Ecological Applications, 6(2), 1996, pp. 573–593
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ELK POPULATION PROCESSES IN YELLOWSTONE NATIONAL PARK UNDER THE POLICY OF NATURAL REGULATION[1]

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Abstract. The interrelations of weather, plant production and abundance, and elk population dynamics on Yellowstone's northern winter range were examined for a 23-yr period when there was minimal human offtake from the herd. Significant correlations between precipitation and plant production, between elk population responses and precipitation, and between elk population responses and elk population density strongly suggested that forage limited elk population growth. Although population responses to density have been documented previously in Yellowstone, responses to precipitation have not. Correlations between elk population responses and annual precipitation were presumably consequences of plant growth responses to precipitation and subsequent effects on elk nutritional status. Population regulation was most consistently achieved through the responses of juveniles rather than adults. Winter mortality of juveniles was primarily correlated with elk numbers, whereas recruitment was primarily correlated with precipitation. Adult mortality rates were not significantly correlated with elk numbers, but were correlated with precipitation. Per capita rate of increase was negatively correlated with elk number, but 55% of the variance was density-independent. There was evidence that winter weather affected the elk, but season-long weather indices had poor predictive power. A stage-structured population model using regression equations of mortality and recruitment rate responses to precipitation and elk numbers, predicted that the population could vary within a range of ≈16 400 ± 2500 sighted elk (mean ± 1 SD).

Key words: Cervus elaphus; *elk; natural regulation; population; Yellowstone National Park.*

INTRODUCTION

The effectiveness of ecological controls on ungulate populations, even in the largest wildlife reserves, is still debated. Ungulate populations may be regulated without human interference through food limitation (Caughley 1976, Sinclair 1977, Sinclair et al. 1985, Novellie 1986, Fryxell 1987, Dublin et al. 1990, Owen-Smith 1990), predation (Bergerud et al. 1983, Messier and Crete 1985, Borner et al. 1987, Fryxell et al. 1988), disease (e.g., Sinclair et al. 1985), and weather (e.g., Picton 1979, 1984, Mech et al. 1987, Merrill and Boyce 1991). Although food-limited ungulate populations should tend towards dynamic equilibria with forage (Caughley 1976), a population may be unable to track the dynamic equilibrium when interannual forage variability is high (Caughley 1987, DeAngelis and Waterhouse 1987, Ellis and Swift 1988). There is a broad continuum of human disruption of these natural mechanisms. Unnaturally large ungulate concentrations and attendant range damage may occur where wildlife reserves are small in comparison to the ungulate's natural range, particularly where reserve boundaries do not circumscribe an ecologically complete habitat, or where migratory or dispersal movements have been impaired (Jewell and Holt 1981, Owen-Smith 1983, Coughenour 1992). Impaired dispersal is not a problem in very large African and Alaskan unfenced wildlife reserves, however (e.g., Murie 1944, Sinclair and Norton-Griffiths 1979, Fryxell and Sinclair 1988). Somewhere along this spectrum lies the northern Yellowstone elk (*Cervus elaphus*) population of Yellowstone National Park (hereafter YNP). YNP is a moderately large (889 571 ha), unfenced reserve, partially surrounded by human land use and hunting corridors that act as partial barriers to ungulate movements and, until 1995, lacked the most significant predator of ungulates, the wolf (*Canis lupis*).

If one management objective is to conserve natural processes within the reserve, then human controls on ungulate populations are justifiable if, and only if, there is scientific evidence that ecological limitations on population growth have broken down and the habitat is not ecologically complete (Cole 1971). Otherwise, human interventions could interfere with the natural processes of population regulation. Conversely, nonintervention should be justified with evidence that natural population processes are intact. The 1916 U.S. National Park Service (NPS) Organic Act directed that the fundamental purpose of the parks is to "conserve the scenery and the natural and historic objects and the wild life therein." Conditions within parks should "be maintained as nearly as possible in the conditions that prevailed when the area was first visited by white man. A national park should represent a vignette of primitive America" and the NPS should make an effort to restore "an illusion of primitive America" (Leopold et al. 1963). The preservation of pristine ecosystems and,

[1] Manuscript received 28 March 1994; revised 6 June 1995; accepted 6 June 1995.

thus, natural processes, has been a part of NPS management philosopy throughout the agency's existence (Houston 1971, Baur 1987).

Human interventions and noninterventions with the northern Yellowstone elk herd have been controversial. For ≥70 yr, there have been divergent viewpoints on the nature and effectiveness of ecological limitations on that population (see Houston 1982 and Coughenour and Singer 1991 for reviews). The herd was intensively culled from 1935 to 1968. On average, 2040 elk were removed each year in an attempt to alleviate or prevent presumed range damage. By 1935, early park managers believed elk were too abundant because they were protected from hunting inside the park, wolves (*Canis lupis*) were eliminated by the 1930s, native American hunters were absent, and migrations out of the park were impaired by human occupation and unrestricted hunting (Graves and Nelson 1919, Skinner 1928, Grimm 1939, Cahalane 1943, Pengelly 1963). The carrying capacity of the winter range has been calculated at 5000–7000 elk, based upon numerous questionable assumptions about available foraging area, forage production, forage requirements, and proper levels of use to maintain good range condition (Grimm 1939, Cooper 1963). Artificial regulation was partly based on the assumption that elk populations with low rates of increase and high mortalities were unnatural (Cole 1971). Thus, "economic carrying capacity," i.e., the number of animals that maximizes animal production and minimizes "wastage," was apparently confused with the nonconsumptive "ecological carrying capacity," i.e., the number of animals that results from food limitation (Houston 1971, Caughley 1976, and see Coughenour and Singer 1991).

From 1962 to 1968, negative public sentiments about large elk culls increased to national proportions (Olsen 1962, 1968, Kay 1990). Private hunters, in particular, objected to the government culls. In 1967, U.S. Senator McGee (Wyoming) chaired a subcommittee which led to a hearing and a directive from the U.S. Department of Interior and the NPS to stop the culling (Kay 1990).

From 1967 to 1969, the policy of artificial regulation was questioned on scientific grounds, in view of the paucity of data about how populations of ungulates were regulated in pristine ecosystems, questionable assumptions about the role of predation, theoretical and empirical evidence that herbivores should come into a natural balance with their forage, and the clear mandate that natural processes be preserved in national parks (Cole 1971). Furthermore, elk appeared to have an ecologically complete habitat, including ample winter as well as summer range within the protected area (Cole 1971). Thus, there appeared to be a strong possibility that artificial regulation was inconsistent with the objectives and management policies of natural areas (Cole 1971).

Since 1968, the northern Yellowstone elk herd has been managed under a philosophy of natural regulation, on the premise that most of the elk herd existed in an ecologically complete habitat and that " . . . over a series of years, naturally regulated ungulate populations were self-regulating units. They regulated their own mortality and compensatory natality in relation to available winter food and their population size" (Cole 1971, Houston 1976). Food limitation is the central mechanism of the natural regulation hypothesis. Predation was proposed to assist, but not be essential to, the natural regulation process. Recent analyses have suggested that wolf reintroduction might reduce northern Yellowstone elk herd size by 5 to 30% (Boyce 1993, Mack and Singer 1993). There are divergent views about the effect of hunting by native Americans (Houston 1982, Kay 1990).

TABLE 1. Northern Yellowstone elk counted during winter censuses, sightability-corrected estimates, and offtake from the regular hunt (≈19 October–30 November) including Montana units 313 and 316, and the late hunt (usually 15 December–15 February).

Year	Actual winter count	Sightability-corrected winter count	Regular hunt offtake	Late hunt offtake
1968/1969	4305		46	
1969/1970	5593		50	
1970/1971	7281		82	
1971/1972	8215		149	
1972/1973	9981		265	
1973/1974	10 529		316	
1974/1975	12 607		252	
1975/1976	12 014		327	1207
1976/1977	8980*		219	
1977/1978	12 680		239	803
1978/1979	10 838		311	70
1979/1980	10 108		189	487
1981/1982	16 019		344	1015
1985/1986	16 286		456	1059
1986/1987	17 007	23 350	893	843
1987/1988	18 913	22 779	379	215
1988/1989	10 991*	22 048	487	2352
1989/1990	14 829	20 964	833	423
1990/1991	9451*	16 036	301	684

* The actual count was considered to be poor. See *Methods: Elk population analyses* for method of correction.

Under the natural regulation policy, the herd grew from <4000 elk in 1967 to ≈12 000 by 1975 (Table 1). Hunting offtake outside the park was increased from 165 elk/yr from 1968 to 1975 to 1246 elk/yr from 1975 to 1991, but the herd nevertheless grew to nearly 19 000 sighted elk by 1988. Vegetation on windswept and often snow-free areas, a small fraction (<5%) of the winter range, was fully utilized by elk even at the end of the period of artificial reductions (Cole 1971, Houston 1976, Cayot et al. 1979). Herbaceous vegetation on the winter range has not degraded (Houston 1982, Coughenour 1991, Frank and McNaughton 1992, 1993, Coughenour et al. 1995; F. J. Singer, K. K. Symonds, and A. Harding, *unpublished manuscript*), but riparian woody plants, particularly willows (*Salix* spp.) and aspen (*Populus tremuloides*), have declined. Most of the

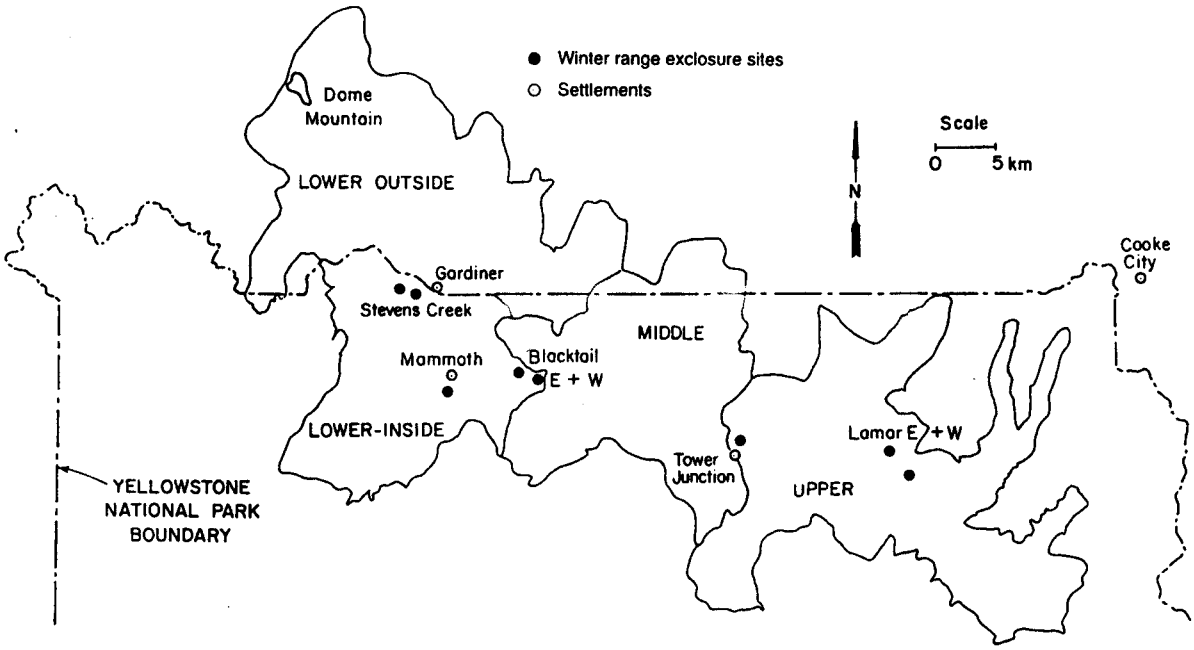

FIG. 1. The northern Yellowstone elk winter range showing outside, lower, middle, and upper elk count sectors.

willow declines occurred during the 1920s to 1940s (Kay 1990, Singer et al. 1994), when 10 000–15 000 elk were believed present. Aspen cover has declined since the park was established, and there has been very little recruitment of large-stemmed aspen stands since 1870–1890, which was an ecologically unique period (Warren 1926, Romme et al. 1995).

Our objective here is to investigate whether or not the northern Yellowstone elk herd has been limited by food and winter weather under the natural regulation policy from 1969 to 1991. The potential effects of elk on vegetation and soils, and the appropriateness of the plant–herbivore system are treated elsewhere and are beyond the scope of this study. Previous research has provided evidence that the northern Yellowstone elk herd is regulated by density-dependent competition, presumably for food (Houston 1982, Merrill and Boyce 1991). There has been little documentation showing that ecological carrying capacity varies in response to interannual forage production. Elk die-offs and poor recruitment have long been associated with severe winter weather (Skinner 1928, Pengelly 1963, Houston 1982, Merrill and Boyce 1991). We examine elk population and distribution data collected on Yellowstone's northern winter range from 1969 to 1990, forage production and precipitation data from 1935 to 1988, and 1969–1990 weather data to determine whether or not forage supply, precipitation, and winter weather have limited the size and growth rate of the elk population. If forage limits elk population growth we expect to observe the following relations:

1) Intraspecific competition for a limited supply of available forage will result in significant positive correlations between population size and mortality and negative correlations between population size and recruitment. As population size increases, the proportion of newborns and subadults in the population will decline.

2) Forage production will be positively affected by precipitation.

3) Population parameters will be correlated with annual precipitation. Recruitment rates should be higher and mortality rates lower during, or immediately following, wet years. If plant growth is limited by water and elk are limited by plant production, then significant positive correlations should be observed between population growth and precipitation or between recruitment and precipitation (e.g., Owen-Smith 1990).

4) Population responses will be time-lagged behind precipitation. Winter calf mortality should be negatively correlated, and summer calf recruitment should be positively correlated with plant growth in the previous summer. Higher winter calf proportions will be positively correlated with precipitation two summers prior, since winter calf proportion reflects previous winter and summer mortality.

METHODS

Study area

The current northern Yellowstone elk winter range encompasses lands inside and outside the northern portion of the park, mainly at low elevations in the Lamar and Yellowstone River valleys (Fig. 1). Houston (1982) delimited an area of 100 000 ha, including 17 000 ha of land outside the park that was available to elk by

1982. The elk range has expanded, however. A current range size of 140 000 ha was defined by connecting outermost animal locations observed during aerial surveys from 1986 to 1990. About 100 000 ha of the 140 000 ha lie within YNP and 40 000 ha lie north of the park boundary on Gallatin National Forest and private lands. The boundary shown in Fig. 1 corresponds to the outermost perimeter of elk count units covering 141 921 ha, of which 97 238 ha lie within the park. Two new count units at the northernmost end of the range were added in 1986, bringing the total area counted to 148 893 ha.

Elevations of the northern winter range vary from 1500 to 2400 m. Mean annual precipitation ranges from 24 cm at Gardiner, Montana (1731 m elevation), to 39 cm at Mammoth (2032 m), 41 cm at Tower (2056 m), 35 cm at the Lamar Ranger Station (2112 m), and 65 cm at Cooke City (2445 m). Most of the northern winter range is steppe or shrubsteppe (55%), dominated especially by Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrass (*Pseudoroegnaria spicatum*), and big sagebrush (*Artemisia tridentata*). Conifer forests (*Pseudotsuga menziesii, Pinus contorta*) cover 41% of the range, along with small amounts of aspen (*Populus tremuloides,* 2.0%) and willow (*Salix* spp., 0.4%).

Weather data

Daily precipitation, snowfall, and minimum and maximum temperatures in the study area were recorded from 1929 to 1991 at Mammoth Hot Springs, 1931 to 1991 at Tower Falls, 1929 to 1976 at Lamar Valley, 1936 to 1991 at Gardiner, and 1967 to 1991 at Cooke City. Precipitation data were summarized by site and season (fall, September–October; winter, November–March; spring, April–May; summer, June–August). Precipitation from September of the preceding year through August of a given year was summed to yield "water-year precipitation," which is meaningful because fall and winter precipitation may be stored in the snowpack or soil, and because plant growth measurements were always made prior to mid-September. Gardiner, Montana precipitation data were used in correlations with plant growth measurements for the "lower" winter range (Fig. 1). The average of precipitation data at Mammoth, Tower, and Lamar was used in correlations of plant growth measurements on the "upper" winter range. Water-year precipitation for the winter range as a whole was obtained by averaging Gardiner, Mammoth, Lamar and Tower data.

Winter severity indices were calculated using probit analyses of April snow depths and minimum winter temperatures (Farnes 1996). The percent probability of nonexceedence (PN) of the mean was subtracted by 50% and divided by 12.25 to compress the range of 1% through 99% (PN) to −4 through +4. Farnes's index ranged from −4 = most severe, to 0 = normal, to +4 = most mild. Separate indices were calculated for snow and temperature. A combined snow and temperature severity index was calculated as the average of the snow and temperature severity indices.

Forage biomass

Herbaceous biomass production data collected in Yellowstone were utilized in our analyses of production–precipitation relationships. Measurements of herbaceous (grass, forb, half-shrub) standing crops on the Yellowstone winter range were made by park personnel using "volume plots" in 1935–1941, 1947 (n = 14–16 plots/yr), 1949, and 1950 (n = 4 plots/yr) (Grimm, 1935–1938, Gammill, 1939–1941, Kittams 1948–1950). All herbage was clipped from a 32.7 × 32.7 m area in mid- to late summer, air-dried, and weighed. Herbaceous plant growth was studied in more detail from 1986 to 1988 (Coughenour 1991, Singer 1995). In mid- to late summer, peak standing crops were sampled inside and outside 2-ha exclosures constructed from 1958 to 1962. In 1986, biomass was measured in 10 1-m^2 quadrats; in 1987, 15 0.25-m^2 quadrats were randomly located within each of 10 × 10 m paired plots at each exclosure (Singer 1995). Plots were paired inside vs. outside with respect to slope, aspect, and soil. There were two plot pairs at Mammoth, two at Blacktail, one at Junction Butte, two at Lamar, and two at Stevens Creek. In 1987 and 1988, biomass was sampled in four 0.25-m^2 circular quadrats randomly located within each of four 5 × 5 m plot pairs at each of four exclosures (Coughenour 1991). Biomass on all quadrats was clipped to ground level, sorted, oven-dried, and weighed. Green standing biomass of grass and forbs plus dead forb biomass was taken as a best estimate of current season production, since nearly all standing dead grass appeared to be carried over from prior seasons. In 1987, when biomass was sampled on two dates, the maximal of the two values was taken as being the "peak" biomass for the season. Data taken outside the Mammoth exclosure in 1986 were not used because a local group of elk had not migrated off the winter range and had been grazing there prior to sampling.

Forage measurements taken from lower winter range sites at 1500–2000-m elevation were distinguished from those taken from higher winter range sites. The lower winter range included areas below Mammoth and near the park boundary at Gardiner, Montana (Fig. 1). Lower winter range growing conditions are relatively xeric, and the much lower snowfall, faster melting and wind removal of snow from the slopes result in easy access to forage and high use by wintering elk. Correlations and regressions were calculated separately for the corresponding upper and lower range precipitation data.

Elk population analyses

Elk total numbers and ratios of calves, yearling males (spikes), and bulls to cows from 1969 to 1990 were estimated by YNP biologists (Barmore 1980, Houston

1982, Singer 1991). Elk were counted from fixed-wing aircraft during a 1–3-d period in early winter (December–January) 1952–1979 (Houston 1982). Two aircraft were used to count elk in the winter of 1981/1982, but no more counts were made until 1985/1986. From 1985/1986 to 1990/1991 elk counts were completed in a single day using four aircraft simultaneously. The winter range was divided into 68 count units based on topographic features. In complete counts, all units were fully surveyed, whereas partial counts were conducted by fully surveying only a portion of the total 68 count units.

Aerial censuses were affected by factors that influence the "sightability" of the animals, such as tree cover, snow cover, group size, and observer. Sightability-corrected estimates can be made by developing an empirical model of how sightability is affected by these factors in each census. Sightability models were derived from the numbers of radio-collared animals observed from fixed-wing aircraft in each census from 1986/1987 to 1990/1991 (Singer and Garton 1994). Unseen animals were radio-located from a second fixed-wing aircraft. Eleven counts during winters of 1986/1987 to 1990/1991 were corrected for sightability (Singer and Garton 1994); however, only five were complete counts conducted during early winter. Six were partial counts or late-winter counts, and thus were not used in our analyses. Three of the five complete counts were "good," with sightability proportions of 0.70–0.91, and two were "poor," with sightabilities of 0.49–0.65 (Table 1).

Since sightability estimates were made in five out of 19 data-years (Table 1), we performed analyses using all 19 years of uncorrected count data rather than omitting 14 years of uncorrected data. However, certain of the counts provided exceptionally low estimates because of poor counting conditions. Those counts were obviously inconsistent with counts in prior and subsequent years. The count in winter 1976/1977 was poor (Houston 1982), so a calibrated sex and age class population projection model (Mack and Singer 1993) was used to estimate the ratio of population size in 1976/1977 to that in 1975/1976, which was 0.82:1. This yielded a sightability-uncorrected estimate, which was used in statistical tests and plots. Counts in winters of 1988/1989 and 1990/1991 were also exceptionally poor. Sightability estimates were available for counts in these two years, however. Sightability-uncorrected estimates for those two years were derived by reducing the sightability-corrected estimates by the mean fraction sighted in the other "good" counts (sightability proportion of 0.75).

Classifications were conducted from helicopters or on the ground. Winter range elk classification samples were separated into four elevation sectors: (1) upper sector, including the Lamar Valley, where winter snow depths are deepest and tend to average 0.6–0.7 m; (2) middle sector where snow depths are only slightly less, ≈0.5 m; (3) lower-inside park sector where the ground is bare or snow depths are <0.3 m; and (4) lower-outside park sector, at lowest elevations with similarly shallow snow depths, and where the 3-mo-long hunting seasons affect the migratory elk (Fig. 1).

In classification counts, "calves" were <1-yr-old animals. "Spikes" were male (bull) elk that would be ≈1.5–1.75-yr-old in December–January (yearlings). "Cows" were female elk >2-yr-old. "Bulls" were male elk >2-yr-old. Calf:cow, spike:cow, and bull:cow ratios were compared between sectors of the early- and late-winter range, using the Friedman two-way analysis by ranks test with count units as replicates. Bull ratios are not reported prior to 1988 for early winter or 1985 for late winter, since classifications were done from the ground along the park roads and trails, and tended to underrepresent higher elevation winter range sites favored by bull elk.

Two annual hunts affect the elk herd as it moves outside the park into Montana. A regular hunt occurs during 19 October to 30 November, and a late hunt occurs 15 December to 15 February. Data on hunter harvests obtained from the Montana Department of Fish and Game were used to estimate pre-hunt elk population sizes. Hunting removals averaged <9% of the herd in these sectors each year (Table 1).

Winter calf mortality rate was calculated as

$$\mathrm{wclfm}_t = \frac{(\mathrm{aclf}_t - \mathrm{ayrl}_{t+1})}{\mathrm{aclf}_t},$$

where aclf_t is number of calves estimated to have been present in autumn of elk-year t (Fig. 2), and ayrl_{t+1} is number of yearlings estimated to be present in autumn of the subsequent elk-year $t + 1$. The number of animals in autumn is estimated as the number in the winter count, plus the number taken off during the regular hunting season. The number of autumn yearlings is

$$\mathrm{ayrl}_{t+1} = \mathrm{aspk}_{t+1}(1 + \mathrm{fmr}),$$

where aspk_{t+1} is the number of yearling males in autumn of year $t + 1$ and fmr is a typical ratio of female to male yearlings (0.66:0.44, Houston 1982). The equation for winter calf mortality thus assumes negligible mortality of yearlings during the summer.

Summer calf mortality rate can be estimated as

$$\mathrm{sclfm}_{t-1} = \frac{(\mathrm{adcow}_t \times \mathrm{brth}_t) - \mathrm{aclf}_t}{(\mathrm{adcow}_t \times \mathrm{brth}_t)},$$

where brth_t is births per adult cow in year t, and adcow_t is number of adult cows in year t. Adult cow number in autumn (adcow) is the total number of pre-hunt (autumn) cows (acow), minus the number of pre-hunt yearling females. The birth (calving) rate is based on observed pregnancy rates, which appear to vary in response to elk density. When the elk population was small in 1967/1968 (4272 elk), a pregnancy rate of 0.87 was observed (Houston 1982). A pregnancy rate of 0.82 was observed in 1952, when the population was

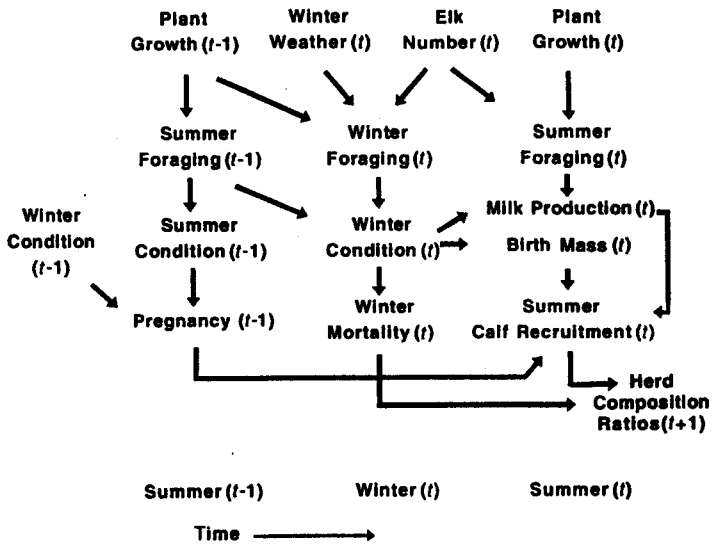

FIG. 2. Causal pathways and time lags between plant growth and elk population responses in elk-years $t - 1$, t, and $t + 1$. An elk-year begins on 1 November.

>13 500 (Houston 1982), and in 1990/1991 a pregnancy rate of 0.82 was noted when the population was 12 024 (T. Lemke, *personal communication*). However, when the population was 17 773 in 1986/1987, a pregnancy rate of 0.61 was observed (T. Lemke, *personal commununication*). Thus, we assumed that pregnancy rate varies in proportion to elk population size within these ranges.

An estimate of calf recruitment rate into the population over the prior summer is

$$\mathrm{clfr}_{t-1} = \frac{\mathrm{aclf}_t}{\mathrm{adcow}_t},$$

expressed as calves per adult cow. This estimator for calf recruitment rate is not influenced by uncertainties in values for pregnancy rates, whereas the summer calf mortality estimator is. Actual recruitment, however, is influenced both by pregnancy and by summer calf mortality. Only if pregnancy rate were a constant would recruitment rate be solely influenced by summer mortality.

Cow mortality was calculated as the difference in cow numbers from one autumn to the next and was corrected for known hunting removals. Furthermore, we accounted for the addition of new cows (yearling females) to the autumn population of the second year. Yearling females were estimated from spike (yearling male) numbers and a yearling female:male ratio of 0.66:0.44 (Houston 1982). Bull mortality was estimated, following Houston (1982), as the difference between bull numbers in year $t + 1$ minus bull numbers in year t and was corrected for hunting offtake. Cow and bull mortalities were converted to mortality rates (number dying per number alive) by dividing the total mortality by the population size at the beginning of the period.

Winter of 1988/1989 mortalities were estimated differently. The direct count in early winter of 1988/1989 was poor (10 908 elk seen), a sightability-corrected estimate was 22 048 elk. Sightability-corrected estimates of two counts made in April 1989 were 12 590 and 13 367 elk, mean 12 978 elk. In total, 2352 elk were removed during the late hunt. Thus, we estimate that 6718 elk died. Lemke and Singer (1989) counted and classified carcasses on and north of the park boundary. They estimated a proportional carcass composition of 0.46 calves, 0.21 bulls, and 0.33 cows. Thus, an estimated 3090 calves, 1410 bulls, and 2217 cows died. Based on early-winter herd composition, the winter mortality rates were then estimated as 0.83 of the calves, 0.60 of the bulls, and 0.14 of the cows. The calf mortality rate is in agreement with the value of 0.84 determined by studies of radio-collared calves marked as newborns (F. J. Singer, K. K. Symonds, and A. Harding, *unpublished manuscript*).

The actual per capita rate of increase (r_a) was defined by

$$\frac{dN}{dt} = r_a N$$

and

$$N_{t+1} = N_t e^{r_a \Delta t},$$

where Δt equals one year and N_t is population size in year t. Thus, r_a was calculated as

$$r_a = \ln\left(\frac{N_{t+1}}{N_t}\right),$$

where N_t is the post-hunt population size in year t (pre-hunt size minus hunting removal), and where N_{t+1} is the pre-hunt population size in year $t + 1$.

An "elk-year" begins just prior to the beginning of the regular hunting season. Changes in herd composition as reflected in calf:cow, spike:cow, and bull:cow ratios were potentially affected by vegetation abundance during the previous two elk-years (Fig. 2). Elk

sex and age ratios in elk-year $t + 1$ (corrected to prehunt) might reflect (1) the effects of plant growth during the summer of elk-year $t - 1$ on summer foraging and calf survivorship in that year ($t - 1$); (2) the effects of plant growth in summer of elk-year $t - 1$ on winter foraging, elk condition, and either winter mortality or summer calf recruitment in year t; (3) the effects of winter weather conditions on elk foraging or thermal stress in elk-year t; or (4) the effects of elk population size in elk-year t on intraspecific competition for forage in winter and summer of year t.

Winter mortality rates in elk-year t could be affected by plant growth in elk-year $t - 1$. Plant growth in year $t - 1$ may affect foraging during winter of year t or it may affect foraging during the summer of year $t - 1$ and elk nutritional status going into winter of year t (Fig. 2). Winter mortality rate in elk-year t might respond to winter weather in the current year through effects on foraging. Winter elk number in year t would affect the mortality rate through competition. Summer calf recruitment in year t could respond to plant growth and total elk population size in year t, but would more probably be affected by the condition of the pregnant female and by calf birth weight, which are affected by foraging in the summer of year $t - 1$ and the winter of year t.

A stage-structured model was constructed with calf, cow, and bull elk classes. Recruitment and mortality rates of each class were modeled using the best equation determined from forward stepwise multiple regression analyses, with precipitation amounts and elk number as the independent variables. The exact equations are given in *Results*. The model was initialized with elk numbers in 1968/1969. The model was tested against observed elk sightings from 1969 to 1990. The model was then run for 30 simulations, 28 yr each, randomly choosing each year of weather from the 1931–1990 data set. Normally distributed stochastic variation with a standard deviation of 25% of observed mean recruitment or mortality rate was added to simulate variance not explained by the regression models.

Results

Aboveground plant biomass

Total live plus dead biomass measured on the early volume plots from 1935 to 1950 varied from 17 to 120 g/m^2 on higher winter range sites and from 14 to 115 g/m^2 on the lower winter range sites. Mean total standing crop was 52.8 ± 25.0 g/m^2 (mean ± 1 SD) on lower winter range sites, compared with 66.6 ± 30.5 g/m^2 on higher winter range sites. Total biomass was significantly correlated with water-year precipitation (Tables 2 and 3). The slope of the regression line indicated an increase of ≈1.8 g/m^2 of biomass for each 1 cm of precipitation. More of the variation in total biomass was explained by seasonal (58–59%) than by total water-year (34%) precipitation models (Table 3). Total biomass appeared to respond most strongly to spring precipitation, but summer and fall precipitation also contributed significantly to explaining the variance. Winter precipitation explained little of the variance in total biomass, and so was eliminated in the backwards regression procedure.

TABLE 2. Correlation coefficients (r) of the 1986–1988 estimates of green herbaceous biomass (g/m^2) inside or outside exclosures, or total (live plus dead) herbaceous biomass outside exclosures 1935–1941, 1947, 1949–1950, 1987–1988, with seasonal or water-year precipitation or elk number. For green biomass inside, n = 18 (3 years × 6 sites); for green biomass outside, n = 16 (sites × years) (Mammoth sites were excluded due to summer grazing). For total biomass outside, n = 24 (sites × years). For total biomass outside, n = 24. * $0.01 < P < 0.05$; ** $P < 0.01$.

Factor	Green biomass		Total biomass
	Outside	Inside	Outside
Precipitation			
Fall	−0.01	0.08	0.25
Winter	0.27	0.72**	0.17
Spring	0.49*	0.14	0.42*
Summer	0.29	0.35	0.49*
Water-year	0.38	0.53*	0.55**
Elk number			0.26

Green plant biomass from 1986 to 1988 was most strongly correlated with winter precipitation inside exclosures and with spring precipitation outside exclosures (Table 2). Green biomass was not correlated with summer or fall precipitation, either inside or outside exclosures. Winter precipitation alone explained 51% of the variance in green biomass inside exclosures, while spring, fall, and summer precipitation amounts were eliminated in the backwards regression analysis (Table 3). Green biomass inside exclosures was more strongly correlated with winter precipitation than with total water-year precipitation.

Elk distributions

The proportion of the elk herd counted north of YNP, including known hunting offtake (Table 4), was not correlated with winter temperature ($r = -0.20$) or snow ($r = -0.41$) severity indices (n = 16 years). The proportion of elk that were counted plus harvested north of the park was not significantly correlated with years since cessation of artificial control in 1968 ($r = 0.21$, $P = 0.43$). However, the total number of elk counted north of the park each winter was weakly correlated with years since cessation of artificial control ($r = 0.47$, $P = 0.06$), suggesting that migration increased. A significant portion of the variance in total elk north of park was related to time and winter severity in a multiple regression analysis ($r^2 = 0.42$, $P = 0.026$). The numbers of elk counted on Dome Mountain at the northernmost extremity of the winter range increased markedly after 1988 as a result of the large migration in the winter of 1988/1989.

TABLE 3. Backwards elimination regression analysis of green biomass (1986–1988) inside (n = 16) or outside (n = 18) exclosures, or total live-plus-dead biomass outside (n = 20) exclosures (1935–1941, 1947, 1949–1950), with fall (FALL), winter (WINT), spring (SPRN), and summer (SUMR) precipitation amounts (cm) and significant regressions on total water-year (WTYR) precipitation (cm). Value in parentheses is probability of exceeding F, based on Type II sum of squares, followed in the last model by the partial correlation coefficient of the variable. Partial r^2 of eliminated variables can be computed by the difference in r^2 between successive models. All terms not significant at $P < 0.1$ were eliminated to yield the final model.

Dependent variable	Independent variables	r^2	P
Total biomass outside	= −25.79 + 2.30 FALL (0.070) − 0.55 WINT (0.618) + 9.45 SPRN (0.008) + 2.37 SUMR (0.043)	0.59	0.007
	= −27.99 + 2.20 FALL (0.071, 0.10) + 8.92 SPRN (0.007, 0.29) + 2.38 SUMR (0.038, 0.19)	0.58	0.002
	= − 0.33 + 1.83 WTYR (0.340)	0.34	0.007
Green biomass inside	= 10.61 + 2.73 FALL (0.533) + 3.97 WINT (0.002) + 2.03 SPRN (0.620) − 0.79 SUMR (0.345)	0.59	0.021
	= 32.97 + 0.72 FALL (0.648) + 4.01 WINT (0.001) − 0.41 SUMR (0.197)	0.58	0.008
	= 35.70 + 3.98 WINT (0.007) − 0.31 SUMR (0.147)	0.58	0.002
	= 32.60 + 3.74 WINT (0.001, 0.51)	0.51	0.001
	= 34.04 + 0.87 WTYR (0.024)	0.28	0.024
Green biomass outside	= −57.57 + 8.24 FALL (0.030) + 0.37 WINT (0.639) + 9.47 SPRN (0.004) − 1.32 SUMR (0.188)	0.65	0.014
	= −52.56 + 7.65 FALL (0.024) + 9.22 SPRN (0.003) − 1.08 SUMR (0.185)	0.64	0.005
	= −21.87 + 3.79 FALL (0.006, 0.34) + 6.37 SPRN (0.001, 0.24)	0.58	0.003

Calf:cow ratios varied among sectors of the winter range in early winter (Table 5) during seven of nine years for which classification data were available (Friedman test, $P < 0.01$). The Jonkhere ordered-alternative test suggested calf:cow ratios were ordered from highest to lowest in the sectors as follows: lower-outside = lower-inside > middle > upper (S = 36, $P < 0.04$). Spike:cow ratios were lower in the middle and upper sectors during four of eight winters of early-winter classifications (Table 5, $P < 0.05$). These results suggested a greater tendency of cow–calf groups and yearlings to migrate to lower elevations in winter.

Calf:cow ratios differed among various sectors of the winter range during five of six late-winter periods (Friedman test, χ^2_r = 69, $P < 0.01$). The Jonkhere ordered-alternative test indicated calf ratios were ordered from highest to lowest in the sectors as follows: outside = lower > middle > upper (S = 41, $P < 0.03$). Spike:cow ratios varied among sectors during only one of five late winters ($P < 0.05$) and the pattern was opposite that observed during early winters; harvests of spikes outside the park and migrations may have obscured patterns of yearling survivorship. Bull:cow ratios were higher in the middle and upper sectors of winter range than in the lower sectors during three winters, 1985–1988 ($P < 0.05$). The response was reversed in the winter of 1988/1989, when more bulls were observed outside the park ($P < 0.05$) in late winter. However, this could have resulted from the unusually high hunting offtake of cows (1864) relative to bulls (48) in the winter hunt in 1988/1989.

Calf:cow ratios declined in some or all sectors between early and late winter during four of five winters in which data were available (Table 5), suggesting significant differential overwinter mortality rate of calves compared to cows. Low relative mortality of calves in winter 1989/1990 could have been the result of a moderate winter and reduced population size. Spike:cow ratios declined over all winters. Bull:cow ratios declined during two winters and increased in two winters.

Elk population responses

Negative correlations were observed between winter spike:cow ratio and elk number in the previous elk-year (r = −0.84, $P < 0.001$), and between bull:cow ratio and elk number in the previous elk-year (r = −0.78, $P < 0.001$). Calf:cow ratio was not significantly correlated with population size (r = −0.43). Calf:cow

TABLE 4. Winter severity indices and numbers of elk north of Yellowstone National Park, 1970–1991.

Year	Winter temperature severity index*	Winter snow severity index*	No. elk counted north of park†	Proportion of herd north of park‡	No. elk counted on Dome Mountain, north of park
1970/1971	1.5	−3.2	600	0.082	
1971/1972	0.7	−2.6	1300	0.158	
1972/1973	2.9	2.9	800	0.080	
1973/1974	0.0	−3.8	800	0.076	
1974/1975	0.7	−2.0	2786	0.221	
1975/1976	2.0	−3.4	1700	0.189	60
1976/1977	3.1	3.3	500	0.039	80
1977/1978	1.1	−2.4	2,000	0.203	258
1978/1979	−4.0	−1.6	1500	0.138	389
1979/1980	−0.4	1.4			
1980/1981	3.0	3.8			
1981/1982	−0.3	−1.9	1097	0.068	
1982/1983	3.1	1.0			
1983/1984	−2.9	2.1			
1984/1985	−2.6	0.3			477
1985/1986	0.9	1.4	2998	0.184	135
1986/1987	2.7	3.7	1723	0.101	298
1987/1988	1.5	3.1	483	0.026	105
1988/1989	−3.3	−1.9	5290	0.338	1938
1989/1990	1.5	−0.6	3400	0.229	2139
1990/1991	−3.4	1.5	1400	0.097	722

* The ranking index varies from −4.0, most severe, to +4.0, mildest (Farnes 1996).
† Data from Houston (1982) and F. J. Singer (*unpublished data*).
‡ Includes elk taken in the regular hunt prior to the count.

and bull:cow ratios were positively correlated with precipitation in year $t - 2$ (Fig. 3). Spike:cow ratio was also correlated with precipitation, but the relationship was weaker ($y = -3.9 + 0.34x$, $r^2 = 0.27$). Calf:cow ratio was positively correlated with winter ($r = 0.47$, $P < 0.05$) and summer ($r = 0.48$, $P < 0.05$) precipitation in year $t - 2$. Spike:cow ratio was significantly correlated with winter precipitation in year $t - 2$ only ($r = 0.44$, $P < 0.05$). Bull:cow ratio was not significantly correlated with precipitation in any single season.

Herd composition was not significantly correlated with any measure of winter weather severity including winter temperature, winter snowfall, winter temperature severity index, winter snow severity index, winter snow and temperature index, or snow water contents in year $t - 1$. Correlations between spring precipitation in year $t - 1$ and calf:cow ($r = -0.40$), spike:cow ($r = -0.40$), and bull:cow ($r = -0.30$) ratios were nearly, but were not, statistically significant ($P > 0.05$).

Forward stepwise multiple regression analyses of herd composition parameters showed the sensitivity of calf:cow ratio to precipitation (Table 6). Winter and summer precipitation, or water-year precipitation, were included in the best models for calf:cow ratio. Elk numbers did not enter into calf:cow ratio models. Elk numbers entered first into models for spike:cow and bull:cow ratios. Water-year precipitation explained less of the variance in spike:cow and bull:cow ratios than did elk numbers. Fall and spring precipitation amounts both helped to explain variations in bull:cow ratios. No seasonal precipitation amount entered significantly into the spike:cow ratio model.

Calf mortality rates were generally higher than cow and bull mortality rates. Summer calf mortality rate was 0.52 ± 0.16 (mean ± 1 SD), $n = 16$ years. Mean winter calf mortality rate was 0.32 ± 0.29, $n = 15$ years. Mean cow mortality rate was 0.08 ± 0.09, $n = 15$ years. Mean bull mortality rate was 0.18 ± 0.18, $n = 15$ years. Summer calf mortality rate was significantly higher than winter calf mortality rate ($P = 0.05$, $t = 2.0$). Summer calf mortality rate was negatively correlated with precipitation (Fig. 4A), but it was not correlated with elk population size ($r = 0.33$) or any winter severity index, including winter and spring precipitation, or temperature or snow severity indices in year t. Summer calf recruitment rate was positively correlated with winter ($r = 0.52$, $P < 0.05$), summer ($r = 0.54$, $P < 0.05$), and water-year precipitation (Fig. 4B), and negatively correlated with elk number (Fig. 5A). Winter calf mortality rate was negatively correlated with fall ($r = -0.54$) and water-year precipitation (Fig. 4C) in year $t - 1$. Winter mortality rate was strongly correlated with elk number (Fig. 5B). There were no correlations between winter calf mortality rate and any measure of winter weather severity, although winter mortality rate was correlated with spring precipitation in year t ($r = 0.61$, $P < 0.05$).

Cow mortality rate was not correlated with water-year precipitation ($r = -0.02$) or elk number ($r = 0.28$). Although cow mortality was not correlated with any measure of winter weather severity in year t, it was

TABLE 5. Elk herd composition on lower, middle, and upper sectors of the northern Yellowstone winter range and outside the park boundary in early and late winter. "Lower-in" and "Lower-out" refer to lower sectors inside and outside the park, respectively.

	No. calves per 100 cows		No. spikes per 100 cows		No. bulls per 100 cows		Sample size	
	Early	Late	Early	Late	Early	Late	Early	Late
1982/1983								
Lower-in	46		6				780	
Upper	27*		7				250	
Total	41		6				1030	
1983/1984								
Lower-in	47		18				581	
Upper	25*		5*				364	
Total	38		12				945	
1984/1985								
Lower-in	48		12				433	
Upper	24*		3*				461	
Total	34		7				894	
1985/1986								
Lower-out	56	35		3		1	3039	779
Lower-in	66	57*		4		18	583	414
Middle	52	25		3		32	305	1565
Upper	32*	20*†		5		28*	2446	454
Total	48	30†	4	3	26	21	5363	3212
1986/1987								
Lower-out	42	32*		4		6	1930	1759
Lower-in	46	22		6		16	1253	2276
Middle	36	18		6		18	895	4836
Upper	21*	19*†		13*		50*	1496	522
Total	33	22†	7	6	16	16	5574	9393
1987/1988								
Lower-out	44	21*		5		2	1560	724
Lower-in	48	27†		4		8	485	1497
Middle	40	21†		4		27	985	2672
Upper	32*	17		5		168*	1667	356
Total	40	25†	5	4	19	26	4967	7470
1988/1989								
Lower-out	30	19				27		1615
Lower-in	18	8†	7	3	19	14	956	817
Middle	25*	6†	2	3	31	20	962	794
Upper	24	4*†	2	1	28*	10*	695	1011
Total		9†	3	2	26	19†	2613	4237
1989/1990								
Lower-out		37*		4		32		413
Lower-in	21	41	3	3	19	19	737	1109
Middle	19	15	4	3	22	18	3255	1131
Upper	18	19†	6*	3	17*	13†	1487	287
Total	19	20	5	3†	20	14†	5479	2940
1990/1991								
Lower-out	28	21					319	357
Lower-in	42	27	10		12		2207	624
Middle	23	30	8		15		1281	288
Upper	21*	27	5		13		2210	1627
Total	27	26	6		13		6017	2896

* Significant difference among winter range areas ($P < 0.05$).
† Significant difference between early and late season ($P < 0.05$).

positively correlated with precipitation in the previous spring ($r = 0.54$, $P < 0.05$). Bull mortality rate was negatively correlated with water-year precipitation (Fig. 4D), and with fall ($r = -0.75$, $P < 0.01$) and summer ($r = -0.78$, $P < 0.01$) precipitation in the previous year. Like cow mortality, bull mortality was positively correlated with spring precipitation in the previous year ($r = 0.54$, $P < 0.01$), and was not correlated with any measure of winter weather severity in the current year. Bull mortality rate was not significantly correlated with elk number ($r = 0.39$).

Per capita rate of increase was not significantly correlated with water-year precipitation ($r = 0.46$, $P = 0.06$), but a trend was present. Per capita rate of in-

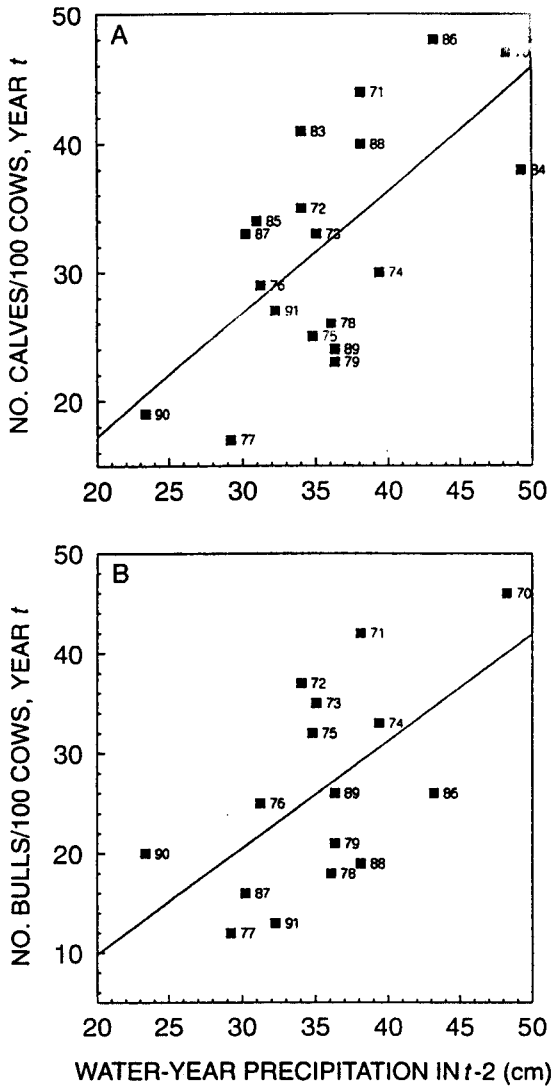

FIG. 3. Relations between ratios in early winter 1970–1990 (year t) to water-year precipitation of two seasons prior (year $t - 2$): (A) calf:cow, $y = -1.9 + 0.95x$, $r^2 = 0.43$; and (B) bull:cow, $y = -11.6 + 1.07x$, $r^2 = 0.36$. Points are labeled by year, where year 68 is winter 1967/1968, for example.

crease was positively correlated with fall precipitation ($r = 0.58$, $P < 0.05$) and negatively correlated with spring precipitation ($r = -0.49$, $P < 0.05$) in year $t - 1$. The per capita rate of increase was negatively correlated with total elk numbers (Fig. 6, Table 7). By definition of carrying capacity, K, in the logistic equation, the actual per capita rate of increase (r_a) is equal to zero when population size (N) equals K:

$$\frac{dN}{dt} = rN\left(\frac{K - N}{N}\right), \quad \text{and}$$

$$r_a = r\left(\frac{K - N}{N}\right),$$

where r is the intrinsic rate of increase. In Fig. 6, along the lowest line of r_a vs. N, $r_a = 0$ at ≈10 000 sighted elk. Conversely, the uppermost line of r_a vs. N in Fig. 6 defines a maximal K of ≈18 000 sighted elk.

Forward stepwise regression analyses indicated that summer calf recruitment was most closely tied to precipitation rather than to elk number (Table 7). Summer and winter precipitation were both retained in the best model. Elk number entered the model first, followed by winter and then summer precipitation. Then elk number was removed in the forward stepwise regression procedure, to leave only winter and summer precipitation in the final model. The final model based upon precipitation had a higher r^2 and was more significant than the model based upon elk number alone (Table 7). The most significant models for summer calf mortality included summer and winter, or water-year, precipitation.

In contrast, elk number was the first variable to enter the model for winter calf mortality rate (Table 7). Fall precipitation contributed less to the regression. When the number of elk counted was excluded from the analysis, fall and winter precipitation both entered as significant negative terms in a model for winter calf mortality rate. The only significant regression model for cow mortality rate included a positive effect of spring precipitation the prior year. Bull mortality rate was best modeled as decreasing in response to summer and fall precipitation, although water-year precipitation was also a moderately good predictor. The number of elk counted was not a significant correlate with bull mortality rate. The best model for per capita rate of increase included elk numbers and fall precipitation. Although spring precipitation was a significant correlate with per capita rate of increase ($r = -0.49$, $P < 0.05$), it did not significantly enter the model (Table 7). No model of per capita rate of increase based upon water-year precipitation was significant.

The empirical elk population model was based upon equations developed in Table 7. The best stepwise regression equation for calf recruitment rate included summer and winter precipitation. The best winter calf mortality equation included fall precipitation and elk numbers. Cow mortality was best predicted from spring precipitation and bull mortality was best predicted from fall and summer precipitation. The empirical population model predicted observed numbers of sighted elk from 1969 to 1990 well, using annual hunt rates of 2% of calves and cows and 5% of bulls (Fig. 7). Over the 30 stochastic simulations using the same hunting rates, elk numbers increased, then fluctuated about 16 400 ± 2500 sighted elk (mean ± 1 SD), varying from lows of ≈10 000 to highs of ≈23 000 elk (Fig. 8).

DISCUSSION

Plant biomass responses to precipitation

The positive correlation of aboveground plant biomass with water-year precipitation is in agreement with many studies that have shown that grassland primary

TABLE 6. Forward stepwise regression analyses of the arcsine of calf, spike, and bull ratios during elk-year t against precipitation in the winter (WINT), fall (FALL), summer (SUMR), and spring (SPRN) of elk-year $t - 1$, and winter elk numbers (ELK) in elk-year t; or against water-year precipitation (WTYR) and ELK. Value in parentheses is probability of exceeding F. Partial r^2 of eliminated variables can be computed by the difference in r^2 between models. All terms in the last model are significant at the $P = 0.15$ level. Variables not entered in the last model did not meet the $P = 0.15$ significance level. Number of years is given in n.

Dependent variable	Independent variables	r^2	P	n
Arcsine(calf : cow$_t$)	$= 0.156 + 0.016\ \mathrm{WINT}_{t-2}$	0.23	0.036	19
	$= 0.056 + 0.014\ \mathrm{WINT}_{t-2}$ (0.047) $+ 0.009\ \mathrm{SUMR}_{t-2}$ (0.051)	0.40	0.017	19
	$= -0.032 + 0.010\ \mathrm{WTYR}_{t-2}$	0.41	0.003	19
Arcsine(spike : cow$_t$)	$= 0.018 - 8.03 \times 10^{-6}\ \mathrm{ELK}_{t-2}$	0.71	0.001	16
	$= 0.085 + 0.0022\ \mathrm{WTYR}_{t-2}$ (0.117) $- 6.5 \times 10^{-6}\ \mathrm{ELK}_{t-1}$ (0.002)	0.77	0.001	16
Arcsine(bull : cow$_t$)	$= 0.502 - 1.97 \times 10^{-5}\ \mathrm{ELK}_{t-2}$	0.60	0.007	15
	$= 0.401 + 0.011\ \mathrm{FALL}_{t-2}$ (0.149) $- 1.69 \times 10^{-5}\ \mathrm{ELK}_{t-2}$ (0.003)	0.67	0.001	15
	$= 0.214 + 0.229\ \mathrm{FALL}_{t-2}$ (0.030) $+ 0.220\ \mathrm{SPRN}_{t-2}$ (0.091) $- 1.86 \times 10^{-5}\ \mathrm{ELK}_{t-2}$ (0.001)	0.75	0.001	15
	$= 0.229 + 0.0063\ \mathrm{WTYR}_{t-2}$ (0.141) $- 1.52 \times 10^{-5}\ \mathrm{ELK}_{t-1}$ (0.011)	0.67	0.001	15

productivity is influenced by precipitation (Sims and Singh 1978, Webb et al. 1978, Sala et al. 1988). Most grasslands are water-limited, and are commonly replaced by forests in more mesic climates (e.g., Borchert 1950). The variance in plant biomass data from Yellowstone was not fully explained by precipitation, however. The unexplained variance could have been caused by differences in plants, soils, and landscape positions among plots and sampling sites, and by differences in sampling methodologies. More extensive sampling, integrating over a broader area, could provide a tighter correlation, as more of the among-plot and among-site variance is averaged out (e.g., Sala et al. 1988). Ideally, long-term plant growth data should be collected from the same sites every year, so as not to confound site and climate effects. Although the ideal long-term data set was not available, we believe the evidence shows that forage biomass is positively affected by precipitation on the northern Yellowstone elk winter range. Data from many other grassland studies support this conclusion.

Plant biomass production was influenced by the distribution of annual precipitation among seasons. Plant biomass was predicted more accurately from equations based upon seasonal precipitation amounts than upon total water-year precipitation. The fact that green and total biomass amounts outside exclosures were correlated with spring, summer, and fall precipitation, whereas green biomass inside exclosures was correlated mainly with winter precipitation, suggests that grazing alters the importance of precipitation in different seasons. Possibly, the accumulation of standing dead shoots inside exclosures reduced evaporative losses of winter precipitation from bare soil, and increased interception of spring precipitation by dead leaves and litter, with consequent evaporative loss from these surfaces. By summer, however, soil moisture was not significantly different inside vs. outside exclosures (Coughenour 1991, Singer and Harter 1995). Total biomass outside exclosures in 1988 was comparable to that in 1987 (Singer et al. 1989, Coughenour 1991), despite the drought in the summer of 1988. Regression results indicated that spring precipitation contributed more grams of total biomass per centimetre of water than did precipitation in other seasons. The correlations between spring precipitation and green and total biomass outside exclosures suggest that above-average spring precipitation in 1988 could have supported ample plant growth, but the dry summer of 1988 caused earlier senescence.

The increase in elk numbers from 1969 to 1988 has apparently had little effect on peak herbaceous standing crop on the winter range. Forage biomass measured from 1986 to 1988, when 16 000–19 000 elk were counted, was similar to forage biomass from 1935 to 1950, when 10 000–13 000 elk were counted. This is consistent with comparisons of current live standing crop and total cover inside and outside exclosures (Coughenour 1991, Coughenour et al. 1995, Singer 1995) and aboveground primary production (Frank and McNaughton 1992, 1993), which have failed to show conclusive negative effects of elk herbivory on herbaceous vegetation.

Elk population responses

The hypothesis that the northern Yellowstone elk herd is nutritionally limited was supported by two relationships. First, the elk appeared to respond to precipitation. Elk population responses to precipitation were most likely caused by variations in forage pro-

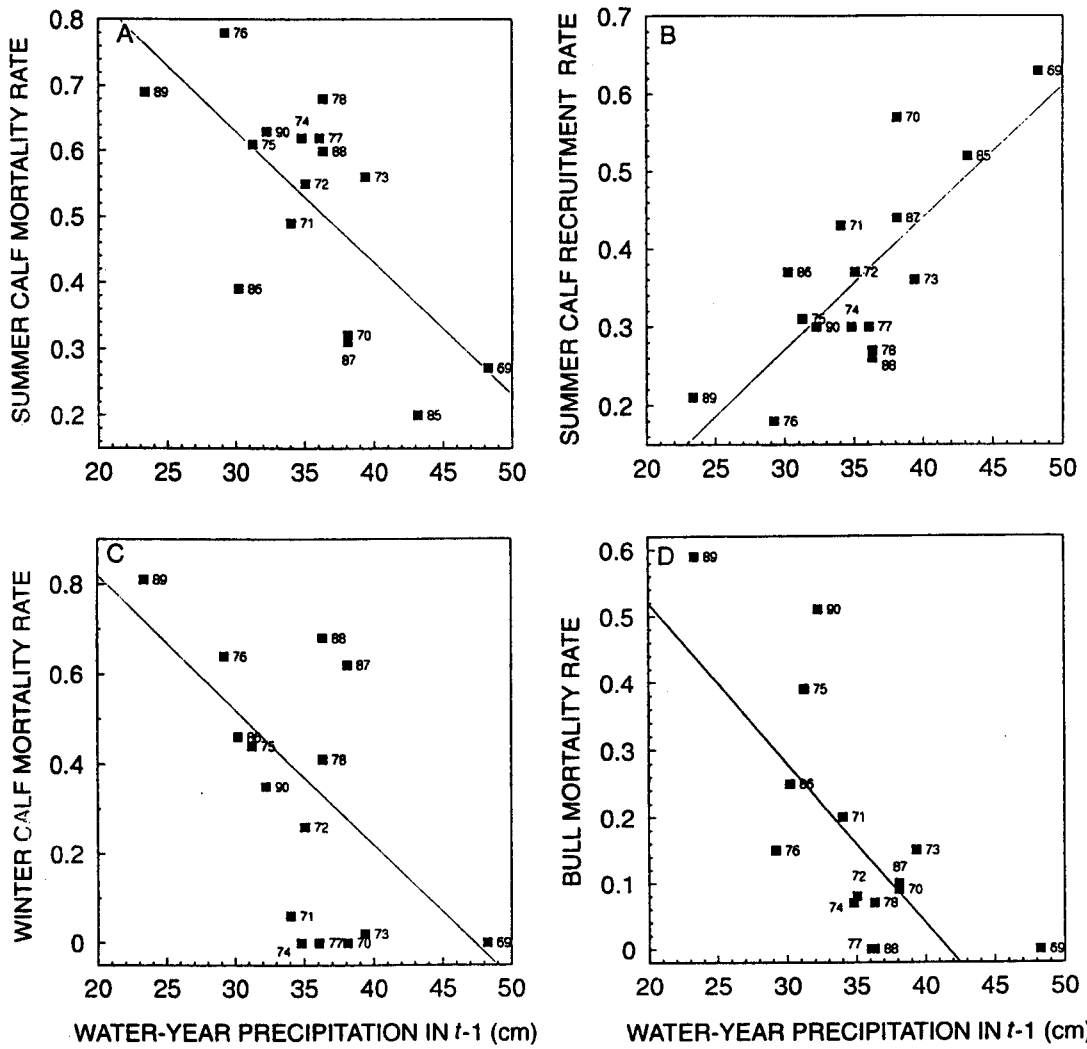

FIG. 4. Year t responses to prior water-year precipitation (year $t - 1$) of (A) summer calf mortality; (B) summer calf recruitment; (C) winter calf mortality, $y = 1.42 - 0.03x$, $r^2 = 0.37$, $P = 0.01$; and (D) bull mortality (see Table 7 for other regression equations and significance). Points are labeled by year, where 68 is summer of 1968 or winter of 1967/1968, for example.

ductivity, given that we have shown forage abundance to be correlated with precipitation. Second, the elk population grew less rapidly when elk were more abundant. This strongly suggests that the elk were competing for a limiting resource. Because elk are not limited by water and are nonterritorial during winter (Boyd 1978), the limiting resource was most probably food.

Population recruitment appeared to be strongly influenced by precipitation. The early winter calf:cow ratio was highly correlated with precipitation, but was not significantly correlated with population size. Precipitation strongly affected summer calf recruitment and mortality. In contrast, elk numbers had little or no effect on the calf:cow ratio, summer mortality, or recruitment. The correlation between precipitation and recruitment rate was stronger than that between precipitation and summer mortality, suggesting that natality rate could also have been influenced by precipitation. The weak response to population size is consistent with red deer (*Cervus elaphus*) summer calf survival, which also did not vary in relation to population size (Guinness et al. 1978, Clutton-Brock et al. 1982). Survival rates of juvenile kudu (*Tragelaphus strepceris*) were also more strongly influenced by rainfall than by population density (Owen-Smith 1990). Survival rates of African buffalo (*Syncerus cafer*) calves were not significantly correlated with population density, although a trend was evident and the sample size was small (Sinclair 1977). Juvenile buffalo mortality may have been more influenced by precipitation. The buffalo population was mainly regulated through the adults, because adult mortality was tightly coupled with population size but juvenile mortality was not.

Calf survival during winter was probably influenced

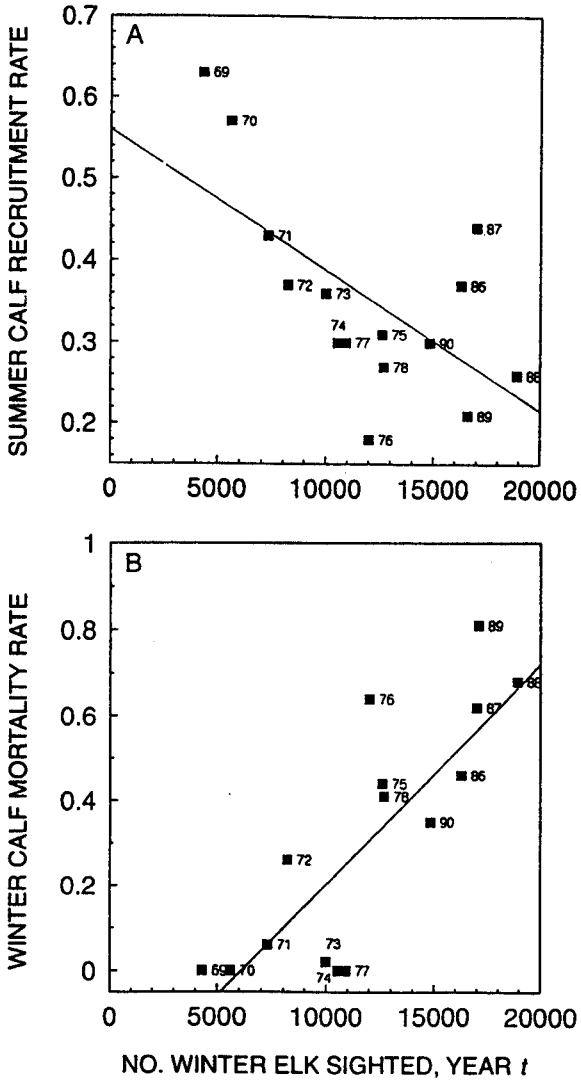

FIG. 5. (A) Summer calf recruitment, and (B) winter calf mortality responses in year t to winter elk number in year t (see Table 7 for regression equations). Points are labeled as in Fig. 4.

by different factors than was survival during summer. Seasonal foraging environments are different, as are the processes leading up to winter vs. summer stresses (Fig. 2). The apparent effect of elk density on winter calf mortality rate was stronger than the apparent effect of precipitation. In studies by Lowe (1969), Guinness et al. (1978), Staines (1978), and Clutton-Brock et al. (1987), winter survival of elk and red deer (*Cervus elaphus*) calves similarly declined with increasing population size. During the winter, foraging area is restricted by deeper snows at higher elevations. This probably amplifies calf mortality responses to elk density. Nevertheless, fluctuations in forage density within the available foraging area influenced winter mortality, as suggested by a significant correlation between winter calf mortality and precipitation in the previous year.

Winter weather and foraging conditions are likely to be more stressful during winter than summer. Decreasing potassium:creatinine ratios and increasing urea:creatinine ratios through the winter indicated increasing nutritional deprivation and catabolism of lean body, respectively (DelGiudice et al. 1991). Much of the effect of winter stress upon cows carrying calves may not be exhibited until summer, however, when the cumulative over-winter stress affects mortality and recruitment of spring-born calves. The fact that calf mortality rate in summer (mean 0.52) exceeded that in winter (mean 0.33; $t = 2.5$, $0.01 < P < 0.05$) is consistent with the hypothesis that winter stress has less of an effect on the 6–8 mo-old overwintering calves than on the smaller newborns in spring and summer. Similarly, winter mortality in red deer was determined by birth date, population density, and home range, but summer calf mortality was determined by calf birth weight and age of the cow (Guinness et al. 1978). Differences in juvenile mortality in donkeys were related to the nutrition of lactating females (Choquenot 1991). Mech et al. (1987) found that snow accumulation in the winter prior to birth strongly affected survivorship of juvenile deer and moose. Owen-Smith (1990) also found that juvenile kudu survivorship was correlated with rainfall in the preceding year, through effects on the nutritional status of adult females.

A large fraction of the variance in bull mortality rate was explained by precipitation, yet elk population size did not affect bull mortality rate. In other studies, survival rates of adult males declined with increasing population size (Anderson 1958, Flook 1970, Clutton-Brock et al. 1982). Bulls may be more sensitive to plant

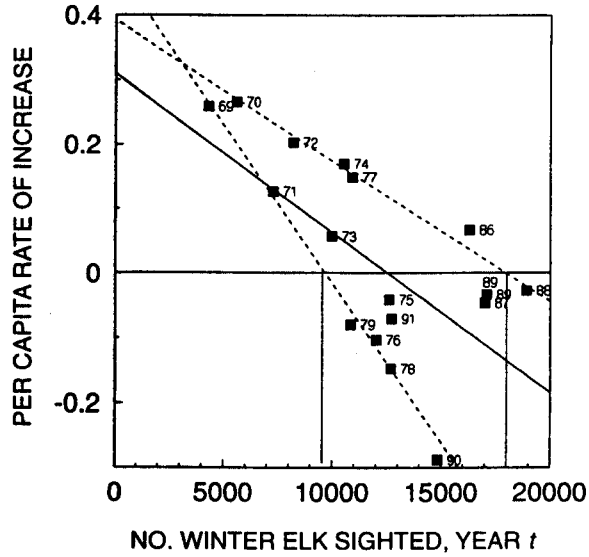

FIG. 6. Elk population per capita rate of increase in year t vs. winter elk number (see Table 7 for regression). Minimum and maximum lines (dashed) are related to corresponding ecological carrying capacity (K) values, where rate of increase (r_a) equals zero.

TABLE 7. Forward stepwise regression analyses of elk recruitment and mortality rates during elk-year t and per capita rate of increase (r_n) against precipitation in the winter (WINT), fall (FALL), summer (SUMR), and spring (SPRN) of elk-year $t - 1$, and winter elk numbers (ELK) in elk-year t; or against water-year precipitation (WTYR) and ELK. Value in parentheses is probability of exceeding F. Partial r^2 of added or eliminated variables can be computed by the difference in r^2 between models. All terms in the last model are significant at the $P = 0.15$ level. Variables not entered in last model did not meet the $P = 0.15$ significance level. Number of years is given as n.

Dependent variable	Independent variables	r^2	P	n
Summer calf recruitment rate	$= 0.570 - 1.8 \times 10^{-5}\ \mathrm{ELK}_{t-1}$	0.42	0.009	15
	$= 0.320 - 1.3 \times 10^{-5}\ \mathrm{ELK}_{t-1}$ (0.050) $+0.018\ \mathrm{WINT}_{t-1}$ (0.090)	0.55	0.008	15
	$= 0.116 - 0.843 \times 10^{-5}\ \mathrm{ELK}_{t-1}$ (0.196) $+ 0.020\ \mathrm{WINT}_{t-1}$ (0.043) $+ 0.010\ \mathrm{SUMR}_{t-1}$ (0.010)	0.66	0.007	15
	$= -0.083 + 0.024\ \mathrm{WINT}_{t-1}$ (0.013) $+ 0.016\ \mathrm{SUMR}_{t-1}$ (0.011)	0.57	0.004	16
Summer calf mortality rate	$= 0.754 - 0.0186\ \mathrm{SUMR}_{t-1}$	0.23	0.063	16
	$= 1.01 - 0.025\ \mathrm{WINT}_{t-1}$ (0.093) $- 0.0184\ \mathrm{SUMR}_{t-1}$ (0.051)	0.38	0.044	16
	$= 1.23 - 0.020\ \mathrm{WTYR}_{t-1}$	0.47	0.003	16
Winter calf mortality rate	$= -0.330 + 5.44 \times 10^{-5}\ \mathrm{ELK}_{t-1}$	0.68	0.001	15
	$= -0.090 - 0.027\ \mathrm{FALL}_{t-1}$ (0.140) $+ 4.79 \times 10^{-5}\ \mathrm{ELK}_{t}$ (0.0007)	0.73	0.003	15
Cow mortality rate	$= -0.063 + 0.022\ \mathrm{SPRN}_{t-1}$	0.30	0.036	15
Bull mortality rate	$= 0.581 - 0.033\ \mathrm{SUMR}_{t-1}$ (0.001)	0.60	0.001	15
	$= 0.646 - 0.033\ \mathrm{FALL}_{t-1}$ (0.001) $- 0.022\ \mathrm{SUMR}_{t-1}$ (0.011)	0.77	0.001	15
	$= 1.00 - 0.024\ \mathrm{WTYR}_{t-1}$	0.51	0.003	15
Per capita rate of increase	$= 0.321 - 2.47 \times 10^{-5}\ \mathrm{ELK}_{t}$ (0.003)	0.45	0.003	17
	$= 0.119 + 0.023\ \mathrm{FALL}_{t-1}$ (0.057) $- 1.93 \times 10^{-5}\ \mathrm{ELK}_{t}$ (0.015)	0.57	0.002	17

production because they are more likely to deplete their energy reserves during the rut in fall, and tend to use habitats where foraging is more difficult because of deeper snow, less abundant forage or steeper topography (e.g., Watson and Staines 1978, Clutton-Brock et al. 1982; F. Singer, *unpublished data*). In Yellowstone, there were higher bull:cow ratios at higher elevations in three of five late winters. The poorer habitats that bulls use may be relatively abundant and there may be little competition for them, thus explaining the lack of effect of elk population size. Competition among bulls would be limited to these distinct habitats, where competition between bulls and calf–cow groups would be small or nonexistent. Therefore, either bull mortality rate is regulated in a density-independent manner or density effects arise from competition with

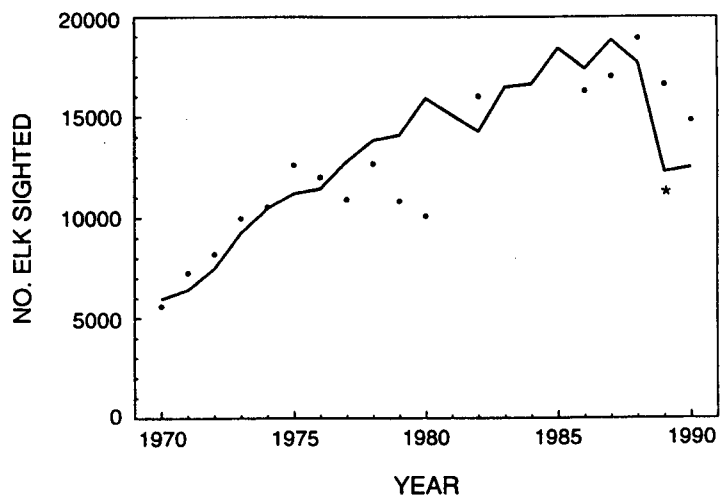

FIG. 7. Comparison of observed (points) and simulated (line) numbers of elk. The asterisk shows the number of elk actually sighted in winter 1988/1989.

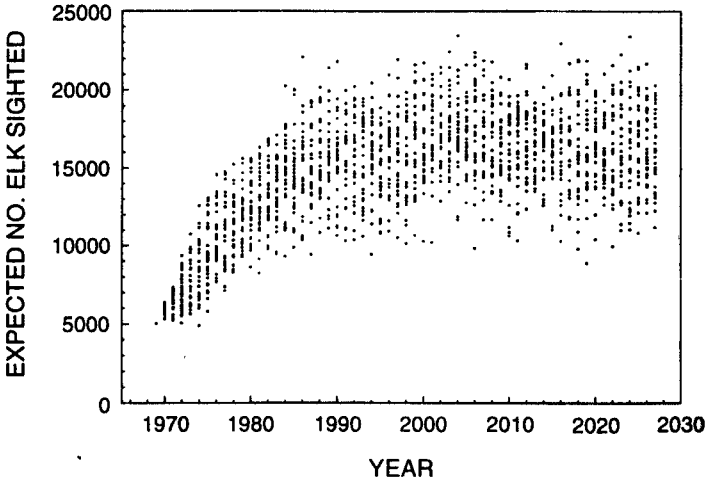

FIG. 8. Number of elk over time in 30 stochastic simulations.

other bulls, rather than with all of the elk in the herd. Bull mortality rate was not correlated with bull density ($r^2 = 0.01$), so the former explanation is more plausible. The susceptibility of bulls to density-independent factors was illustrated when severe snow patterns, coupled with reduced winter forage caused by the 1988 fires and a dry summer, were accompanied by a high bull mortality in winter 1988/1989 (Lemke and Singer 1989, Singer et al. 1989: Fig. 8a). A lower fraction of the older bulls than of cows or spikes migrated from traditional ranges that winter, including winter ranges that had burned (Singer et al. 1989).

Population dynamics were determined primarily by calf, spike, and bull survivorships, whereas cows appeared more resistant to changes in forage and elk number: no cow responses to density or to precipitation effects on forage were observed. Juveniles and males are probably especially vulnerable to changes in forage supply. Calves are competitively subordinate to mature animals in winter foraging (Houston 1982), and may begin winter with smaller energy reserves. Cows that carry calves and then nurse are more prone to experience energy deficits, with the dependent calves suffering disproportionately. Bulls not only experience large energy demands during the rut in fall, but they also may use more marginal habitats than cows. Analogous results were observed in African kudu (Owen-Smith 1990), where precipitation-related calf survival was the key factor in population fluctuations. Cow elk survival was unaffected by precipitation. As with kudu, cow elk conferred population resilience against fluctuations in resource abundance.

Correlations between mortalities in year t and plant growth in year $t - 1$ could have reflected elk responses to forage limitations in the summer or winter (Fig. 2). However, the primary forage limitations probably occurred during winter. Nonforested transitional and summer ranges are more productive than winter ranges because of their higher elevation and precipitation (e.g., Frank and McNaughton 1992, 1993, Merrill et al. 1993). Forested summer range is much less productive but is quite expansive. Nutritionally based estimates of carrying capacity accounting for habitat productivities and areas indicated that summer range K values are at least twofold greater than winter range K values (Coughenour and Singer 1996). Negative correlations between summer range plant production and population rate of increase could be a consequence of higher snowfall limiting elk foraging, while providing increased moisture to support plant growth (Merrill and Boyce 1991).

The number of elk that can be supported varies considerably among years, as indicated by the high unexplained variance (55%) in the correlation between per capita rate of increase and elk number (Fig. 6). This variance translates into a large uncertainty in ecological carrying capacity (K). Although the median K would be 14 000 counted elk, the range of possible K values is quite broad (10 000–18 000 elk). The median K value agrees very closely with the prediction of a population model based upon a regression equation for r_a (Merrill and Boyce 1991).

The empirical state-structured population model provided realistic simulations of elk population dynamics (Fig. 7). The major deviation from observed values occurred in 1979–1980, when fewer elk than predicted were seen. Variability in counting conditions introduces errors into the data, however. The large increase from 1980 to 1982 suggested by the data may not actually have occurred. The ability of the model to simulate the data lends support to its predictions that population size continued to increase throughout the 1980s, but that further increases over the long term should not be expected. Numbers of sighted elk should fluctuate about a mean of ≈16 400, which is ≈2500 more elk than the median K estimated by the r_a vs. N analysis (Fig. 6), and ≈1400 more elk than the K of 15 000 estimated by Houston (1982). The apparent decline between 1975 and 1980 (Fig. 7) gave the impression that the popu-

lation had reached K, and probably biased mathematical estimates of K downwards.

Winter weather effects

We could not document any significant effects of season-long winter severity on elk population dynamics, based on winter severity indices. Merrill and Boyce (1991) found that a modified Lamb's winter severity index was correlated with population rate of increase and spike:cow ratio (an index of yearling recruitment), but there was no correlation with calf:cow ratio. Picton (1984) observed that the intensity of winter effects on Montana elk population growth rates depended upon the size of the elk population relative to carrying capacity (K); climatic effects were significant only when elk populations were at carrying capacity. The northern Yellowstone elk population has varied near or above K (defined as in Fig. 6) since 1974/1975, so mortality and population growth rates should have been correlated with winter severity indices, based upon Picton's observation.

Indices of winter-long severity reflect winter-long average or cumulative conditions and, consequently, are insensitive to short periods of extremely severe weather. For example, a large portion of the die-off in the winter of 1988/1989 occurred in a 2-wk period in late February (T. Lemke, *personal communication*), although that winter was not severe according to the winter-long snow severity index (Table 4). Snow crusting is promoted by short intervals of warm weather, yet no winter severity index accounts for crusting. Winter severity may be more detrimental late in the season than early. In late winter, animals have depleted their energy reserves more completely and forage is more grazed down or weathered. Winter severity could be more detrimental when forage supply is low. The dry summer of 1988/1989 probably produced less forage and the forage probably cured earlier.

Other evidence did suggest that the elk are affected by severe winter weather. Severe winter weather clearly contributed to die-offs in 1974/1975 (Cole 1983), as well as 1919/1920 (Houston 1982) and 1988/1989 (Singer et al. 1991, Coughenour and Singer 1996, Farnes 1996). Physiological evidence of nutritional stress is associated with declines in calf:cow ratios from early to late winter (DelGiudice et al. 1991). Bull and cow mortality rates were positively correlated with spring (April–May) precipitation in the prior year, per capita rate of increase was negatively correlated with spring precipitation in the prior year, and winter calf mortality was positively correlated with spring precipitation in the current year. Spring precipitation could be more stressful because rain-on-snow, or alternating periods of warm and freezing temperatures, would produce a crust; because elk would more probably have exhausted their energy reserves by then; and because the insulating capacity of elk coats might be decreased by wet spring snow or rain during cold temperatures. Early spring precipitation effectively lengthens the winter by restricting access to the summer range. Adult elk would have less time on the summer range, culminating in lower energy reserves the following winter and possibly explaining the 1-yr time lag between spring precipitation and adult mortality.

Elk distributions and foraging appear to be spatially constrained by deep snows. The winter range itself is obviously delimited by deeper snow at higher elevations, and there are probably also important limitations on available foraging area within the outermost perimeter of the winter range. This constraint was noted by Grimm (1939), who estimated that ≈41 000 ha were available during an average February. Houston (1982) estimated that ≈45 000 ha were available during periods of maximum compression. Interannual variations in snow depth and available foraging area contributed to interannual variations in K in a spatial-dynamic ecosystem model (Coughenour and Singer 1996). The density-independent effects of snow cover on elk foraging probably contributed significantly to elk population dynamics. Models of nutritionally based elk carrying capacity and linked energy balance and population processes are sensitive to the effects of snow depth on forage intake rate and habitat selection (Coughenour and Singer 1996). When the population is near carrying capacity, and where forage supply is not as moisture-limited as in grasslands, fluctuating snow depths could be paramount. Thus, Mech et al. (1987) concluded that snow accumulation, with subsequent nutritional limitation, was the main determinant of changes in Minnesota deer and Isle Royale moose populations, despite significant amounts of predation.

Differences in calf:cow and yearling male:cow ratios among elevations suggest that cows with calves and yearlings had a greater tendency to migrate to lower elevations than did cows without calves (Table 5). These movements are especially significant because winter calf mortality greatly affects population growth rate. If cow–calf groups are restricted to a smaller area during winter than the herd as a whole, then available forage is effectively reduced and competition is effectively elevated.

Increased migrations have probably mitigated the effects of winter severity and drought on elk populations through increases in forage. Data from early counts, 1916–1962, indicated that 15–30% of the herd migrated outside the park in most years, with up to 60% migrating during very severe winters and <10% during mild winters (Houston 1982). The fraction migrating remained mostly well below 15% from 1964 to 1974. The numbers of elk migrating north of YNP then increased in response to severe weather during the winter of 1974/1975, with subsequent migrating proportions exceeding 15% in half of the years counted. Reduced disturbances from livestock grazing, largely due to recent land acquisitions (Olsen and Black 1990), probably reinforced the increased migrations. Higher num-

bers of animals migrating outside the park could have reflected increased total herd size because the proportion of the herd migrating did not increase (Table 4), but the herd may have increased, in part, because more elk migrated out of the park. According to a nutritional model of carrying capacity (Coughenour and Singer 1996), areas outside the park provide 36% of the total elk winter range forage base.

Implications for elk management policy

Management of elk in YNP has been controversial (Pengelly 1963, Cole 1971, Beetle 1974, Cayot et al. 1979, Chase 1986, Baur 1987, Kay 1990, Boyce 1991*a*, Coughenour and Singer 1991), largely because there have been many different conceptual models for elk population regulation. Several resource managers and authors have felt that the elk herd cannot regulate itself at a level that prevents range damage because predators are absent and humans have preempted winter range habitat outside the park (Rush 1932, Cahalane 1943, Chase 1986, Kay 1990). Others have hypothesized that there is an ecologically complete habitat for elk in and just outside northern YNP, and food, rather than predation, controls elk population sizes in nature (Cole 1971, 1983, Houston 1982, Boyce 1991*b*). There are multiple definitions of carrying capacity, each one appropriate to a unique set of management objectives (Caughley 1976, McNab 1985, Coughenour and Singer 1991). Some authors have interpreted ecological carrying capacity as a stable equilibrium between elk and forage, whereas others allow that carrying capacity may be dynamic, so the elk population can never reach a steady state.

This analysis of the Yellowstone elk population data indicates that forage supply does limit the population. Although there is density-dependent competition for food, density-independent fluctuations in forage supply and forage availability prevent the population from ever attaining a static equilibrium. Density-independent factors include fluctuating precipitation and forage production, and variations in snow depth, areal extent, and hardness. Variability of spring precipitation is another source of density independence: cow and bull mortality rates are higher and intrinsic rate of increase tends to be lower following a year with a wet spring. Although cow mortality varies independently from density, density-dependent calf and bull mortality is sufficient to regulate the population. Insensitivity of cow mortality to precipitation or forage production is stabilizing and provides population "inertia." Together, these response patterns indicate that population regulation is "density-vague," and numbers should vary rather than attain a static equilibrium. The demographic properties of the population will ensure its persistence despite this variability.

Ecological carrying capacity (ECC) estimates based upon these data should be carefully interpreted. The median ECC based on an assumed intrinsic rate of increase of zero at equilibrium is 14 000 elk whereas the empirical population model suggests 16 400 elk. The fraction of elk actually sighted during counts is much lower (≈75% in good counts). Thus, actual mean ECC is ≈22 000 elk. A nutritionally based estimate of actual mean ECC is 21 000 elk (Coughenour and Singer 1995). These estimates may be higher than the earlier 14 000–15 000 sighted elk at ECC estimated by Houston (1982) and Merrill and Boyce (1991), because elk use of lands outside the park has increased since their estimates. These estimates are much higher than the earlier estimates of carrying capacity (Grimm 1939, Cooper 1963) for many reasons. Both of the earlier estimates were based on assumptions that no winter range existed outside the park. Mean areas available for foraging during the winter (due to snow) were of 42 000 ha (Grimm 1939) or 18 300–27 800 ha (Cooper 1963), which precluded use of any of the forage on the remaining one-half to two-thirds of the area at any point during the winter. Cooper assumed that no forage in woodlands or forests should be utilized, and provided no forage production data for the winter range. The "forage acre factor" method used by Grimm (1939) was abandoned long ago because it is inaccurate and based on questionable assumptions (Houston 1982).

Food limitation of the elk population is but one of several phenomena suggested to be valid criteria for continued application of the natural regulation policy. It was also suggested that herbivory should not cause vegetation to retrogress to early successional states (Cole 1971, 1983). Data from short- and long-term elk exclosures indicate that herbaceous vegetation did not retrogress from 1968 to 1990 (Houston 1982, Frank 1990, Coughenour 1991, Frank and McNaughton 1992, 1993, Coughenour et al. 1995, Singer and Harter 1995). Elk browsing suppressed the heights and diameters of aspen and riparian willow, however, long prior to termination of human controls on elk in 1968 (Kay 1990, Chadde and Kay 1991, Singer et al. 1994). Decline in beaver, drier climate, fire suppression, altered hydrology, and market hunting for elk prior to 1870 may also have affected these plant species, in combination with herbivory (Singer et al. 1994, Romme et al. 1995). Importantly, aspen and willow are small components (1–5%) of the elk diet (Singer and Norland 1994) and they have not been shown to limit elk population size. Thus, elk abundance is regulated by herbaceous plants and is, and probably always has been, largely decoupled from woody browse. Finally, models suggest that recently reintroduced wolves may lower elk numbers by 5 to 30% (Boyce 1993, Mack and Singer 1993), but it is unlikely that 5–30% fewer elk would result in increased aspen and willow, since leader use of those species did not decline during the period of reductions to <4500 elk (Barmore 1980, Singer et al. 1994).

Observed and empirically simulated population responses support the hypothesis that the northern Yellowstone elk herd is regulated through food limitation,

through both density-independent fluctuations in total available forage and density-dependent fluctuations in the forage available to each elk. These findings are consistent with other analyses of Yellowstone elk (Barmore 1980, Houston 1982), red deer (Guinness et al. 1978), and many other large herbivores (e.g., Sinclair 1977, Sinclair et al. 1985, Novellie 1986, Mech et al. 1987, Sheperd and Caughley 1987, Messier et al. 1988, Dublin et al. 1990, Owen-Smith 1990, Choquenot 1991). Whether past, current, or future numbers of elk are "acceptable" or "natural," or whether *a* self-regulated elk–plant system with minimal human intervention is more or less desirable than other alternatives, or *other* elk–plant systems, are different questions requiring different methods of assessment.

Acknowledgments

This research was funded by the United States National Park Service. We thank David Vales, Don Despain, C. Les Marcum, Harold Picton, Mark Boyce, Steve Keay, Marco Festa-Bianchet, and five anonymous reviewers for thoughtful comments on various versions of this report. Discussions with Dave Swift and Jim Ellis were useful. John Mack developed information on population size and composition and conducted elk classifications 1988–1991. E. O. Garton derived elk sightability models. We thank John Varley and the rest of the Yellowstone National Park research staff for invaluable scientific and logistical support.

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