low elevation grasslands in river valleys where elk congregate in winter. If a wolf pack occupies such an area in the winter, it is likely to produce pups shortly before elk migrate to high elevation summer ranges, leaving the wolves with a local prey base that is suddenly dominated by cattle. Largely as a result of situations like this, human-caused mortality takes more than one-fifth of Montana's wolf population each year, mainly through predator-control operations in response to predation on livestock. Despite these genuine conflicts, wolf predation on livestock in the region has remained low relative to other causes of death (<1% of all livestock losses in the northern Rockies, according to the U.S. Fish and Wildlife Service), and the wolf population has grown numerically and expanded geographically.

The third concern, which has proved well founded, focused on the potential impact of wolf predation on elk populations. Although the causes are very different, Rocky Mountain elk and wolf populations have followed similar trajectories over the last 200 years, both driven by humans. While people were intentionally eradicating wolves and other predators, they were simultaneously (though unintentionally) eliminating elk through over-hunting. Where the journals of Lewis and Clark described herds of thousands, elk had dwindled to only seven relict populations in the entire state of Montana by the turn of the 20th century. Beginning in the early 1900s, programs to reintroduce elk into their former range and to promote population growth allowed elk to recover in the Yellowstone area and elsewhere. By the turn of the 21st century, elk were widely distributed in mountainous areas, and had attained high densities in many places, including the Greater Yellowstone Ecosystem (GYE).

Like almost everything in the conservation and management of large animals in the United States, the return of the elk was attended by complications and controversies. While most hunters favored policies that maintained large numbers of elk, others argued that the Yellowstone population had grown so dense that it was altering the plant community on which it depended. Others noted that by feeding hay to elk in winter, elk populations were kept artificially large, potentially exacerbating conflict with ranching. This is a major catch-22, because the current intention of winter feeding (in the Wyoming portion of the GYE) is not to increase elk numbers, but to keep elk from aggregating on ranches and competing with cattle for food. Finally, in response to clumped food sources, elk cluster at atypically high densities on feed-grounds, thereby creating conditions that may promote the transmission and persistence of brucellosis within the elk herd. *Brucella* infection can induce abortion in cattle (particularly in first-time breeders), so the persistence of *Brucella* in Yellowstone wildlife has become an economic issue, necessitating testing and vaccination programs for cattle. Although the elk population was originally infected by cattle, subsequent vaccination programs have eradicated *Brucella* from the US outside the Yellowstone region.

As these complex, intertwined issues illustrate, there is no widespread consensus on the number of elk that is desirable for the Yellowstone ecosystem; the desired outcome depends on the value that different individuals place on different things. Of course, from the perspective of ecosystem function, adjectives like 'desirable' do not have to enter the analysis. An ecosystem shifts among states through time in a manner that depends on the interactions of the species that are present. There may be equilibrium points to which the system tends to return, provided that driving forces like the climate remain relatively constant, but the modern view is that ecosystems are dynamic, and their state depends on multiple factors, from predator-prey ratios to wildfire and drought.

▲ PHOTO 5.2 This elk calf was born in the Gallatin Canyon portion of the Greater Yellowstone Ecosystem. The presence of wolves leads to broad changes in elk grouping, foraging behavior, habitat selection, diet, and nutrition. These "risk effects" are associated with a decrease in the progesterone levels of female elk during gestation and therefore reduced calf production. (David Christianson)

From the perspective of ecology, the dominant question with respect to wolf reintroduction was, and still is: "How will the addition of wolves alter the elk population, and what consequences will responses by the elk have for other species?" Ecological experiments like a large-scale wolf reintroduction are rare, so it is interesting to go back and consider what answers were offered to this question prior to the reintroduction, how those answers compare to the outcomes that have been observed thus far, and what we have learned.

Wolf Recovery

In terms of rapidly establishing an ecologically functional predator population in a large area, wolf reintroduction in the GYE has been a success. From the release of 31 individuals in 1995 and 1996, the GYE population grew to 376 individuals in 31 breeding packs by December 2006. Geographically, the population expanded to include portions of Wyoming, Montana and Idaho. The Northern Rockies population held 1,243 known wolves and 90 breeding packs at the end of 2006, which constituted 24% of the 5,251 known wolves in the lower 48 states. The Mexican Gray Wolf population in Arizona and New Mexico held only 59 individuals, and the remaining 3,949 wolves were in the Great Lakes population. In addition, Alaska held an estimated 6,000 to 7,000 wolves. In one decade, the recovery of wolves in Central Idaho and GYE has had a substantial effect on national wolf numbers, and particularly on their geographic distribution.

Predicted Responses of Elk Numbers to Wolf Recovery

Prior to wolf reintroduction, there was not complete unanimity about the likely effect on Yellowstone elk numbers, but the most widely-accepted prediction (from the National Park Service's environmental impact statement) was based on the well-studied Northern Range herd, and predicted a decline of 5% - 30%. At the time of reintroduction, the National Park Service summarized this consensus view as follows:

Gray wolves are being restored, but not because park managers think the wolves will "control" the number of elk. Instead, fifteen North American wolf experts predict that 100 wolves in Yellowstone would reduce the elk by less than 20%, 10 years after reintroduction. Computer modeling of population dynamics on the northern winter range predicts that 75 wolves would kill 1,000 elk per winter, but that the elk would be able to maintain their populations under this level of predation, and with only a slight decline in the level of hunter harvest.

In the 1970s, other authors had also argued that predation by wolves would be largely compensatory, meaning that wolves would kill elk that would have died anyway, or that the rates of survival and reproduction of the survivors would improve due to reduced competition for food. In these authors' view, wolves were not predicted to reduce the elk population appreciably. At the other extreme, several authors noted that wolf predation has stronger effects on the dynamics of their dominant prey in ecosystems with multiple predators (such as grizzly bears and mountain lions), and predicted that elk numbers would decline by as much as 50%.

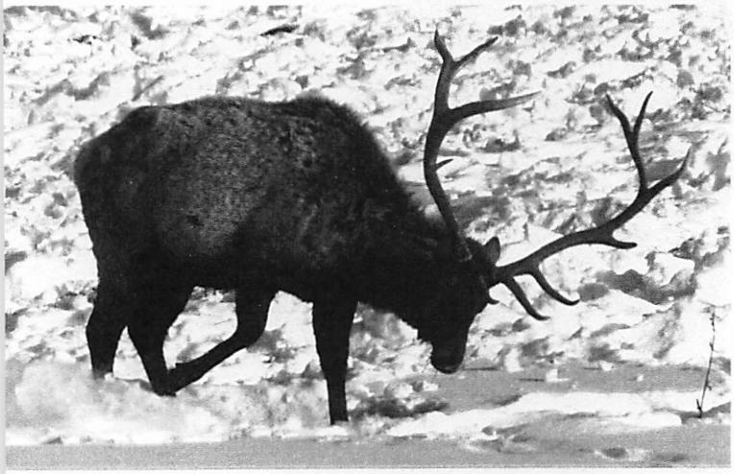
Actual Responses of Elk Numbers to Wolf Recovery

By the winter of 2007 - 2008, elk numbers had declined farther than predicted by any of these studies. The northern range herd has steadily declined from approximately 17,000 in 1995 to less than 7,000 in 2006, a reduction of 60%, or triple the consensus prediction of a 20% decline. Elk in the small, nonmigratory Madison-Firehole population in the center of the park have declined by more than 60%. Elk in the Gallatin Canyon have also declined significantly since 1995, from around 1738 to around 1101 - a 37% reduction. These patterns are striking, but when evaluating population trends, one must keep in mind that no species is limited exclusively by a single factor, and elk are not limited only by wolves. Consequently, one must consider the possibility that the strength of other limiting factors might have increased during the same period. This question has seen considerable attention, and some authors have suggested that predation by wolves is not likely to be the primary cause of the decline, which they attribute to a combination of dry weather and 'supercompensatory' effects of human harvest, in which each elk harvested causes the population to decline by more than one individual.

However, most data suggest that wolf predation is the dominant ecological process driving the decline of Yellowstone elk. First, there is the observation that elk constitute approximately 90% of the prey taken by GYE wolves, and wolves account for more than 90% of the observed predation on adult elk. Grizzly bears also take a substantial number of newborn elk, but bear predation is rare for elk older than a few months. Second there is the abrupt nature of the decline, it's timing, and its relation to trends in elk populations outside of the wolf recovery area. For several decades prior to 1995, elk numbers were rising in the GYE, as in the rest of Montana. Elk populations in areas of Montana with little wolf presence have mostly continued their growth, and many Elk Management Units in Montana are now well above their target population sizes. Overall, there are now more elk in Montana than at any time since the late 1800s. This pattern contrasts sharply with population trends for GYE elk, and strongly suggests that general climatic trends have been favorable for elk in the years since 1998.

Considered mechanistically, it is not surprising that the span of dry years coinciding with wolf recovery has been climatically favorable for elk. A great deal of research shows that winter starvation is a strong limiting factor for elk, and that the strength of this effect is dependent on the severity of winter snowfall. Yellowstone elk feed primarily by grazing on grasses, rather than browsing woody vegetation. Yellowstone elk lose body mass steadily during the winter, and this negative energy balance is exacerbated by long winters with deep or heavy snow. In contrast, recent variation in levels of summer rainfall does not appear to cause enough variation in the amount of grass available to have much effect on elk numbers. Overall, the benefits of low-snow winters have been stronger than the costs of low-rain summers. As an aside, it is notable that most climate models predict increased precipitation for the Northern Rockies, but less snow accumulation due to warmer temperatures. If this pattern does emerge, one would expect elk populations to increase. Whether these changes will be enough to offset the effects of wolf predation will be an interesting research question for the future.

Many Yellowstone elk migrate out of the park to lower elevation winter ranges, and are consequently exposed to human harvest. Thus, changes in the pattern of human harvest could potentially explain the decline in GYE elk since 1995. While human harvest does contribute to elk mortality, harvest levels in the GYE have declined substantially since 1995, rather than increasing. General hunting season quotas established by the Montana Department of Fish Wildlife and Parks have been reduced for Elk Management Units in the GYE, and late season population control hunts of antlerless elk in units directly north and west of the park have been reduced by more than half, or closed altogether. This pattern of reduced harvest is in contrast to many Elk Management Units outside the core wolf recovery area, where quotas have been liberalized, hunting seasons have been extended, and the state is actively promoting increased harvest to limit ongoing elk population growth (at a statewide rate of 2.8% annually).



▲ PHOTO 5.3 Elk consume large amounts of energy as they use their hooves and muzzles to dig craters in loose snow to expose dry grass and leaves. When the snow gets too deep or develops a layer of hard crust, they are likely to shift their feeding to less nutritious woody twigs. When wolves are present they relocate into timber to avoid detection, again shifting to a diet with a high proportion of woody browse. (Scott Creel)

Grizzly bears are capable of killing adult elk, but they obtain meat mainly by scavenging winter-killed elk when they emerge from hibernation and by predation on newborn elk. In the first few weeks of life, elk calves remain stationary and hidden while the mother is away, and bears are the most common predator of Yellowstone elk during this 'hiding' period. Grizzly bears have been increasing in the GYE over the period of wolf recovery. For the ecosystem as a whole, it is likely that the limiting effect of bears is stronger now than it was when wolves were reintroduced in1995. However, this change in bear numbers began many years before the elk trajectory shifted from growth to decline, and changes in bear numbers since 1995 have been relatively small in comparison to the 12-fold increase in the number of wolves. Moreover, the increase in the size of the GYE bear population is mostly due to geographic expansion and increased bear numbers on the periphery of the ecosystem, while grizzly bear density in the core of the ecosystem (where elk have declined most) has changed little, if at all, since 1995. In addition, Yellowstone wolves have largely been specialists on elk, while grizzly bears are omnivores whose diets include many elements other than meat. For these reasons, grizzly bear predation is not likely to have increased enough to be a large driver of the changes in elk population dynamics.

To summarize, GYE elk populations have declined substantially since 1995, while wolves have increased by a factor of 12. The observed decrease in elk numbers was larger than expected, and is not well-explained by ecological limiting factors other than wolves. These observations raise an interesting question that must be answered if ecology is to become a better predictive science: why was the effect of wolf predation on elk dynamics larger than anticipated?

Direct Predation and Risk Effects

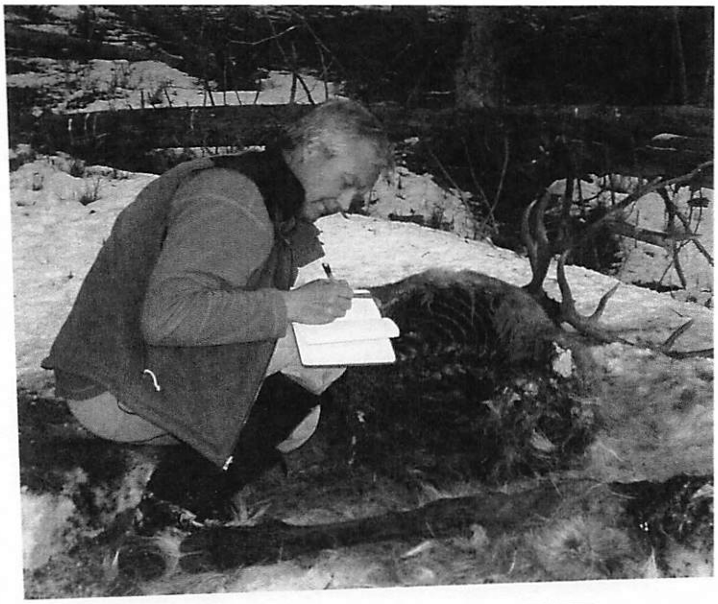
Why was the observed effect of wolf recovery on elk dynamics larger than anticipated? To address this question, reconsider the Park Service's summary of the pre-reintroduction environmental impact statement:

Fifteen North American wolf experts predict that 100 wolves in

Yellowstone would reduce the elk by less than 20%, 10 years after reintroduction. Computer modeling of population dynamics on the northern winter range predicts that 75 wolves would kill 1,000 elk per winter...

In my opinion, 'kill' is the single most important word in this statement, because it reveals the logical structure of the mathematical models of predation that were used to evaluate the likely impact of wolves on elk. In essence, these models assumed that the population growth rate of elk would depend on the population's size (with competition for food slowing growth as the population increased), minus some number of individuals that were eaten by wolves. At first glance, this seems a very reasonable way to incorporate the effects of predation on the dynamics of prey. However, this logic is incomplete in a subtle but important way. Predators do not affect their prey only by killing them. Predators also affect prey by inducing changes in their behavior. When predation risk is low or absent, prey move through the landscape and harvest food in one way. When predation risk is high, most prey species modify their behavior, and the constraints that predators place on their behavior can carry costs in terms of survival or reproduction. For a broad set of prey species, behavioral responses to predation risk include changes in habitat use, diet, movement patterns, grouping patterns, increased vigilance levels and reduced foraging time.

A large body of experimental and observational research shows that these behavioral responses are induced by an increase in the risk of predation. Some research has shown that these responses are effective in reducing the rate of predation, though this point is not as well demonstrated. Nonetheless, logic suggests that the primary benefit of anti-predator behavior is to reduce the rate of predation, and any such benefit is automatically taken into account by field studies that measure the rate of predation. For example, if elk reduce their vulnerability by moving into wooded habitats to avoid detection, then the predation rate that is measured in the field will reflect this effect, even if the researcher isn't aware of the habitat shift. In contrast, the costs of anti-predator behavior are far more subtle and difficult to demonstrate and quantify. To extend the example, a shift into wooded



▲ PHOTO 5.4 The direct impact of predation is obvious to detect and easy to understand. When wolves prey on elk, adult males are killed more often than would be expected if elk were selected randomly with respect to sex. Risk effects, or the costs of antipredator behavior, are more subtle to detect, but also have a strong effect on elk demography and population dynamics. (John Winnie)

habitats may reduce predation, but it might also carry a cost through reduced access to preferred feeding sites. If one does not design research carefully to consider such a cost, it is easily missed or attributed to causes other than predation. Because the costs of anti-predator behavior are not obvious and are difficult to measure, they have mainly been studied in experiments with invertebrates or small vertebrates in controlled settings. These costs are usually not considered in analyses of vertebrate predator-prey interactions, and they were not considered in pre-release assessments of the likely impact of wolves on elk dynamics.

Recent reviews of studies with invertebrate predator-prey systems suggest that the costs of anti-predator behavior, or 'risk effects', can affect the dynamics of prey just as strongly as direct killing itself. In other words, changes in prey behavior, habitat selection, foraging patterns and diet can alter the survival or reproduction of prey just as much as direct predation itself, or even more. When risk effects occur, it is a serious oversimplification to model the impact of predation simply by subtracting out the number of prey animals that are directly killed. If risk effects are important in large vertebrate systems like wolves and elk in the GYE, then risk effects might explain the mismatch between the predicted effect of wolves on elk dynamics (which was based only on direct predation) and the substantially larger effect that was observed. It seems logical to hypothesize that risk effects are at least as strong in vertebrates as in the better-studied invertebrates, because the complexity of the vertebrate brain allows great behavioral flexibility, and the anti-predator responses of vertebrates are consequently strong and multifaceted.

Fundamentally, risk effects are the costs of anti-predator behavior. If risk effects alter the population dynamics of elk, then elk should show clear behavioral responses to the presence of wolves, in a manner that affects processes that are important to survival and reproduction. For GYE elk, winter starvation was the dominant ecological limiting factor prior to wolf recovery, so anti-predator responses that affect winter foraging are a logical target for research.

The Study Area

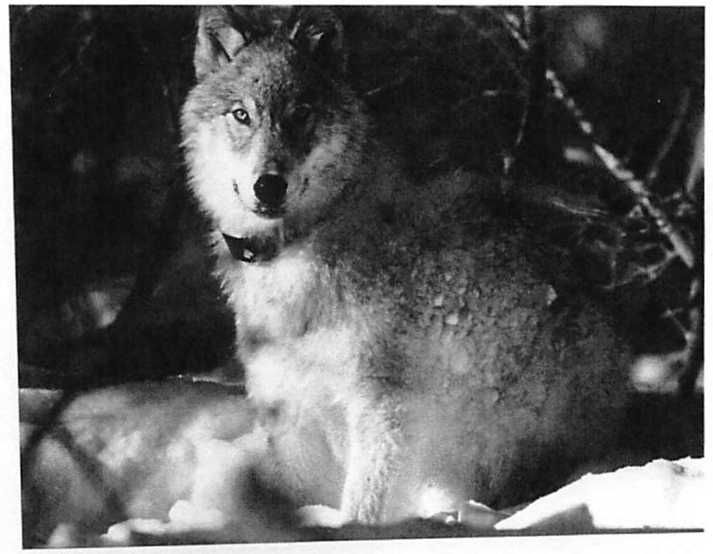
We studied the behavioral responses of elk to wolves using a variety of techniques, on a study site in the Gallatin Canyon, in the NW portion of the GYE. Our site covers 125.8 km^2 and included four drainages of the Gallatin River (Porcupine, 30.3 km^2; Taylor, 56.0 km^2; Tepee, 13.1 km^2; Daly, 26.4 km^2), on a combination of national forest, national park, state, and private land. These drainages form the primary winter range for a subpopulation of elk that has averaged 1642 elk in 50 annual counts conducted by Montana Fish Wildlife and Parks since the 1920s. These elk migrate to higher elevations in the summer, typically moving southeast into the Fan Creek and Upper Gallatin portions of the National Park. In fall and early winter, some elk pass through the site en route to winter range on the lower Madison River, but the majority of elk on the study area in winter engage only in localized movements, usually within a single drainage. Movement between Tepee and Daly Creeks is common, as these two drainages are easily linked by short movements over and around Crown Butte.

South-facing slopes and valley bottoms are generally a mixture of open sage (*Artemesia* spp.) and grassland (dominated by Idaho fescue, *Festuca idahoensis*, and bluebunch wheatgrass, *Agropyron spicatum*) with riparian areas bordering small creeks and the upper Gallatin River. North-facing slopes and higher elevations are primarily coniferous forest (lodgepole pine, *Pinus contorta* and Douglas fir, *Pseudotsuga menziessii*) broken by occasional small meadows. Elevation ranges from 1975 m to 2432 m above sea level. Two characteristis of the upper Gallatin drainage provided good conditions for testing our hypotheses. First, a short growing season and harsh winters mean that elk face energetically difficult conditions, so anything that precludes optimal foraging is likely to be costly. Also, there are notable differences in body condition between cows and bulls during the winter study season, which allows comparisons between the sexes to refine tests about the effects of predation risk. Second, wolves enter and leave each of the four drainages many times per winter, creating substantial variation in predation pressure within and between drainages. The data considered here were collected during periods that elk were on their winter range, beginning around 1 January each year and ending at melt out in late May or early June. Data on behavioral and distributional responses come mainly from three winters (2001 – 2003) and data on dietary and nutritional responses come mainly from three subsequent winters (2004 – 2007).

Wolves

Wolves colonized the study area in 1997. During the years of our study (2001 – 2007), the study area held from one to three packs totaling five to seventeen individuals. Packs denned successfully in the Daly and Taylor drainages, and apparently unsuccessfully in the Porcupine drainage. Each of the pack's home ranges included areas that were outside of our study area, so wolves commonly moved into and out of each drainage repeatedly throughout each winter of study. While walking fixed transect routes, and during daily visits to drainages, we continuously checked for signs that wolves were present within a drainage on that day. We considered wolves present within a drainage if we locatec them via VHF radiotelemetry, found a fresh kill, fresh

▲ PHOTO 5.5 Using a global positioning unit, we followed the track of foraging elk to sample the plants that elk consumed in the presence and absence of wolves, to quantify effect of predation risk on diet and nutrition. (Scott Creel)



▲ PHOTO 5.6 We determined if wolves were present within each drainage of our study area in multiple ways, including VHF radio collars, fresh kills, scat and fresh tracks. (U.S. Fish and Wildlife Service)

scat, or fresh tracks in snow, mud or loose soil. Averaged across all study drainages, wolves were present on 39.8% of days. The number of radiocollared wolves in the study area varied within and between years because of mortality and dispersal. In the Chief Joseph pack, zero to six wolves carried radiocollars. In the Sentinel pack, zero to two wolves carried radiocollars, and no wolves were collared in the short-lived pack in the Porcupine drainage. If wolves denned in a drainage (typically near 5 April), we scored all days during the denning period as having wolves present. Because not all wolves in the study area were radiocollared and we undoubtedly missed some physical evidence of their presence, it is likely that we failed to detect wolves on some days. This classification is conservative in that failure to detect wolf presence might mask responses by elk to wolves (type II errors, in statistical parlance), but should not create apparent differences where none exist (type I errors).

Elk

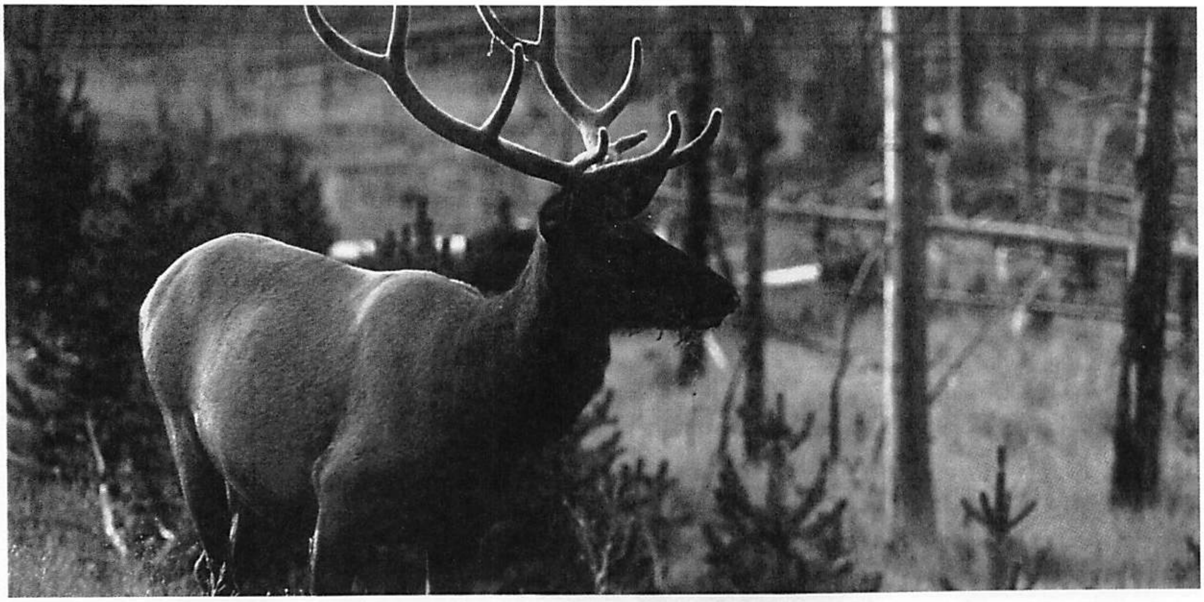
Elk in the study area are part of a seasonally migratory population (Mean +/- SE = 1642 elk, minimum and maximum counts of 789 and 3028 for the years 1928 - 2005) that winters along the tributaries of the upper Gallatin River from the northwest corner of Yellowstone National Park, north to Big Sky, Montana. Summer range for most of the population is at higher elevations within western Yellowstone National Park. The migration route and winter range have changed little over the past 75 years. Based on winter ground counts of 1143 herds, most elk herds are small – a maximum of 253 individuals and concentrated in the four study area drainages, avoiding the steep, rocky terrain typical of the rest of the region. Based on VHF radiotelemetry and GPS telemetry data, elk rarely moved between drainages during the study period based on 20,400 fixes from 47 individuals over two years. Moose, mule deer and white-tailed deer were present in the study area at low densities. Elk made up more than 90% of our ungulate observations, and more than 90% of wolf kills that we detected were elk.

Behavioral Responses of Elk to the Presence of Wolves

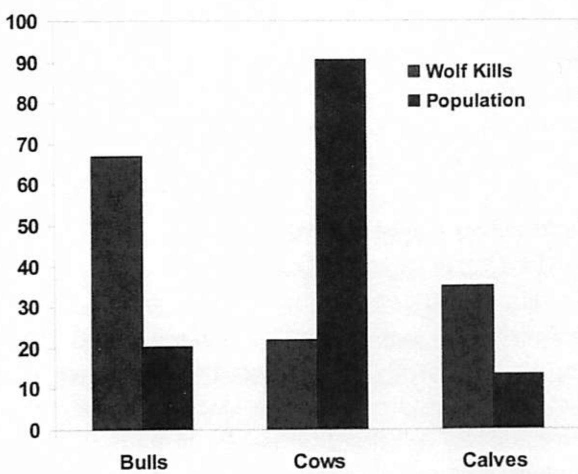
In virtually every aspect of their behavior and ecology, elk responded to the presence of wolves. For all of the results that follow, the basic method of analysis was to compare some aspect of elk behavior or ecology (herd size, for example) on days that wolves were known to be present within that drainage to data for the same elk, in the same location, on days that wolves were not detectably present.

VIGILANCE AND FORAGING

Overall, elk spend more time vigilant, and consequently less time foraging, on days that wolves are nearby. This response is driven entirely by the behavior of females, who respond strongly to the presence of wolves. Bulls, in contrast, do not increase their level of vigilance in response to wolves, and consequently do not decrease their feeding rate.



▲ PHOTO 5.7 Elk are more vigilant on days that wolves are locally present within a drainage, and consequently forage less. This response is driven entirely by the responses of females. Bulls are not more vigilant in response to wolf presence, and consequently do not reduce their feeding time. (U.S. Fish and Wildlife Service)

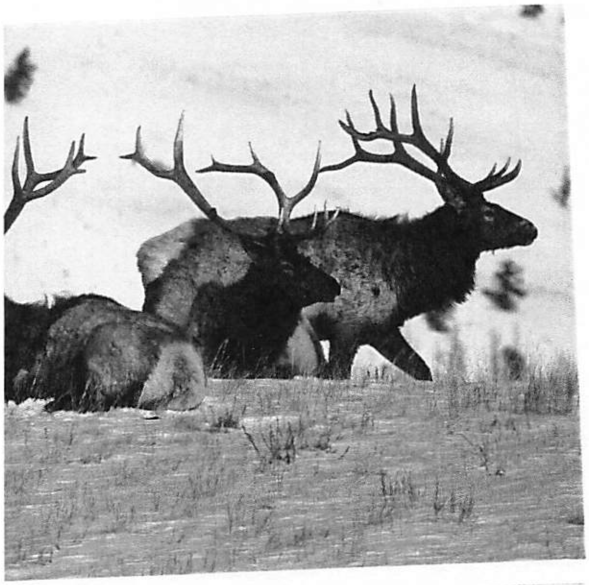


▲ FIGURE 5.1 Bull elk are killed by wolves more frequently than expected, based on their representation in the population. Cow elk are killed less often than expected. Calves, like bulls, are killed more often than expected, but only after the first six months of life (these data are restricted to winter, when calves are 6-10 months old). (Scott Creel, Dave Christianson & John Winnie)

This sex difference does not arise because bulls are less vulnerable to wolves. In fact, direct data show that bulls are killed more often than expected by chance, while cows are killed less often than expected. Instead, it appears that bulls respond weakly to predation risk because they are less able to pay the energetic costs of reducing their foraging time. The fat content of bone marrow is a sensitive measure of the degree of starvation, because fat stores in bone marrow are among the last to be depleted when an animal is running a negative energy budget. Bull elk enter winter in a depleted condition, in comparison to cows. Following their exertions in the fall rut, the marrow fat of bulls in early winter is depleted to levels typical of cows at the end of winter. This is an interesting example of differences between the sexes in behavior being driven by variation in the costs (starvation risk), rather than the benefits (reduced predation risk), which tend to be considered first.

HERD SIZE

For species that are typically found in herds or flocks, it is generally argued that shifting into larger groups should reduce the risk of predation. This can occur for two basic reasons. First, larger groups may be better able to detect or deter predators. In this situation, the risk that any member of the group will be killed decreases as the group gets larger. This is known as the 'many eyes' hypothesis. Second, it is possible that groups are no better are detecting or deterring predators, or that these benefits are offset by an increased likelihood that predators will find and attack larger groups. In this case, the risk that someone in the group will die may hold constant or even increase as group size increases, but this risk is 'diluted' among a larger number of individuals. To illustrate, natural selection should favor prey who choose to be in a group of five victims in 1000, rather than a group of two victims in 100. This is known as the 'dilution of risk' hypothesis.

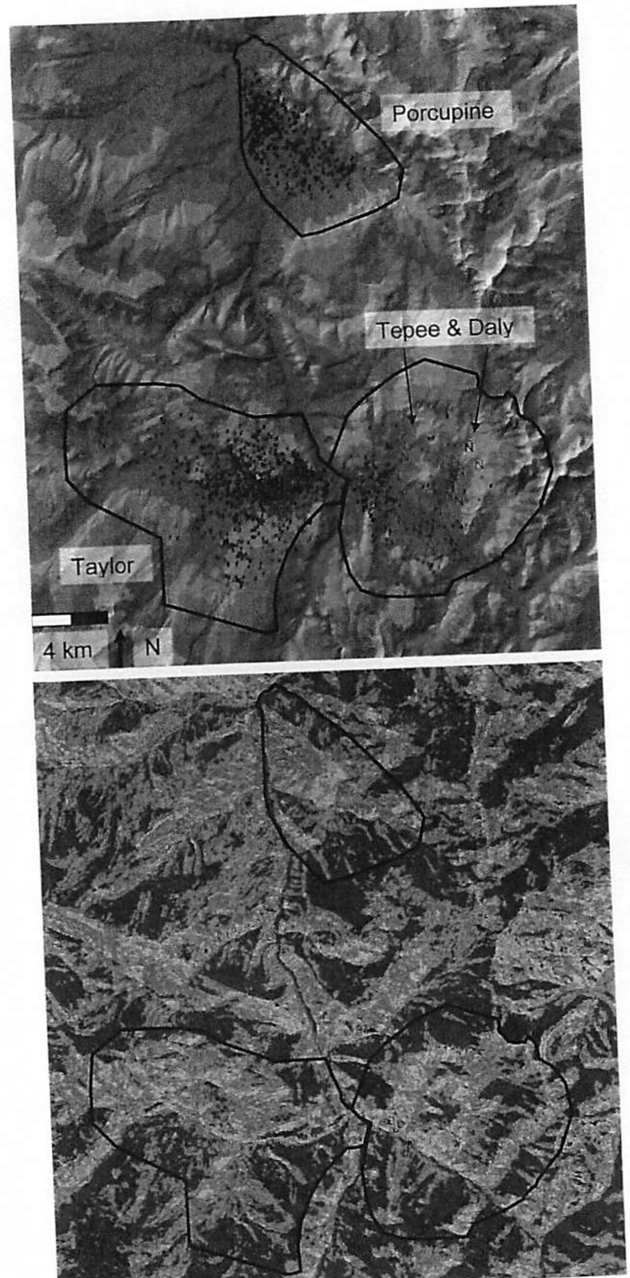


▲ PHOTO 5.8 Changes in elk distribution are associated with changes in behavior and habitat selection. On days that wolves are not present, elk are likely found in open grasslands and sage meadows. When wolves are present, they move into woodland edges and are less detectable when local predation risk is high. (Ken McElroy)

Given the well established benefits of many eyes and dilution of risk, the general expectation is that herd size should increase in response to predation risk. It is consequently somewhat surprising that Gallatin elk formed significantly smaller herds on days that wolves were present, in comparison to the same elk on days that wolves were absent. While our research did not directly establish the function of breaking into smaller herds, a logical suggestion is that smaller herds might be less detectable. This interpretation is reinforced by data which I discuss below.

HABITAT SELECTION

In the Gallatin, wolf kills were more common in grassy areas far from woodland edges than in areas closer to cover. This pattern was also observed in the Northern Range, where kills were most common in flat, grassy areas far from timber but close to rivers. Elk prefer open grassy meadows when wolves are absent, but in response to the patterns just described, move into coniferous woodland when wolves are in the area. In our data, this response could be seen in two ways. First, we recorded the locations of all elk herds that we spotted while



▲ FIGURES 5.2 The top image shows habitats on the Gallatin Canyon winter range, color scaled with grassland in areas of red and yellow, and coniferous woodland in areas of purple and blue. The bottom image displays the four drainages that form the three main winter ranges of elk in the Gallatin Canyon outlined in black, with the locations of wolf killed elk (blue crosses) and the locations of GPS-collared elk when wolves were present (red) and absent (black). Elk were more likely to occupy wooded areas on days that wolves were present, leaving their preferred foraging sites in open areas dominated by grasses. (Scott Creel & John Winnie) walking fixed transects - herds were much more likely to move far into the open on days that wolves were absent. Second, we used radio collars with onboard GPS units to record more than 20,000 locations from elk that were sampled at two hour intervals, around the clock, for two years. The GPS data also showed that elk are substantially more likely to be in wooded locations when wolves were present, and more likely to be in grassland areas when wolves were absent.

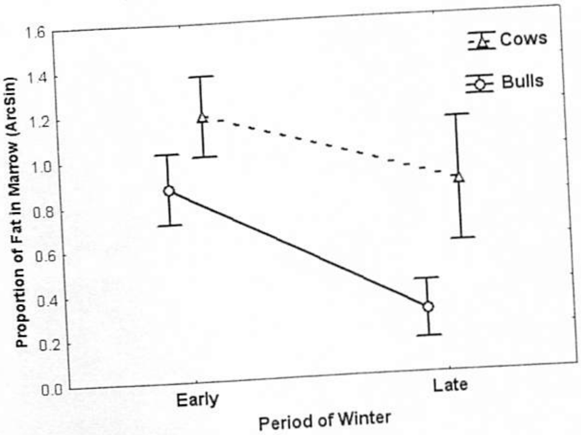
DIET AND NUTRITION

Parallel to shifts in habitat selection, the diets of elk change when wolves are present. Female elk browse on woody vegetation more and graze on grasses less. Males show less pronounced responses. The dietary shift provoked by wolves affects the quality and quantity of food that elk obtain. Surprisingly, the quality of the diet actually improves in response to wolves (higher nitrogen content, no decrease in digestible energy content). However, the quantity of food obtained goes down, and this effect is large enough to overwhelm the change in quality. The net effect of wolf presence in winter is an increase in the rate of body mass loss due to changing feeding habits.

Measuring Risk Effects on Reproduction and Population Dynamics

One of the biggest challenges for field research on risk effects is to document a causal chain from behavioral responses to risk, to physiological or energetic costs of these responses, and then to changes in survival or reproduction that affect population dynamics. For risk effects to be important, this chain must exist, but very few studies in the wild have examined every link in the chain. Consequently, an important final stage of this study was to test whether the responses we detected were associated with changes in elk demography and dynamics.

We first addressed this question by measuring progesterone levels, using non-invasively collected scat samples. Progesterone is a steroid hormone secreted by the ovaries, and in all mammals, progesterone levels increase dramatically during pregnancy, particularly

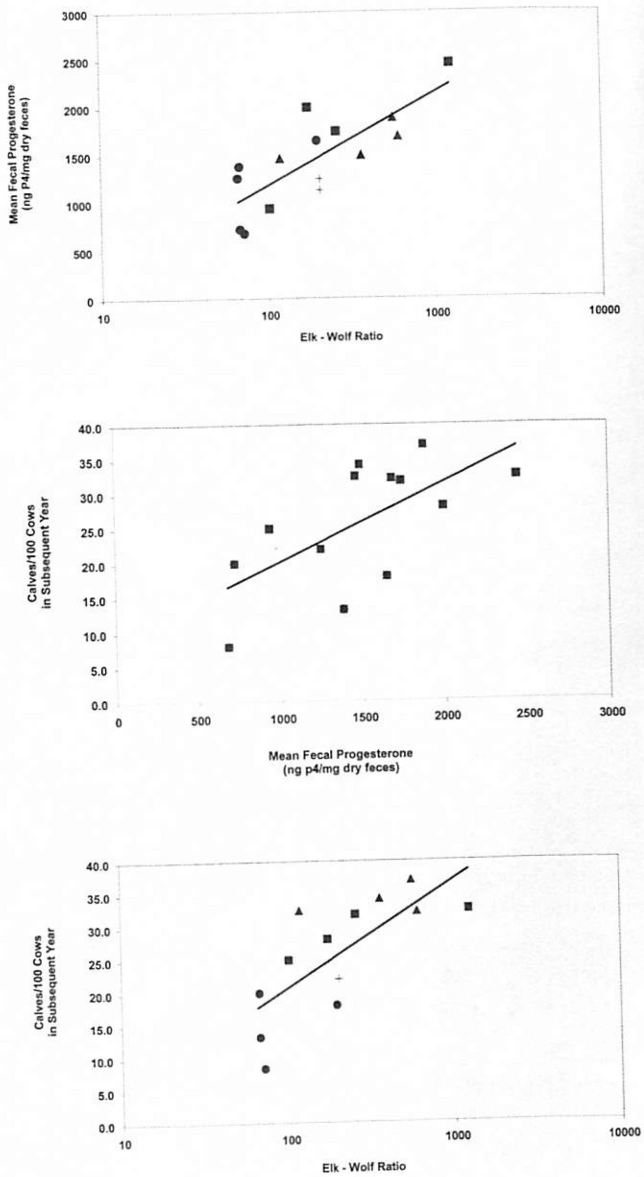


▲ FIGURE 5.3 Bull elk have lower fat stores than cow elk during winter, due to fat depletion as a consequence of competition for mates during the fall rutting season. Bulls enter winter with fat stores comparable to those of cows in late winter. Because of more limited energy stores, the antipredator responses of bulls are more highly constrained than those of cows, due to the real prospect of starvation before the spring green-up. (Scott Creel, Dave Christianson & John Winnie)

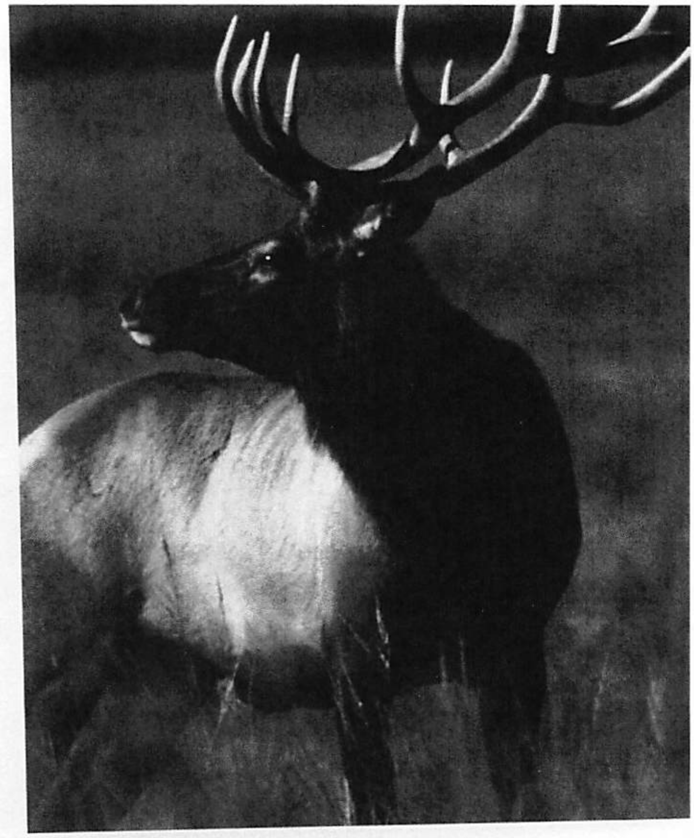
during the third trimester. Progesterone is cleared from the blood by the liver and passes into the feces intact, so measurements of progesterone in scat samples can be used to determine whether or not a female is pregnant. We collected fecal pellets from elk on five winter ranges between 2002 and 2006, and used immunoassays to measure progesterone concentrations for 1465 samples collected between March 15 and May 15, in the third trimester of gestation. When we examined the relationship between the mean progesterone level for a population and the level of predation pressure (measured as the elk-wolf ratio), we found that progesterone levels were dramatically lower in populations with high wolf-elk ratios. We then tested whether this physiological response was associated with calf production, and found that progesterone levels were a good predictor of calf numbers the following year. These results can be combined to show that calf production declines rather strongly as predation pressure increases. For these populations calf production is a good predictor of changes in population size.

Prior to describing our research results, I stated that:

GYE elk populations have declined substantially since 1995, while wolves have increased by a factor of 12. The observed decrease in elk numbers was larger than expected, and is not well-explained



▲ FIGURE 5.4 There are clear relationships between predation pressure (as measured by the ratio of elk to wolves), progesterone levels (an indicator of pregnancy), and calf production. (top) Across populations and years, progesterone levels are higher in populations with high elk:wolf ratios. (middle) In turn, progesterone levels are related to calf recruitment. (bottom) Consequently, calf production is significantly lower in populations with greater predation pressure. Overall, populations with high per-capita levels of predation had lower progesterone levels and produced fewer calves. While the possibility is rarely considered, these data show that predation can affect prey numbers by reducing reproduction, not only by decreasing survival. (Scott Creel, John Winnie, Dave Christianson & Stewart Liley)



▲ PHOTO 5.9 This Yellowstone bull elk is in its prime. The real impacts on elk populations from wolves are complex and include direct predation as well as behavioral changes. Understanding the ecological and demographic consequences of these behavioral responses is an important part of a complete understanding of wolf-elk dynamics. (U.S. Fish and Wildlife Service)

by ecological limiting factors other than wolves. These observations raise an interesting question that must be answered if ecology is to become a better predictive science: why was the effect of wolf predation on elk dynamics larger than anticipated?

To return to this broad question, one major reason that the impact of wolves on elk dynamics was greater than anticipated is that pre-release assessments considered only direct predation, and ignored risk effects. Subsequent research has revealed that elk, like most prey species, engage in a broad set of behavioral responses to risk, that these responses carry nutritional and physiological costs, and that these costs are associated with a decrease in calf production that helps to explain the observed impact of predation on elk dynamics. Retrospectively, these results help to explain wolf-elk dynamics in the GYE. Prospectively, they suggest that we must broaden our analyses to include risk effects, if we are to accurately predict or measure the impact of predators on prey dynamics.