

# EFFECTS OF THE 1988 FIRES ON UNGULATES IN YELLOWSTONE NATIONAL PARK

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## ABSTRACT

Few ungulates were directly killed by the 1988 fires in Yellowstone National Park. The greatest effects of the fires are expected to be changes in the forage base used by these animals. Only nine percent of the grasslands normally used by elk (*Cervus elaphus*) and bison (*Bison bison*) on the northern range during winter burned; most of the area burned was summer range. Prior to the fires, we studied factors influencing population dynamics of elk and bison in Yellowstone over a 15-year period, and found that three variables—(1) winter severity, (2) summer herbaceous biomass, and (3) population size—accounted for most of the year-to-year variance in per capita population growth rates for both species. The dynamics of elk and bison populations were modelled by incorporating these three parameters into a stochastic difference equation for each species. Our results suggest that at the beginning of the winter of 1988-89, the elk and bison populations were above average carrying capacity due to a series of mild winters. High over-winter mortality during the spring of 1989 was largely a consequence of abnormally high populations, and winter weather of slightly higher than average severity. Studies suggest that drought during the summer of 1988, as well as the burned winter ranges, were additional impinging factors on ungulate populations. We used a range of summer forage conditions extrapolated from literature on post-fire vegetation development to project consequences of the 1988 fires on elk and bison populations. An improved forage base for both elk and bison should enhance recruitment and population size for several years. Then a gradual decline to long-term carrying capacities of approximately 2,500 bison and 16,000 elk overwintering in the Park are projected.

## INTRODUCTION

The 1988 fires in Yellowstone National Park have been extolled by some to be the ecological event of the century. Indeed, nearly 42% of the Park's surface was affected by fires to some degree. This was the largest area burned in the greater Yellowstone landscape in recorded history. High-intensity fires are known to be an integral component of Yellowstone ecology, with extensive fires appearing infrequently, approximately every 300 years (Romme 1982, Romme and Despain 1989a, 1989b).

One of the major concerns about fire effects is the consequence to large mammals, which are key attractions for seasonal visitors to the Park. It is generally believed that the fires will be beneficial to most ungulate species because of an increase in the availability of high-quality forage, particularly in areas formerly dominated by lodgepole pine (*Pinus contorta*). Ungulates also will be benefited because the fires have altered the spatial pattern and juxtaposition of habitat types. The fires created a complex mosaic with an increase in the amount of edge (Knight and Wallace 1989). Elk prefer forest edge where they can feed in close proximity to cover (Thomas 1979, Bobek et al. 1984).

Surveys by the National Park Service revealed that fewer than two percent of the ungulates in Yellowstone National Park were killed by the fires of 1988 (Singer and Schullery 1989, Singer et al. 1989). It appeared that most mortality resulted from asphyxiation. Most animals simply moved away from the fires.

A large number of elk and bison died during the winter of 1988-89. It is unclear whether some of this mortality was attributed to reduced forage availability because of fire. The winter was near average for snowfall and temperature. However, ungulate populations were substantially above average carrying capacity due to several mild winters during the 1980s (Merrill and Boyce 1991). Considering the high elk population going into the 1988-89 winter, heavy losses were not unexpected, irrespective of the fires. Drought during the summer of 1988 was responsible for a reduction in winter range forage production. Production was claimed to be approximately 22% below normal (Singer and Schullery 1989).

Elk and bison populations were further reduced by hunting outside the Park during the 1988-89 winter (see Meagher 1989). A late-season hunt hosted by the Montana Department of Fish, Wildlife and Parks resulted in a kill of 2,400 elk. A highly controversial hunt removed 569 bison.

Studies of ungulates in the western United States have generally shown that diet quality and/or foraging efficiency of ungulates is enhanced as a consequence of fires (Hobbs and Spowart 1984, Urness 1985, Canon et al. 1987). Both elk and bison are attracted to burned areas where new forage is highly nutritious (Penfound 1968, Coppock and Detling 1986). In this paper we extrapolate from our studies on ungulate population dynamics in Yellowstone National Park (Merrill and Boyce 1991) to project probable consequences of the 1988 fires on the size of future elk and bison populations.

## BACKGROUND

We used Landsat satellite imagery to characterize summer ranges on the Northern Range of northeastern Yellowstone National Park from 1972 through 1987. During the summer of 1987, vegetation was sampled in 1,300 plots at 25 sites scattered across the northern range. Linear combinations of 3 Multi-

Spectral Scanner (MSS) wave lengths were used to estimate average green herbaceous phytomass over a 300 km<sup>2</sup> study area. Only grasslands were sampled. Forested vegetation types were eliminated from our calculations. Based upon the among-site variation for 1987 we then estimated green herbaceous phytomass for Landsat images from 1972 to 1987. Details of methods are given by Merrill et al. (1988).

Estimates of green herbaceous phytomass exhibited a strong pattern dependent upon the date of the satellite pass. We suspect this is largely attributed to annual variations in phenology. To standardize for this effect, we calculated the residuals from an average seasonal decline in green phytomass represented by a maxima function. Deviations from this phenological pattern were a quadratic function of winter precipitation, implying that winter snowpack influences forage greenup and thereby alters the timing of available green forage for ungulates, particularly at higher elevations. Therefore, we will define the negative of these residuals to be an index of forage quality.

After accounting for density dependence and winter severity (Houston 1982), variation in summer range forage quality was significantly correlated with recruitment rates, calf survival, and per capita population growth rates for elk on the northern range. With the addition of spring precipitation, a similar relationship was documented for bison. These relationships allowed us to construct population models to extrapolate effects of changes in summer range on future dynamics of elk and bison.

## MODELLING FORAGE DYNAMICS

Our projections of forage responses are based primarily on patterns in plant succession in lodgepole pine (Basile 1975), sagebrush grasslands (Harniss and Murray 1973, West and Hassan 1985) and sedge meadows after clearcutting or burning. We acknowledge that forage on burned sites may be higher in nutrients after burning (Coppock and Detling 1986) but these changes are likely short lived (< 3 years).

Diet quality also can increase initially because burning removes senescent vegetation which hinders diet selectivity (Hobbs and Spowart 1984, Cannon et al. 1987, Wilms et al. 1980, Coppock and Detling 1986). However, litter cover will return within a few years because summer ranges in Yellowstone are highly productive and do not receive the heavy ungulate use that is evident on winter range. Studies of *Stipa comata* in North Dakota found a return to prefire mulch structure after four years, although stands of *Agropyron smithii* took longer to restore mulch structure (Dix 1960).

We submit that the major change after fires will be in relative availability of various forage species. Forb diversity will increase and forb production will peak 5-10 years after the disturbance in lodgepole pine communities. Thereafter there will be a decline (Basile 1975), possibly due to allelopathic influences of lodgepole pine trees and canopy closure. Elk are expected to

benefit from the increase in forbs because they are highly nutritious (Cook 1972), have high breakdown rates (Spalinger et al. 1986), and afford greater foraging efficiency (Canon et al. 1987, Merrill 1987). Bison do not make as extensive use of forbs, relying more on grasses and sedges (Meagher 1973). Sedges and grasses are expected to increase, primarily in wet meadows and sagebrush-grasslands (Old 1969, Coupland 1973, Harniss and Murray 1973).

Most anticipated changes in plant communities will enhance the forage available for ungulates. For example, some areas will be converted from tree cover to meadow. Forest encroachment onto these meadows may require a long time. Furthermore, burned aspen stands should undergo extensive suckering and vigorous regrowth (Bartos and Mueggler 1979, Boyce 1989). Burned sagebrush stands will be dominated by grasses and forbs until sagebrush plants become established and grow to maturity (Knight and Wallace 1989). And we anticipate an increase in open woodlands and savannas (Knight and Wallace 1989).

To simulate the effects the 1988 fires on summer range forage, we modelled forage quality,  $Q(t)$ , in year  $t$  as a maxima function which is written

$$Q(t) = At \cdot e^{nt} \quad (1)$$

where  $A$  is a positive constant and  $n$  is a negative constant which together scale the peak in forage quality and the number of years post-fire at which the peak will occur, and  $t$  is time in years.

The year of peak forage quality for the maxima function was scaled relative to variation in available green herbaceous biomass which we documented on the northern range of Yellowstone National Park during the period 1972 through 1987 (Merrill et al. 1988; Merrill and Boyce 1991). We have computed the function with a maximum at one and two standard deviations above average forage (see Figures 1 and 2). Peak forage quality for elk occurs six years after the fires, i.e. in 1994, with forage remaining average in the first year after the fire (Basile 1975, Bartos and Mueggler 1979). Although we do not know how to estimate the actual magnitude of response in forage quality, we propose that the 2 maxima curves encompass the range of probable responses.

## POPULATION PROJECTIONS

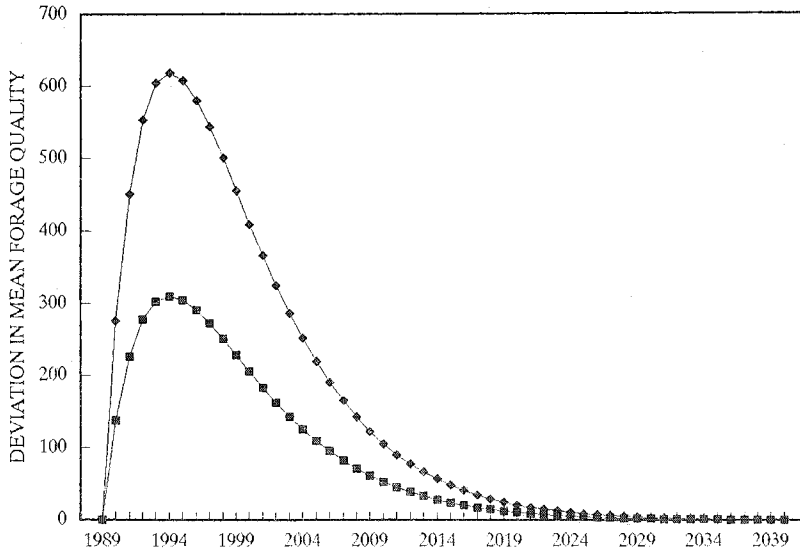
Ungulate response to summer range variation was estimated by fitting the per capita growth rate to a linear combination of effects attributable to population size in year  $t$ ,  $N(t)$ , winter severity (Lambs Index, see Houston 1982),  $S(t)$ , and forage quality on summer range,  $Q(t)$ :

$$\ln[N(t+1)/N(t)] = r - (r/K)N(t) - aS(t) + bQ(t) \quad (2)$$

$r$  is the logistic potential growth rate, and  $K$  is the carrying capacity where  $N(t+1)/N(t) = 1$ . Multiple regression coefficients,  $r$ ,  $(r/K)$ ,  $a$ , and  $b$ , were estimated by least squares (Merrill and Boyce 1991).

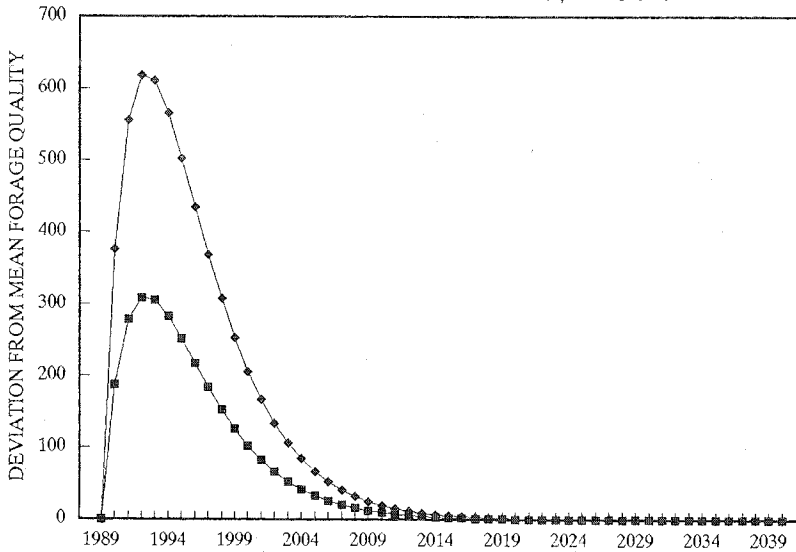
**Figure 1. Predicted deviations from mean forage quality for elk after the 1988 fires in Yellowstone National Park. Curves are generated using the maxima function,  $y = 336 \cdot t \cdot e^{-0.2t}$  for the higher curve, and  $y = 168 \cdot t \cdot e^{-0.2t}$  for the lower curve.**

**PROJECTED SUMMER RANGE PRODUCTION**  
IN YELLOWSTONE NATIONAL PARK, WYOMING



**Figure 2. Predicted deviations from mean forage quality for bison subsequent to the 1988 fires in Yellowstone National Park. Curves are generated using the maxima function,  $y = 507 \cdot t \cdot e^{-0.3t}$  for the higher curve, and  $y = 253 \cdot t \cdot e^{-0.3t}$  for the lower curve.**

**PROJECTED BISON SUMMER RANGE**  
IN YELLOWSTONE NATIONAL PARK, WYOMING



This model can be rewritten as a difference equation to project future population size:

$$N(t+1) = N(t) \exp[r - (r/K)N(t) - aS(t) + bQ(t)] \quad (3)$$

We used this model to project a stochastic time series by defining  $S(t)$  and  $Q(t)$  to be independent random variables with normal distributions with variances equal to those observed during the period 1972 through 1987.

In Figure 3 we present the results of deterministic projections of the number of elk wintering in Yellowstone National Park for the next 52 years, based upon forage functions in Figure 1. In Figure 4 we show a stochastic simulation to illustrate the magnitude of fluctuations attributable to climatic unpredictability.

For bison, the projected population sizes are presented in Figures 5 and 6. Again, stochastic fluctuations, especially due to severe winters, cause substantial unpredictability in future population sizes.

## DISCUSSION

Population growth rates for ungulates in Yellowstone National Park are mostly determined by winter severity, population density, and summer forage quality. Our simulations presume that the effects of the 1988 fires will be manifested primarily through the consequences to summer forage composi-

**Figure 3. Predicted population size for elk wintering in Yellowstone National Park for each of the forage response scenarios suggested in Figure 1.**

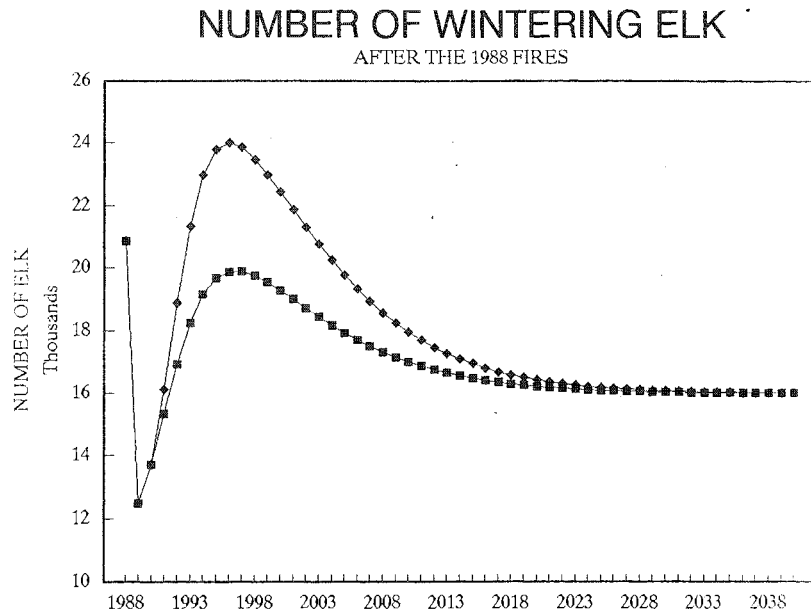


Figure 4. A stochastic simulation of the future population size for elk wintering in Yellowstone National Park.

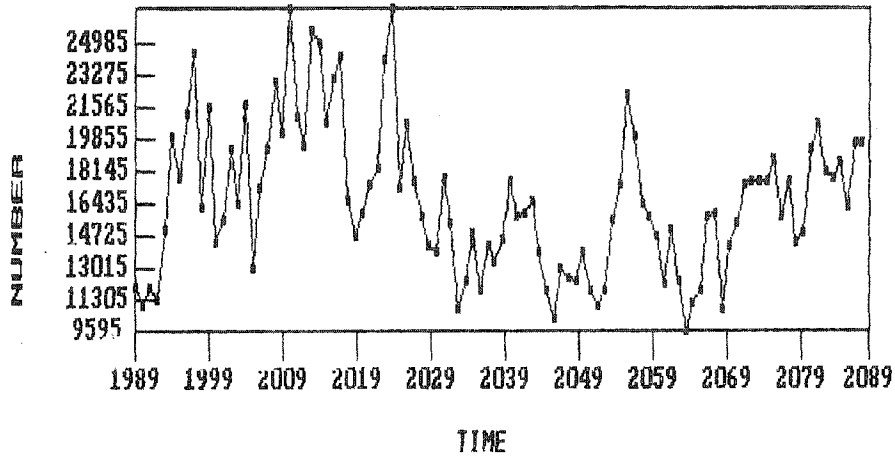
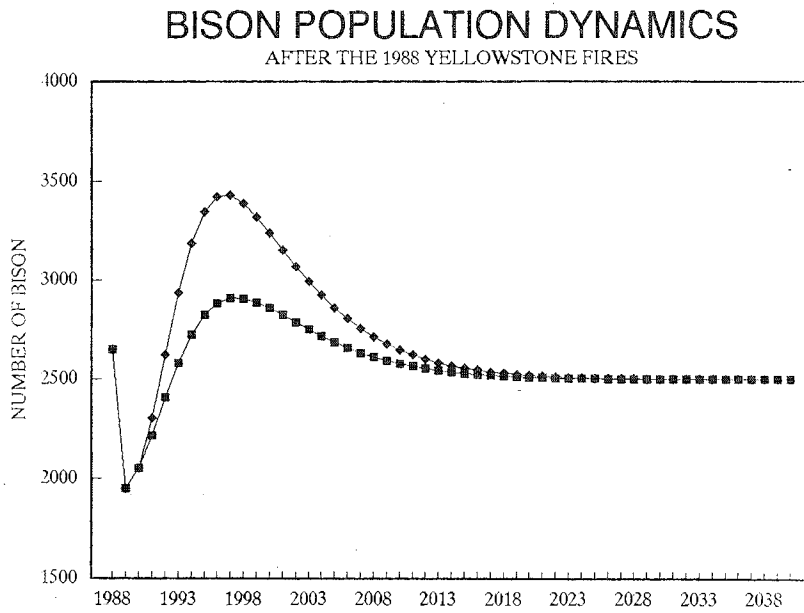
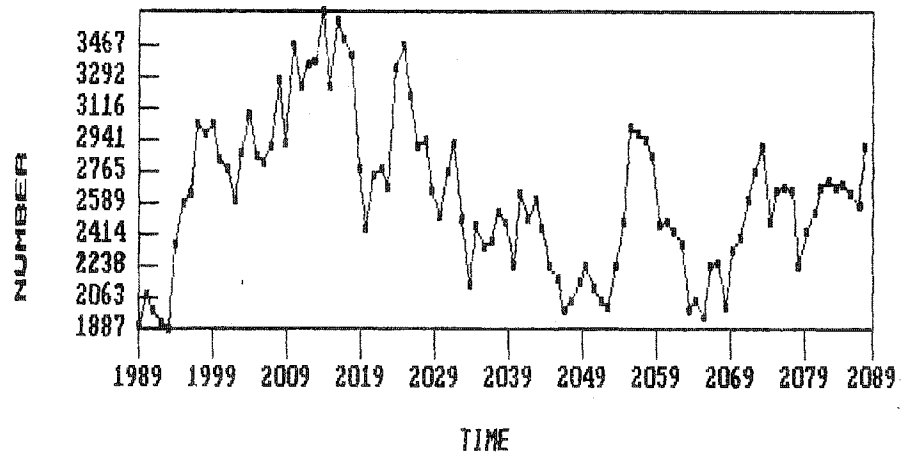


Figure 5. Predicted population size for bison wintering in Yellowstone National Park for each of the forage response scenarios suggested in Figure 2.



**Figure 6. Stochastic simulation of the future population size for bison in Yellowstone National Park after the 1988 fires.**



tion and therefore forage quality. Previous studies have demonstrated that diet quality and foraging efficiency will be enhanced by fire, but we cannot know the extent to which ungulates will use the burned areas, and how much better diets will be compared to prefire diets. Therefore, the scales which we present at Figures 1 and 2 are tenuous. We suspect that our projections are highly conservative, and if anything, the magnitude of population response is likely to be greater. Note that our projections are only within the normal range of variation that has occurred during the past 15 years prior to the fires.

The simulations presented in this paper represent hypotheses based upon our current understanding of factors influencing elk and bison populations in Yellowstone National Park. Our projections are reasonably consistent with patterns of elk population dynamics following fires in the western United States (see Leege 1968 and review by Wright and Bailey 1982). Likewise the curves presented in Figure 3 are largely consistent with observations of Lowe et al. (1978) that maximum elk use of burned sites occurred 7 years after fire, although little preference for burned sites could be seen 20 years after burning. We hope that we will have an opportunity to evaluate our forecasts during the next 25 years.

Large fires in the Greater Yellowstone ecosystem during the summer of 1988 offer a unique opportunity to study the role of fire in the ecology of ungulates in the Rocky Mountains. Numerous monitoring programs have been initiated to document the changes occurring since the fires. However, the fires will have multiple consequences to the vegetation and the animals. Therefore, in addition to monitoring studies, experimental work will be necessary to untangle the mechanisms causing responses by ungulates. Experimental manipulations that are "heavy on the land" may not be appropriate for



Yellowstone National Park; it may be necessary to conduct such experiments on National Forest lands adjacent to the Park. However, certain experimental studies may be conducted within the Park, and current investigations include use of exclosures and tame animals within the boundaries of the Park. The population projections presented in this paper form the basis for a model to anticipate the consequences of wolf recovery in Yellowstone (Boyce 1990). The beneficial effects of the fires on ungulates in Yellowstone may enhance the probability for success of proposed wolf recovery in Yellowstone National Park.

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