DENSITY DEPENDENCE, COMPENSATION, AND ENVIRONMENTAL EFFECTS ON ELK CALF MORTALITY IN YELLOWSTONE NATIONAL PARK

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Abstract: We studied survival of radiocollared elk (*Cervus elaphus*) calves in Yellowstone National Park from 1987 to 1990, and survival of calves computed from population estimates from 1968 to 1992. We hypothesized that summer and winter survival of elk calves and mass of neonates were inversely related to population size, measures of environmental severity, and timing of births. Herd-wide survival estimates based on winter counts, reported harvests, and herd classifications, suggested that winter survival of elk calves was related inversely to estimated size of the elk population during winter ($P = 0.0002$), but we found no correlation with an index of winter severity ($P = 0.51$). Summer survival of elk calves also was correlated inversely with the estimated size of the elk population the previous winter ($P = 0.03$). Summer survival of radiocollared calves averaged 0.65 ($n = 127$ marked calves) from 1987 to 1990, the losses mostly due to predation (22%). Winter survival of calves averaged 0.72 ($n = 88$ marked calves entered the winter period), with losses due mostly to malnutrition (58%). Summer survival of radiocollared calves was positively correlated with estimated birth weight ($P = 0.001$). Survival of radiocollared calves during winters 1987–90 was correlated positively with early calving and mildness of the winter (in contrast to herd-wide survival estimates), and was inversely correlated with estimated elk population size that winter ($P = 0.006$). Winter survival of radiocollared calves was lower during 1988–89 following the drought and large fires than the other 3 winters ($P < 0.001$). Predation on elk calves during summer doubled after the drought and fires of 1988 (13% calf losses to predation before the fires vs. 29% after the fires). Potential compensation existed between components of calf mortality: predators killed more light ($P = 0.041$) and more late born calves ($P = 0.146$); calves were born later and lighter ($P = 0.048$) following severe weather conditions; and heavier born calves survived at a higher rate ($P = 0.006$). Our results are consistent with the hypothesis that density-dependent mortality of calves during winter due to malnutrition, and summer mortality of calves due to predation were partially compensatory but severe environmental conditions produced largely additive components to both summer (increased predation) and winter (increased malnutrition) mortality.

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Ungulates have not been culled within Yellowstone National Park (YNP) since 1969, following the adoption of an experimental policy of natural regulation (Cole 1971, Houston 1982). From 1938 to 1968, elk were reduced by trapping and shooting within the park boundaries. Elk that migrate north of the park are hunted and sport harvests have averaged 9% (range 3–12%) of the estimated herd in recent years (Houston 1982, Mack and Singer 1993*a*), but hunter harvest alone is not considered sufficient to regulate or limit the population (Houston 1982, Merrill and Boyce 1991, Mack and Singer 1993*a*). Regulation is the process by which a population returns to an equilibrium density through density dependent changes in mortality and natality. Limitation is the process which lowers density through density-independent changes in population production or loss (Sinclair 1989:199, Boutin 1992). The distinction between regulation and limitation is important for interpreting the potential effects of wolf (*Canis lupus*) reintroduction to Yellowstone.

Population regulation of the northern Yellow-

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stone elk population could occur through a variety of mechanisms, including density-dependent declines in conception or pregnancy rates (Verme 1965, 1969; Trainer 1971, Thorne et al. 1976), declines in neonatal survival, related to declines in birth weights (Verme 1969, Thorne et al. 1976, Clutton-Brock et al. 1982, 1987), or declines in over-winter survival of juveniles at higher elk densities (Staines 1978, Clutton-Brock et al. 1982, 1987; Houston 1982). Previous studies of the northern Yellowstone population conducted through 1979 demonstrated density dependence in pregnancy rates of cows (Rush 1932, Houston 1982:32), and density dependence in the mortality of elk calves during summer and winter as determined from herd classifications (W. J. Barmore, unpubl. data; Houston 1982:49, Dennis and Taper 1994). Following these studies which ended in 1979, the elk population continued to increase, possibly in response to milder winters in the 1980s and acquisition of elk winter ranges north of the park (Singer 1991, Coughenour and Singer 1996), providing additional opportunities to test for density dependence. We extended these earlier tests of density dependence in the elk population based upon herd classifications (Houston 1982, Merrill and Boyce 1991, Dennis and Taper 1994), to a total of 21 years of data, and we instrumented a sample of elk calves for 4 years (1987–90). Several climatic and environmental effects occurred during our studies in 1988–89, including a severe drought, a series of large fires, and a severe winter (Schullery 1989, Singer et al. 1989), that provided an opportunity to assess the effects of large stochastic environmental variation on juvenile elk survival. As an additional way of looking at the effects of environmental severity, we compared calf survival in 2 study areas where snow depths varied about twofold each winter, but where elk densities were similar.

Predation was not considered essential for natural regulation management when the policy was adopted (Cole 1971; Houston 1971, 1976). Density-dependence alone was considered sufficient to regulate the elk population (Cole 1971, Houston 1971), but the return of wolves to the system was later considered essential to natural regulation (Peek 1980), because wolves were later reported to limit or regulate ungulates (Bergerud et al. 1983, Gasaway et al. 1992, Messier and Crete 1985, Messier 1994). Predation on elk, especially by grizzly bears (*Ursus arctos*), was later determined to be a more significant factor in YNP based upon visual observations. This increase in bear predation was possibly a consequence of the learning of predatory behavior following closure of the YNP garbage dumps (Cole 1972, Mattson et al. 1991, French and French 1990). But the rates of predation on elk, in the absence of wolves, were still unknown. Wolf recovery was under consideration when our study was initiated, and wolves were returned to the area during February 1995, following nearly a decade of studies of their predicted effects (U.S. Fish and Wildl. Serv. 1987, Yellowstone Natl. Park 1990, Cook 1993). One question of particular interest is, will the recovery of wolves be an additive component of elk mortality, or will wolf predation simply compensate for winter starvation of ungulates? Compensatory mortality occurs when one form of mortality decreases mortality from other causes (Bartmann et al. 1992), due to density dependence in mortality factors (McCullough 1979, 1984). Bear predation on ungulates might be compensatory if bears kill calves in poor condition that were already predisposed to mortality from other causes (Boutin 1992). However, compensation has yet to be verified in studies of bear predation on ungulates (Boutin 1992).

As evidence for natural regulation and compensation among mortality factors, we hypothesized that: (1) calf survival would be inversely related to population density, (2) survival of calves would be related to body mass at birth and to early birthdate, (3) heavier and early born calves would survive at a higher rate, (4) survival of calves would be unrelated to environmental severity compared among different years and compared between 2 study areas with widely differing snow depths, and (5) survival of calves would be reduced due to either direct or indirect effects of the fires of 1988.

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STUDY AREA

The study was conducted on the winter, calving, and summer ranges of the northern Yellowstone elk herd (Houston 1982, Singer 1991). We selected 2 study areas for the capture of elk calves. The Gardiner study area encompassed 86 km^2 between 1,700 and 2,500 m in the lower elevation quarter of the winter range described in DelGuidice et al. (1991). The Lamar study area encompassed 115 km^2 between 2,000 and 2,600 m in the upper elevation quarter of the winter range, 35 km upstream from the Gardiner study area. Snow depths on the Gardiner study area (10–20 cm) were typically about half that of the Lamar study area (20–45 cm). Precipitation averaged 35 cm on the Gardiner study area and 55 cm on the Lamar study area (Houston 1982, DelGuidice et al. 1991). Spring precipitation was near normal during the study, but winter precipitation was <50% of average in both winters 1986–87 and 1987–88. Summer precipitation was 69% below normal in 1988 and June and July temperatures were 5 C and 0.5 C above normal, respectively, creating the most severe drought conditions in 52 years for the area (Schullery 1989, Singer et al. 1989). We rated the winter of 1988 to 1989 as the second-most severe (index = −2.8) of the 21 years of data using a winter severity index developed by Farnes (1994). Snows were deep and hard packed that winter, and 3 separate arctic storm fronts of several days duration accompanied by severe winds and extreme cold (−17 to −21 C) occurred.

Most of the study area was grasslands, and upland shrub communities dominated by big sagebrush (*Artemisia tridentata*) (37.3% of the study area) (Mueggler and Stewart 1980, Despain 1991:157–158). Forty-one percent of the study area was coniferous forest, dominated by Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) (Steele et al. 1983). Key calving habitats included dense stands of big sagebrush shrubby cinquefoil (*Potentilla fruticosa*) or silver sagebrush (*Artemisia cana*) at the edges of wet meadows or conifer stands (Johnson 1951, Murie 1940).

Drought conditions in 1988, combined with a series of dry storm fronts, lightning, and above-average winds produced the most significant fire season in the area in about 300 years (Schullery 1989, Singer et al. 1989). About 27% of winter range of the northern Yellowstone elk population burned in 1988, including about 11,427 ha of grasslands and upland shrublands, and about 15,580 ha of coniferous forests. About 30% of the summer range burned, including 149,700 ha of coniferous forests and 12,300 ha of grasslands and meadows.

The size of the Northern Yellowstone elk population was about 22,780 ± 830 elk before the fires in 1988 and following 9 years of mild winters (Singer et al. 1989). By spring 1989, after the drought and fires of 1988 and the severe winter of 1988–89, the elk population declined to about 14,220 ± 650 elk, due to increased winter mortality and increased harvests of elk north of the park (Singer et al. 1989).

Coyotes (*Canis latrans*) (about 400 animals total) and black bears (*Ursus americanus*) are common on the northern range, whereas grizzly bears are seasonally abundant during spring and some fall seasons (about 50–60 grizzlies). A few mountain lions (*Puma concolor*) (17–20 adults) occur mostly in the rocky canyons of the Yellowstone River, where little elk calving occurred (Houston 1982; R. Crabtree, B. Blanchard and K. Murphy, unpubl. data). Gray wolves, the most significant predator of elk, were extirpated from the park about 1926 (Houston 1982). Sympatric ungulates include bison (*Bison bison*), moose (*Alces alces*), mule deer (*Odocoileus hemionus*), pronghorns (*Antilocapra americana*), and bighorns (*Ovis canadensis*).

METHODS

Population Estimates

Elk were counted during early winter, usually in December 1969–79, from a single, fixed-wing PA-18 Supercub (Houston 1982:16–17). From 1986 on, 4 Supercubs were used simultaneously to count the winter range both inside and outside the park during the same day (Singer 1991,

Mack and Singer 1993*b*). Aerial counts provided a highly variable underestimate of the actual elk population size, due to visibility bias (Samuel et al. 1987, Singer and Garton 1994). Therefore, we estimated size of the elk population in 2 ways: (1) we reconstructed estimates of the elk population from 1976 to 1992 using a Leslie matrix population model (Mack and Singer 1993*b*, Coughenour and Singer 1996), and (2) we estimated the elk population from 1987 to 1991 using visibility corrections obtained from logistic regression of visibility parameters gathered from 154 searches for 47 radiocollared adult elk (Samuel et al. 1987, Singer et al. 1989, Singer and Garton 1994).

We estimated cow:calf:yearling bull:older bull ratios during early winter (Dec) from a helicopter in a random sample of about one-quarter of the winter range (22 of 66 count units) from 1985 to 1991. Similar classification data were gathered from 1971 to 1980 by Houston (1982: 29). Pregnancy rates, age structure, and hunter harvest for the matrix model were estimated from carcasses examined during periodic reductions of the northern Yellowstone elk population, 1932–67 (Kittams 1953, Greer 1966, Houston 1982:36–44), and from a mandatory check station for elk harvested north of the park each fall and winter 1976–92 (Houston 1982; Mont. Dep. Fish, Wildl. and Parks, unpubl. data).

The number of mature cows present in the autumn following the summer in question, that is the number counted in the following winter (*wcow*) plus the number taken off in the regular hunt (*hcow*), less the number of yearling females is:

$$adcow_{t+1} = (wcow_{t+1} + hcow_{t+1}) - [(wyrlm_{t+1} + hyrlm_{t+1}) \times 1.5]$$

where *wyrlm* and *hyrlm* are numbers of yearling males in winter count and hunted, and where 1.5 is the estimated ratio of female to male yearlings (Houston 1982). The number of calves present in the following autumn is:

$$aclf_{t+1} = wclf_{t+1} + hclf_{t+1}$$

and the number of yearling males (spikes) was similarly:

$$aspk_{t+1} = wspk_{t+1} + hspk_{t+1}$$

where *wclf* and *hclf* are calf numbers in winter count and hunted, respectively, and *wspk* and *hspk* are analagous numbers in yearling males. The formula to calculate winter calf mortality rate in year t is:

$$wclfm_t = (aclf_t - yrlt_{t+1})/aclf_t$$

where $yrlt_{t+1}$ is total number of yearlings present in autumn of the next year calculated as:

$$yrlt_{t+1} = aspk_{t+1} \times (1 + 1.5)$$

which assumes negligible mortality of yearlings in the summer. Winter survival equals:

$$wclfs_t = 1.0 - wclfm_t.$$

Summer calf production rate in year *t* is simply

$$clfr_t = aclf_{t+1} \,/\, adcow_{t+1}\,.$$

Thus, production rate reflects variations in birth rate as well as summer mortality rate.

Summer calf mortality rate can be computed as:

$$sclfm_{t-1} = [(adcow_t \times brth_t) - aclf_t] \div (adcow_t \times brth_t)$$

where $brth_t$ is births per adult cow which varies from 0.61 to 0.87 inversely with population size as explained in Coughenour and Singer (1996).

We examined the relation between elk calf survival and estimated elk population sizes using linear regression. We used visibility-corrected estimates of elk population size as the best estimate of elk population size in winters 1986–87 through 1990–91 (Unsworth et al. 1990). We used a Leslie matrix estimate of population size for winters 1975–76 through 1985–86, and we multiplied the mean ratio of these estimates to counts in the respective years (1.38) to estimate populations in winters 1968–69 through 1974–75. Hereafter, we simply refer to these as the estimated elk populations. Because we know uncorrected aerial counts of elk (hereafter referred to as counted elk) were undercounted due to poor counting conditions during winters of 1976–77, 1988–89, and 1989–90, we adjusted these 3 counts upwards from the previous year's population size and the estimated calf crop as described in Houston (1982:22–23).

Calf Capturing and Monitoring

We located newborn calves from helicopter, horseback, and foot surveys, and captured them by hand during summers 1987–90. We attempted to capture only calves ≤2 days old, identified by a wet coat, wobbly stance, and an attached umbilical cord (Johnson 1951), but some calves ≥2 days old were captured. We weighed all

calves and recorded their sex, hair moisture, and dentition. We measured body contour length, hair moisture, dentition, new hoof growth, dew claw wear, hind foot length, and width of navel (Johnson 1951, Haugen and Speake 1958, Garner et al. 1985). Ages of calves were estimated as: (1) 0–1 day, (2) 2–4 days, and (3) 5+ days based upon these criteria. We classed calves as heavy (mass $>\bar{x}$ + 1 SD), average, or light (mass $<\bar{x}$ + 1 SD) for each age class. We estimated birth weight for each age class (a, b, c) on the assumption that calves weighed: age class a = 100% of birth weight, age class b = 118% of birth weight, and age class c = 161% of birth weight based on growth rates of elk calves (Thorne et al. 1976). We placed expandable, mortality-sensing radiocollars on the captured calves that were designed to break off after 12 months of useful life (Schlegel 1976; Bear 1989, as modified by Telonics Inc., Mesa, Ariz.). The transmitters doubled in pulse rate after 4 hours of inactivity as an indicator of mortality. Following their release, we estimated the percent shrub cover >0.3 tall within a 3-m radius area surrounding the hiding site where the calf was first detected.

We monitored radiosignals from calves twice daily, once at dawn and again at dusk from a fixed-wing aircraft or from the ground from 17 May to 10 July. We monitored calves less frequently, about 5 times weekly from 11 July to 1 October, and about 3 times weekly through the remainder of the calf's first year. We investigated nearly all mortalities during summer within 12 hours of detecting a mortality signal and generally within fewer hours. We determined causes of death from signs of predation or scavenging, such as tracks, scat, distinctive wounds, distinctive consumption patterns, bed sites, or hair samples (O'Gara 1978, Garner et al. 1985, Larsen et al. 1989). We collected and identified hair of predators found at each site based on color, texture, medullar and cuticle scale patterns. We reported the species of predator causing a death only if a definite identification was made from a sighting, tracks, hair analysis, and if blood stains or hemorrhage indicated a violent death. Typically more time lapsed before detecting mortalities during winter, but physical evidence at the site included tracks and sign in snow. We concluded most winter mortality of calves was due to undernutrition based on: (1) the necropsies of 8 whole carcasses of calves found dead in winter that determined undernutrition as the cause of death (Wildl. Diagnostic Lab, Bozeman, Mont.), and (2) extensive condition sampling of the population during all the winters of the study that suggested undernutrition in many elk by late winter (DelGuidice et al. 1991, DelGuidice and Singer 1995).

Calf Survival

We computed finite rates of summer, winter, and annual survival of radiocollared calves as the number of calves that survived those intervals divided by the number alive at the beginning of each interval. We defined the survival intervals as: summer (capture date–31 Aug.), winter (1 Nov–15 May), and annual (summer plus winter). Further, we inspected rates of survival from predation only during the summer interval (capture date–31 Aug.) when most predation occurred. We used logistic regression (PROC CATMOD, SAS Inst. Inc. 1987) to determine the statistical relation between survival during each period (lived vs. died) and several categorical and continuous variables (Lee 1980, Bartman et al. 1992). Categorical variables were study area (Lamar/Gardiner), year, sex, and birth period (early = May, late = Jun). Continuous variables were estimated birth weight, summer precipitation during both the present (t) and previous year ($t-1$), winter severity at t or $t-1$, and estimated elk population size at t or $t-1$. We estimated summer precipitation as the total precipitation during June and July summed from both study areas during 1987–91. We used a winter severity index for 1968–1992 ranging from −4.0 (most severe) to +4.0 (most mild) that integrates minimum daily temperatures, snow water equivalent, and June–July precipitation as a predictor of winter forage (Farnes, unpubl. data).

We coded animals dying as 0 and surviving as 1; thus a positive parameter in the statistical model indicated a positive relation to survival, whereas a negative parameter indicated a negative relation. We excluded from the analyses calves harvested outside of the park during fall hunts (n = 4), calves dying due to study-induced abandonment (n = 5), and calves dying of undetermined causes (n = 5). We selected the model for each interval from among all possible combinations of parameters as the model with

the lowest value of Akaike's Information Criterion (AIC) (Sakamoto et al. 1986). The lowest AIC selects the best model based on the principle of parsimony, or the tradeoff between the number of parameters included in the model, model bias, and variance of the estimate as described in Burnham and Anderson (1991). We report only models with the lowest AIC value for the 3 survival intervals plus predation only measured during summer. The AIC value for each model is calculated as AIC = -2 (log-likelihood) + $2p$, where p = the number of parameters in the model.

Secondary effects of the fires of 1988, such as reductions in hiding cover, may have influenced elk calf survival. We examined capture site characteristics to determine whether calves were more poorly hidden following the fires of 1988. We determined decreases in big sagebrush and conifer cover following the fires using the park's Geographic Information System (GRASS) and comparative aerial photos taken before and after the fires (D. Despain, A. Rodman, P. Schullery, and H. Shovic, Yellowstone Natl. Park, unpubl. data). We used Chi-square contingency tables to determine if forest cover varied and the Kruskal-Wallis test to determine whether shrub cover at capture sites varied before and after the fires of 1988. We used logistic regression (PROC CATMOD, SAS Inst. Inc. 1987) to determine whether predation on calves (vs. mortality due to all other fates) was correlated with percent shrub cover and distance from forest cover at capture site and year.

RESULTS

Calf Survival Based Upon Population Reconstruction

Summer survival of elk calves, based on herd-wide estimates of calf recruitment to fall, was correlated negatively to estimated population size at t ($r^2 = 0.23$, $P = 0.06$) and at $t-1$ ($r^2 = 0.29$, $P = 0.03$; Table 1). Winter survival of elk calves, based on population reconstruction, was correlated inversely with estimated elk at t ($r^2 = 0.64$, $P = 0.0002$) and with estimated elk at $t-1$ ($r^2 = 0.62$, $P = 0.005$). Winter survival of elk calves was not correlated with the Farnes index of winter severity at t ($P = 0.514$). Ratios of calves were lower in the Lamar study area with more severe winters ($\bar{x}$ = 22, 95% *CI* = 16–28) than in the Gardiner study area ($\bar{x}$ = 42, 95% *CI* = 32–52), 1982–91. Also as expected, our indicator of recruitment, yearling male ratios, was lower in Lamar ($\bar{x}$ 4.6, 95% *CI* = 3.5–5.7) than in Gardiner ($\bar{x}$ = 9.3, 95% *CI* = 5.9–12.7).

Causes and Rates of Mortality of Radiocollared Calves, 1987–90

Seasonal survival rates of radiocollared calves were roughly equivalent during winter ($\bar{x} = 0.65 \pm 0.13$) and during summer ($\bar{x} = 0.72 \pm 0.32$) (Table 2). Summer survival differed among years ($P < 0.001$) and was highest in 1988 (95% *CI* = 0.72–0.98) following the very mild winter of 1987–88, and was lowest in 1990 (95% *CI* = 0.33–0.67) the second summer following the severe environmental events of 1988–89. Winter survival of radiocollared calves was also lower the winter of 1988–89 ($\bar{x} = 0.16$, 95% *CI* = 0.05–0.27) following the severe environmental events, than during the other 3 years ($\bar{x} = 0.91$, 95% *CI* = 0.80–1.00; Table 2).

Predation was the greatest source of mortality, accounting for 29 (43.9%) of all known mortalities and winter malnutrition was the second leading cause of elk calf mortality (22.7% of mortalities; Table 3). All but one instance of predation occurred during summer. Grizzlies and black bears preyed on 15 calves (23% of total mortality of marked calves) and coyotes preyed on 11 calves (16.9% of all calves that died). Most mortalities (n = 21) during summer occurred between 3 and 10 days of age, with the remaining (n = 18) mortalities occurring between 16 and 42 days of age. No elk calves older than 28 days were killed by bears. Only 7 elk calves died from predation after 21 June during all 4 years. A single case of mountain lion predation occurred on a calf that was nearly 1 year old.

Multiple kills by grizzlies were observed in 2 of 29 confirmed instances of predation. In the first, a radiocollared 7-day-old calf was killed by a grizzly bear and was found 2-m from an unmarked calf of about the same age which was also killed by a grizzly. Based on signs, both calves were apparently bedded in big sagebrush about 3 m apart and killed after brief chases. In the second instance, a radiocollared calf, 28 days old, was buried on top of an unmarked calf of about the same age. One calf was carried about 14 m and the other about 60 m from their kill sites to the common burial site.

Table 1. Calculated winter calf survival rates and summer calf production rate, and supporting information to perform the calculations as in Coughenour and Singer (1996). Years are numbered such that 1968–69 refers to winter 1968–69 and summer 1969. Compositions of the winter count were estimated by combining composition data (e.g., calf : cow ratios) with the total winter count of elk.

	Calf response			Winter count—no. of elk							Regular elk hunt			
Year	Summer calf recruitment rate	Summer calf mortality rate	Winter calf survival rate	Total count	Sightability corrected (±90% CI)	Population reconstruction[a]	Bulls	Cows	Yearling males	Calves	Cows	Yearling males	Calves	Winter severity index[b]
1968–69	0.63	0.27	1.0	4,309			857	2,198	264	989	24	4	7	+0.8
1969–70	0.57	0.32	1.0	5,593			1,225	2,663	453	1,252	25	4	11	+0.3
1970–71	0.43	0.49	0.94	7,282			1,522	3,623	543	1,594	28	23	14	−0.6
1971–72	0.37	0.55	0.74	8,215			1,643	4,441	577	1,554	57	26	6	−1.2
1972–73	0.36	0.56	0.98	9,981			1,985	5,671	454	1,871	128	10	29	+0.4
1873–74	0.30	0.62	1.00	10,529			1,985	6,071	722	1,805	155	25	36	−1.8
1974–75	0.31	0.61	0.56	12,607			2,401	7,504	825	1,876	109	28	23	−1.1
1975–76	0.18	0.78	0.36	12,014		15,797	1,889	7,556	378	2,191	61	46	5	−0.6
1976–77	0.30	0.62	1.00	8,980[c]		13,305	816	6,803	204	1,157	53	68	2	+3.3
1977–78	0.27	0.68	0.59	12,680		15,350	1,502	8,342	667	2,169	44	45	0	−0.4
1978–79				10,838		15,364	1,507	7,177	431	1,723	51	81	3	−2.7
1979–80						16,203					39	74	2	0.0
1980–81						16,743					40	97	1	+2.7
1981–82				16,019		17,699					52	81	11	+0.6
1982–83			0.76[h]			19,523			849[h]	5,800[h]	39	125	4	+1.8
1983–84			0.52[h]			20,837			1,637[h]	5,656[h]	38	135	28	+0.3
1984–85	0.52	0.20	0.28[h]			21,115			1,120[h]	5,439[h]	75	72	4	−0.1
1985–86	0.37[e]	0.39[e]	0.54	16,286		22,115	2,379	9,149	366	4,392	89	120	15	+0.8
1986–87	0.44[e]	0.31[e]	0.38[e]	17,007	23,350 (±1,192)	19,825	2,395[e]	14,968[e]	1,048[e]	4,939[e]	328	183	72	+2.9
1987–88	0.26[e]	0.60[e]	0.32[e]	18,913	22,779 (±834)	21,706	2,639[e]	13,860[e]	694[e]	5,556[e]	97	62	59	+2.5
1988–89	0.20[e]	0.69[e]	0.17[f]	10,991[c]	22,048 (±1,467)	20,619	3,722[e]	14,317[e]	573[e]	3,436[e]	102	144	9	−2.8
1989–90	0.30[e]	0.63[e]	0.35[e]	14,829	20,964 (±1,103)	17,843	2,912[e]	14,558[e]	728[e]	2,766[e]	426	126	48	+0.4
1990–91	0.78[eg]		1.00[eg]	9,451[c]	16,036 (±1,578)	17,950	1,428[e]	10,984[e]	659[e]	2,966[e]	59	77	2	−1.3
1991–92				12,720	18,600[d]	19,025	1,029[e]	7,353[e]	809[e]	3,529[e]	29	1,088	9	+1.4

[a] Based on POP-II model. Late hunt harvests were added to population estimates as described in Mack and Singer (1993*b*) and METHODS.
[b] The ranking index varies from −4.0, most severe, to +4.0, mildest (Farnes 1996).
[c] Census conditions were poor and count was abnormally low.
[d] No sightability correction available, this estimate was derived from the spring 1991 aerial corrected count of 12,590 ± 746 elk, plus an estimated 5,318 calves born and surviving to fall 1991. The calf estimate was based on the cow pregnancy rate, corrected with the summer survival rate for elk calves.
[e] Estimate based upon sightability-corrected count.
[f] Estimated based upon more detailed carcass counts (Coughenour and Singer 1996).
[g] Estimates probably too high.
[h] Estimates based on reconstructed population size and observed calf : cow and spike : cow ratios.

Table 2. Summer, winter, and annual survival rates (S) of radiocollared elk calves, Yellowstone National Park, 1987–90.

Year	Summer			Winter			Annual		
	N	S	SE	*N*	S	SE	*N*	S	SE
1987	30	0.558[ab]	0.079	17	0.857[a]	0.074	30	0.478[a]	0.079
1988	29	0.846[a]	0.065	25	0.160[b]	0.066	29	0.135[b]	0.056
1989	36	0.679[ab]	0.076	24	0.920[a]	0.054	36	0.624[a]	0.080
1990	32	0.502[b]	0.084	16	0.941[a]	0.055	32	0.472[a]	0.083
Total, 1987–90	127	0.646	0.132	82	0.719	0.3251	127	0.427	0.179

[ab] Different superscripts in a column denote differences in survival rates ($P < 0.001$, logistic regression).

Factors Influencing Survival of Radiocollared Calves

Survival of elk calves and avoidance of predation during summer was correlated negatively with estimated birth mass ($P = 0.006$, 0.05, Table 4). Further, survival during summer was correlated negatively with elk population size at $t-1$ (Table 4). Neither sex ($P = 0.770$), study area ($P = 0.96$), nor precipitation at t ($P = 0.416$) affected survival of radiocollared elk calves during summer. Calves dying from predation weighed less at birth than those surviving from predation (Fig. 1). Late born calves survived at a lower rate than early born calves during all intervals (Table 4). Late births were correlated positively to estimated elk population size at $t-1$ ($P = 0.005$). More calves were born late in 1989 ($P = 0.030$), the spring following the severe environmental events of 1988–89 (Fig. 2). The ratio of early:late born calves was only 0.46:1.00 in 1989, but early:late calves were nearly equal (0.96:1.00) the other 3 years (Fig. 2).

Survival of calves during winter was correlated negatively to late calving period ($P = 0.065$), winter severity at t, estimated elk population size at t, and precipitation at t (Table 4). Annual survival of calves was correlated negatively with late birth period ($P = 0.01$) and birth mass was correlated positively with annual survival ($P = 0.006$). Calves born following mild winters were heavier than calves born following normal or severe winters ($P = 0.029$, Fig. 1). Further, survival of calves during winter was lower in the Lamar area with deeper snows ($\bar{x} = 0.66$) than in the Gardiner area with more shallow snows ($\bar{x} = 0.80$, $P = 0.034$). Calves were born later in the Lamar area (with more severe winters) than in the Gardiner area ($\chi^2 = 3.79$, 1 df, $P = 0.056$, Fig. 2). Male calves were born later than female calves in both areas ($\chi^2 = 4.45$, 1 df, $P = 0.035$), and more male calves were captured in the Lamar area where winters were more severe (158 M:100 F in Lamar, $P = 0.01$, 110 M:100 F in Gardiner, $P = 0.59$, Fig. 2).

The fires of 1988 increased vulnerability of elk calves to predation. Overall predation rates doubled following the fires (29% of all marked

Table 3. Causes of mortality of radiocollared elk calves in Yellowstone National Park, 1987–90.

Cause	Summer		Winter		Total	
	No.	%	No.	%	No.	%
Predation						
Grizzly bear	11	28			11	16.9
Black bear	1	3			1	1.5
Unknown bear sp.	3	8			3	4.6
Coyote	11	28			11	16.9
Eagle	1	3			1	1.5
Mountain lion			1	3	1	1.5
Unknown predator	1	3			1	1.5
TOTAL PREDATION	28	72	1	3	29	44.6
Starvation	1	3	15	58	16	24.6
Disease	3	8	1	3	4	6.1
Hunter harvest			4	15	4	6.1
Accident	2	6	1	3	3	4.5
Unknown	5	13	4	15	9	13.9
GRAND TOTAL	39	100	26	100	65	100.0

Table 4. Best biological models describing elk calf survival during summer, winter, and annual periods, and for survival from predators of radiocollared calves, Yellowstone National Park, 1987–90. Only the most parsimonious model variables, developed with logistic regression, and selected based on Akaike's Information Criterion (AIC), are presented for each of the 4 models.

Variable	Summer survival-predation only			Summer survival			Winter survival			Annual survival		
	Parameter	SE	*P*	Parameter	SE	*P*	Parameter	SE	*P*	Parameter	SE	*P*
Estimated birth mass	0.206	0.105	0.050	0.338	0.102	0.001				5.20	3.36	0.006
Calving period	−0.353	0.243	0.146	−0.416	0.227	0.066	−0.747	0.405	0.065	−0.577	0.225	0.010
Winter severity index							−0.983	0.221	0.000	−0.669	0.181	0.002
Estimated population size *t*-1				0.002	0.001	0.017				0.008	0.002	0.005

calves were killed by predators, 95% *CI* = 20–38%) compared to before the fires (13% of calves 95% *CI* = 6–20%). Percent shrub cover at capture sites was higher before the fires ($\bar{x}$ = 52%) than after ($\bar{x}$ = 33%), and the difference approached statistical difference (Kruskal-Wallis statistic = 7.18, 1 df, P = 0.066). Fewer calves were killed in forested habitats after the fires (P = 0.040), suggesting fewer forest ambushes of elk by grizzlies occurred as described by French and French (1990) for conditions before the fires.

DISCUSSION

Summer losses of elk calves, mostly due to predation, were roughly equivalent to winter losses. We concluded individual grizzly bears killed more calves than did individual black bears or coyotes. Grizzly bear and black bear densities were roughly equivalent on the area and coyotes were about 6–7 times as abundant as grizzly bears, yet grizzlies killed as many calves as coyotes and 11 times more calves than black bears. In most other large multi-predator systems, including areas with wolves, grizzlies were the most significant predator on neonatal ungulates (Ballard et al. 1981, Ballard and Larsen 1987, Singer 1987, Boertje et al. 1989, Larsen et al. 1989).

Our results corroborate previous conclusions that density-dependent survival of elk calves may limit or regulate the northern Yellowstone elk population (Houston 1982, Coughenour and Singer 1996). Our extension to 21 years of population data indicated both winter and summer survival of elk calves was density-dependent, while our radiocollaring studies conducted over only 4 years with large environmental variations indicated summer and annual survival was density-dependent. We suspect the stochastic environmental events of 1988–89 overwhelmed the effects of density-dependence on winter survival on elk calves. Density-dependent rates of winter starvation have been reported previously for elk and red deer (Guiness et al. 1978, Houston 1982, Sauer and Boyce 1983). By contrast, our findings of density-dependent relations in summer mortality of calves due to predation appear to be unique (Guiness et al. 1978, Ballard et al. 1981, Franzmann and Schwartz 1986, Crete and Jolicoeur 1987, Boertje et al. 1989). Smaller calves might be easier for predators to catch, or cows in poor condition might give birth to lighter

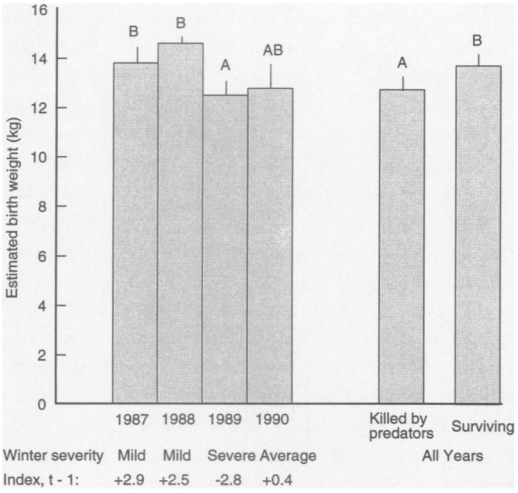

Fig. 1. Estimated birth weights of radiocollared calves and winter severity, 1987–90, and weights of calves killed by predators and those surviving all summers (*t*-tests, $P < 0.05$). Different superscripts denote differences in birth weight ($P < 0.05$).

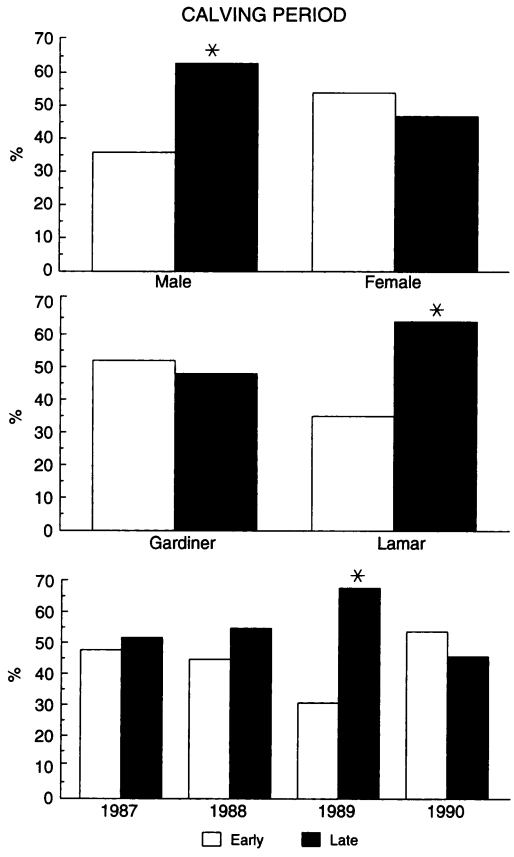

Fig. 2. Elk calves born during the early and late calving periods by sex, study area, and year. A * denotes statistical differences between early and late births.

calves (Clutton-Brock et al. 1982, 1987) and cows in poor condition might visit and nurse the calf less, or not hide the calf as well from predators. Lighter neonates are also reported to survive at lower rates from losses due to stillbirths, starvation, drowning, other accidents, and avian predators (Verme 1969, Thorne et al. 1976, Clutton-Brock et al. 1982, 1987).

Effects of the severe environmental factors of 1988–89 were difficult to separate from the effects of density-dependence. We found no effect of winter severity during the 21-year period when elk populations were mostly below ecological carrying capacity (ECC), (mostly <12,000 elk) but winter severity negatively influenced elk calf survival during the 4-year period when elk numbers (initially) were at or near ECC (>20,000 elk) and when stochastic environmental fluctuations (fire, drought, severe weather) were much larger. Picton (1984) also concluded climatic effects on ungulates were greatest when populations were at or near ECC.

The effects of the various climatic variations including the severe drought of 1988, the large fires of 1988, and the severe winter in 1988–89 were impossible to separate, since these environmental events occurred nearly simultaneously. The effects of these environmental events on elk included: (1) elk forage biomass was reduced, plant senescence was earlier, and elk migrations to the winter range were 4–6 weeks earlier in 1988 (Singer et al. 1989), (2) elk calved later the next spring of 1989, (3) elk calves were born lighter (Fig. 1), (4) predators may have searched harder for elk calves, since other key alternate spring foods were reduced (less bison and elk carrion was available the second winter after the fires due to the ungulate population declines, and some whitebark pine [*Pinus strobus*] stands burned in 1988 where grizzlies previously foraged on pine nut caches), and (5) elk calves may have been less well hidden and predator search efficiency may have increased following the fires of 1988 due to the burning of about one-third the tall shrub and conifer cover. Bears and coyotes needed to search less cover to find calves. Increased predation rates, less shrub cover at calf hiding spots, and fewer calves killed in unburned conifer stands all suggest predators had greater success finding and catching calves in the partially-burned landscape.

The strong influence of environmental factors on calf survival, including a twofold difference in average snow depths, were further supported by our comparisons between the Lamar and Gardiner calving areas. Calves were born later in the higher Lamar area with deeper snows, winter survival of radioed calves was lower, calf: cow ratios were lower, a higher proportion of male calves were captured (this study), and body condition indices were lower than in the Gardiner study area (DelGuidice et al. 1991). Late birth of calves and higher proportion of male calves is typically related to poor condition of cows (Robinette 1966, Mitchell and Lincoln 1973, Reimers et al. 1983).

Potential compensation between components (Boutin 1992) to elk calf mortality in the northern Yellowstone elk population was suggested by the following: (1) predators killed lighter calves and more late-born calves, (2) calves in the population were born later following a winter of reduced body condition for gestating cows (winter 1988–89) and calves were born later each year in the study area with deeper snow, and (3) late-born calves survived at a lower rate than early born calves.

We speculate lighter calves were easier for predators to capture, or were hidden or cared for less by the cow than heavier calves. In contrast, Adams et al. (1995) concluded lighter neonatal caribou (*Rangiper tarandus*) calves were not more vulnerable to grizzlies or wolves in Denali National Park, although with more years of data, Adams et al. (1996) have modified their statements and concluded low birth weights were associated with greater vulnerability to predators. Although we did not study biomass or condition of elk cows, considerable evidence exists that as red deer and elk population densities increase, or experimental per capita food consumption is reduced (the equivalent of a population density increase), cows lose weight, cows conceive later, birthdates are later, calves are lighter, and calf survival is reduced (Mitchell and Lincoln 1973, Thorne et al. 1976, Cothran et al. 1978, Guiness et al. 1978, Clutton-Brock et al. 1982, 1987; Reimers et al. 1983).

As in our study, late-born caribou and red deer calves survived at a lower rate than early- or peak-born calves (Guiness et al. 1978, Boertje et al. 1989, Adams et al. 1995). There may be a lag period between first calving and when predators detect calving, which might result in predators concentrating on calving grounds during later calving times (Adams et al. 1995). Alternatively, late-born calves may have insufficient time to develop body and fat reserves to survive their first winter (Guiness et al. 1978, Berger 1979, Thompson and Turner 1982, Festa-Bianchet 1988). A review of survival studies of radiocollared elk or caribou calves supports our conclusions. Three low density populations (2 heavily hunted and 1 with wolves) experienced 0 winter starvation losses of calves (Schlegel 1976, Adams et al. 1995; Lonner and Schladweiler, Mont. Fish, Wildl. And Parks, unpubl. data), while 2 other lightly harvested, high-density populations without wolves experienced high rates of winter starvation losses of calves (Guiness et al. 1978, Houston 1982).

MANAGEMENT IMPLICATIONS

We recommend using visibility corrected estimates of elk populations for future monitoring of the elk population because it is the most tested technique (Unsworth et al. 1990) and because actual counts were more variable, and biased negatively with biases ranging widely from 0.53 to 0.91 (Table 1). Population reconstruction estimates closely tracked visibility corrections and, therefore, were the second most preferred alternative to actual counts. Accuracy of the population reconstructions were untestable however, therefore we recommend their use only when visibility corrections are unavailable.

Our results are consistent with hypotheses that density-dependent mortality of calves during winter due to malnutrition and during summer due to predation were partially compensatory. We add the caveat, however, that severe environmental conditions may produce largely additive components to both summer (increased predation) and winter (increased malnutrition) mortality.

Wolves were reintroduced into northern Yellowstone in 1995, providing a unique opportunity to evaluate whether the effects of wolves on elk will fall into 1 of 3 predicted scenarios: (1) wolves will be inconsequential to the density-dependent regulation process of elk near some ECC for elk as Cole (1971) and Houston (1971) predicted, (2) wolves will limit or regulate elk at some slightly lower level, perhaps 70–91% of ECC for elk (Boyce 1993, Mack and Singer 1993*a*) or, (3) wolves will limit elk to only one-

half of ECC for elk (Messier and Crete 1985, Gasaway et al. 1992, Lime et al. 1993, Messier 1994).

Following wolf restoration, wolf predation could be partially compensatory with winter malnutrition losses of elk calves, if wolves kill calves that are already predisposed to die of malnutrition. Wolf predation might also be compensatory with other sources of predation (bears, coyotes), but the evidence is equivocal (Ballard and Larsen 1987, Adams et al. 1995). Wolves are potentially more important predators to all ages of elk calves than bears in this system because wolves kill calves later in the summer than bears (Adams et al. 1995) and wolves prefer to kill calves over adult elk during the entire winter season (Pimlott et al. 1969, Carbyn 1983). Fewer elk calves would be predisposed to malnutrition at lower elk densities, and thus wolf predation could switch from largely compensatory to largely additive, if wolves caused elk to decline well below ECC (Gasaway et al. 1992, Messier 1995). Determining the extent of compensation between wolf predation and other causes of elk calf mortality, is critical to setting responsible levels of hunter harvests of elk. We recommend studies be conducted following wolf recovery to test the following hypotheses: (1) the elk population will decline slightly following wolf restoration (8–30%) as predicted by computer modeling (Garton et al. 1990, Mack and Singer 1993*a*, Boyce 1993), and (2) wolf predation will be compensatory with other sources of elk calf mortality or, alternatively, (3) wolf predation on elk neonates will be largely additive to other sources of mortality and, wolf predation will limit the elk population well below (50–66%) current elk population levels (Messier and Crete 1985, Gasaway et al. 1992, Lime et al. 1993).

Our results corroborate earlier findings of density-dependence in the northern Yellowstone elk population (Houston 1982, Merrill and Boyce 1991, Boyce 1993, Dennis and Taper 1995, Coughenour and Singer 1996), and its possible role in regulation of the elk population (Houston 1982). Our finding that, in the absence of wolves, predation by bears and coyotes was a potentially limiting factor on the elk population (predators killed 23% of all marked calves) updates, but does not reject the basic tenet of natural regulation management, that of food mediated density dependence in elk.

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