

Patterns of neonatal mortality of elk in northwest Wyoming

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Abstract: During May and June of 1990–1992, 164 newborn elk (*Cervus elaphus*) of the Jackson elk herd in northwest Wyoming were captured, weighed, aged, and fitted with expandable radio collars. Calves were subsequently monitored twice daily to determine locations and causes of mortality. All neonatal mortality had occurred by 15 July and totaled 15%, 68% of which resulted from predation by black bears (*Ursus americanus*) and coyotes (*Canis latrans*). Mortality of individual elk calves was male-biased but unrelated to birth mass. Early-born calves suffered lower mortality from causes other than predation than late-born calves. However, predation was greater upon early-born calves. Mortality rate of neonatal elk and recruitment rates, measured in early August, were not spatially density-dependent.

Résumé : En mai et juin de 1990–1992, 164 Wapitis (*Cervus elaphus*) nouveau-nés du troupeau de Jackson, dans le nord-ouest du Wyoming, ont été capturés; leur âge et leur masse ont été déterminés et ils ont été munis chacun d'un collier émetteur extensible. Leur position a par la suite été déterminée deux fois par jour et les causes de leur mortalité ont été enregistrées. La totalité des mortalités des nouveau-nés s'est produite avant le 15 juillet et s'élevait à 15%, dont 68% à cause de la prédation par les Ours noirs (*Ursus americanus*) ou les Coyotes (*Canis latrans*). La mortalité affectait surtout les jeunes mâles, mais était indépendante de leur masse à la naissance. Les jeunes nés tôt dans la saison étaient moins souvent victimes de mortalité due à d'autres causes que la prédation que les jeunes nés plus tard dans la saison, mais ils étaient plus souvent victimes de prédation. Le taux de mortalité des wapitis néonates et les taux de recrutement, mesurés en août, n'étaient pas reliés à la densité.

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Introduction

Juvenile mortality is among the most sensitive responses to increasing population density (Eberhardt 1977; Fowler 1987). The rate of mortality often varies widely among populations of the same species (Geist 1971) and can significantly affect recruitment and the rate of increase of cervid populations (Caughley 1977). On the Isle of Rhum, red deer calves born to hinds occupying habitat with relatively low population density (relative abundance of good grazing) had higher birth masses, earlier birth dates, and greater survival than those in high-density habitats (Guinness et al. 1978; Clutton-Brock et al. 1982).

The relationship of spatial forage availability (i.e., population density) to neonatal survival has received limited attention in North American elk. In elk herds that are food-supplemented in winter, variation in forage availability during summer and fall may exceed variation in winter. Among supplemented herds, approximately 35% of the Jackson elk herd in northwest Wyoming and 50% of the elk that winter on the National Elk Refuge (NER) spend summer and fall in Grand Teton National Park (GTNP) (Smith and Robbins 1994). Since GTNP was expanded in size in 1950, the number of elk that summer in the park has quadrupled, despite herd harvests averaging >3000 elk annually (Boyce 1989; Smith and Robbins 1994).

Boyce (1989) speculated that variation in fecundity and (or) calf survival may be responsible for the density-dependent recruitment he reported among Jackson elk that winter on the NER and summer in GTNP. Other studies of elk (Knight 1970; Houston 1982; Sauer and Boyce 1983), Soay sheep (Grubb 1974), mule deer (*Odocoileus hemionus*) (Bartmann et al. 1992), white-tailed deer (*Odocoileus virginianus*) (McCullough 1984), caribou (*Rangifer tarandus*) (Skogland 1985), moose (*Alces alces*) (Pimlott 1959), and other ungulates (Fowler 1987) report density-dependence in recruitment rates due to changes in fecundity and (or) survival of young of the year. Both Boyce (1989) and Smith and Robbins (1994) emphasized the need for information on mortality of juvenile elk to clarify population processes regulating the Jackson elk herd.

Changes in neonatal sex ratios can also alter population growth rates of cervids (Medin and Anderson 1979). Sex bias in neonatal mortality has been reported among several species of cervids (Robinette et al. 1957; Verme 1983; Clutton-Brock et al. 1985a; Skogland 1985; Ozoga and Clute 1988). Owing to a preponderance of female calves in the fall harvest, Boyce (1989, p. 55) speculated that survival during summer may be poorer among male than female calves of the Jackson elk herd.

A 1986 natural resource management plan for GTNP proposed experimental termination of elk reductions in the park to test the hypothesis that the reductions were unnecessary for proper management of the Jackson elk herd (Grand Teton National Park 1986). We conducted research from 1990 to 1993 to evaluate whether this hypothesis (i.e., that natural regulation would stabilize elk numbers in GTNP) was an appropriate management direction for GTNP. This paper

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reports on the contribution of neonatal mortality to regulation of various summer herd segments of the Jackson elk herd. From the foregoing review, we predicted that (i) neonatal mortality of elk would vary inversely with birth mass and positively with birth date, (ii) males would suffer higher mortality than females, and (iii) mortality of elk that were born in GTNP would exceed that of calves born outside the park.

Study area

Boundaries, topography, and vegetative communities of the 5195-km² Jackson elk herd unit in the Snake River watershed of northwest Wyoming were described by Cole (1969), Boyce (1989), and Smith and Robbins (1994). Mean annual temperatures decrease and precipitation and snowfall increase relative to the NER near the southern end of the Jackson Hole valley northward to Yellowstone National Park (Fig. 1) (Smith and Robbins 1994). Elevations range from 1950 to >3650 m. The reporting station at Moran, Wyoming, 2069 m above sea level, near the center of the calving areas on which we captured elk, receives 617 mm of precipitation annually. Monthly temperatures in January and July at Moran average -10.2 and 15.7°C, respectively (National Oceanic and Atmospheric Administration 1992).

From 1990 to 1994, winter censuses of the Jackson herd ranged from 12 905 to 15 066 (Smith 1994). The elk migrate 10–90 km between seasonal ranges. Their summer distribution is subdivided into four relatively distinct units referred to as herd segments: Grand Teton National Park (GTNP), southern Yellowstone National Park (YNP), the Teton Wilderness Area (TW), and the Gros Ventre drainage (GV) (Fig. 1) (Boyce 1989; Smith and Robbins 1994). Adult elk are highly faithful to herd segments but commingle in winter on the NER and other winter ranges in the Jackson herd unit (Boyce 1989; Smith and Robbins 1994).

Over 80% of the elk herd is supplementally fed for approximately 3 months each winter at the NER and at three feeding grounds in the GV. Of the elk that winter on the NER, 48% spend summer in GTNP, 28% in southern YNP, and the remainder in the TW and GV herd segments of the Bridger–Teton National Forest (Fig. 1) (Smith and Robbins 1994). This represents a significant increase in the number of elk summering in GTNP compared with the 29% reported by Cole (1969) during the 1960s. Cole (1969) reported that the highest summer densities of elk in the herd unit (3.8 elk/km²) occurred in the central valley and Uhl Hill areas of GTNP (Fig. 1). In 1991, elk numbers in those areas of GTNP averaged 5.9/km² compared with 2.4/km² outside GTNP (Smith 1994).

Methods

Radiotelemetry was used to investigate calf mortality. Radiotelemetry of neonates has become a widely accepted method for studying cause-specific juvenile mortality and survival rates (White and Garrott 1990). Rates of abandonment of 1–28% have been documented in radio-tagging studies of ungulate neonates (Livezey 1990). With adequate precautions, abandonment has been reduced to insignificant levels (Garrott et al. 1985; Larsen and Gauthier 1989), and handling and tagging does not bias mortality of neonates (Ozoga and Clute 1988).

Captures

During 1990–1992, 164 newborn calves were captured and fitted with radio-transmitter collars within a week of birth. We captured 6 while on foot, 8 from horseback, and 150 from a Hillar 12-E helicopter. A stratified random-sampling design called for capturing two groups of 25 elk neonates during each year, one group that would summer inside GTNP and another that would summer out-

side the park. Captures were allocated among eight distinct calving areas based upon the proportion of adult cows which used each calving area and the probability that animals born in each area would summer inside or outside GTNP (Fig. 2) (Smith and Robbins 1994). Smith and Robbins (1994) found that all radio-collared cows that used calving areas outside GTNP summered outside GTNP, but 33% of cows that used calving areas inside GTNP migrated to summer ranges outside the park. Allocation of captures to the “inside GTNP” and “outside GTNP” samples were calculated as follows:

$$\hat{\delta}_I = \left(\frac{\sum_{i=1}^n P_I j_I}{\sum P_I j_I} \right) 0.5k$$

and

$$\hat{\delta}_O = \left(\frac{\sum_{i=1}^n P_O j_O}{\sum P_O j_O} \right) 0.5k$$

where

$\hat{\delta}_I$ and $\hat{\delta}_O$ are the sample from inside and outside GTNP, respectively

n is the number of calving areas (8)

P_I and P_O are the probability of a calf captured in area I and O, respectively, spending summer in GTNP

j_I and j_O are the number of relocations of radio-collared elk cows using area I and O, respectively, during the calving season (Smith and Robbins 1994)

k is the total number of calves captured each year

Capture efforts by helicopter were rotated among the eight calving areas throughout the periods 27 May – 8 June 1990, 26 May – 9 June 1991, and 27 May – 6 June 1992. Capture efforts from horseback and on foot were made in those calving areas where collars had been cast by calves previously captured from the helicopter. Median dates of capture were 2 June 1990, 3 June 1991, and 3 June 1992. No calves were captured after 30 June.

Captured calves were manually restrained, blindfolded, hobbled, sexed, weighed to the nearest 0.25 kg, and aged. Calves were handled for 4–10 min (\bar{x} = 5.5 min, SE = 0.12 min). An expandable radio collar (Telonics Inc., Mesa, Arizona) weighing 230 g, 1.5% of an elk's birth mass, was placed on each calf. Batteries were configured and collars were designed to last for ≥ 26 months (3 summers). A mortality sensor with a 5-h delay switch was integrated into each transmitter's circuitry.

Estimation of age and birth mass

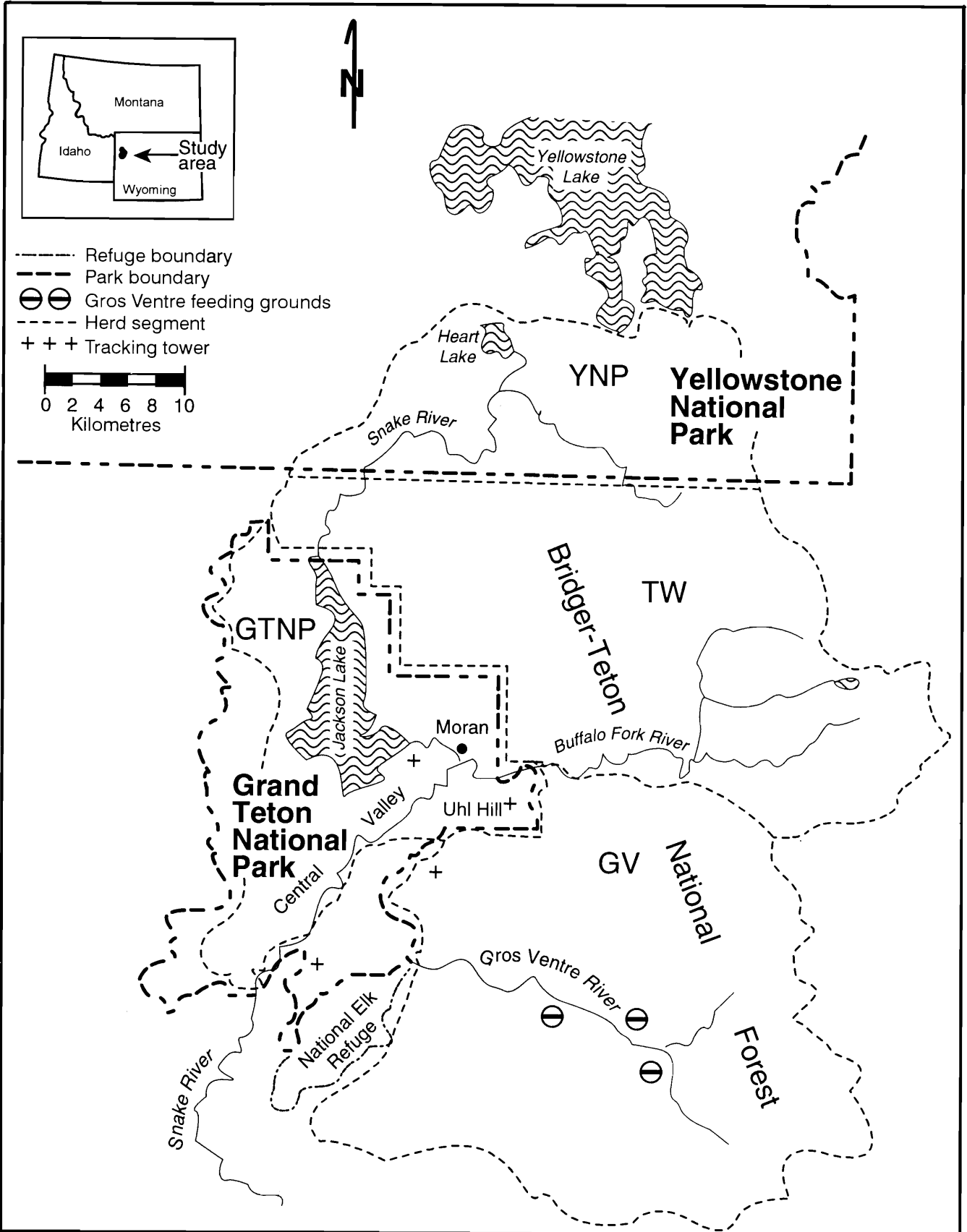
To age neonates we measured the eruption of incisor 1 and the diameter of the umbilicus with a caliper, and categorized the degree of healing of the umbilicus, hardening of the hooves, and stature and coordination of the animal according to Johnson (1951).

Birth masses were estimated from sex-specific daily growth rates of neonates (Smith et al. 1996). We categorized calves by birth mass as heavy-born (greater than the median birth mass of their cohort) or light-born, to test whether birth mass influenced calf mortality. Birth masses of each cohort were further categorized into quartiles for analyses.

Monitoring of transmitters

Radio-collared elk were located once daily through 15 July each year. Azimuths were obtained from four fixed tracking stations surrounding the central valley of GTNP (Fig. 1). Each station included twin 12-element Yagi antennas atop a 6.1-m mast and employed a null-peak tracking system (White and Garrott 1990, pp. 47–74). Transmitters were monitored a second time each day, approximately 12 h after they were located, to determine if they were functioning on active or mortality mode. Most calves, particularly those

Fig. 1. Summer distributions and winter feeding grounds of the four herd segments of the Jackson elk herd: Grand Teton National Park (GTNP), Yellowstone National Park (YNP), Teton Wilderness (TW), and Gros Ventre drainage (GV).



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Fig. 2. Distribution of calves (males–females) captured and radio-collared during 1990–1992 in the Jackson elk herd.

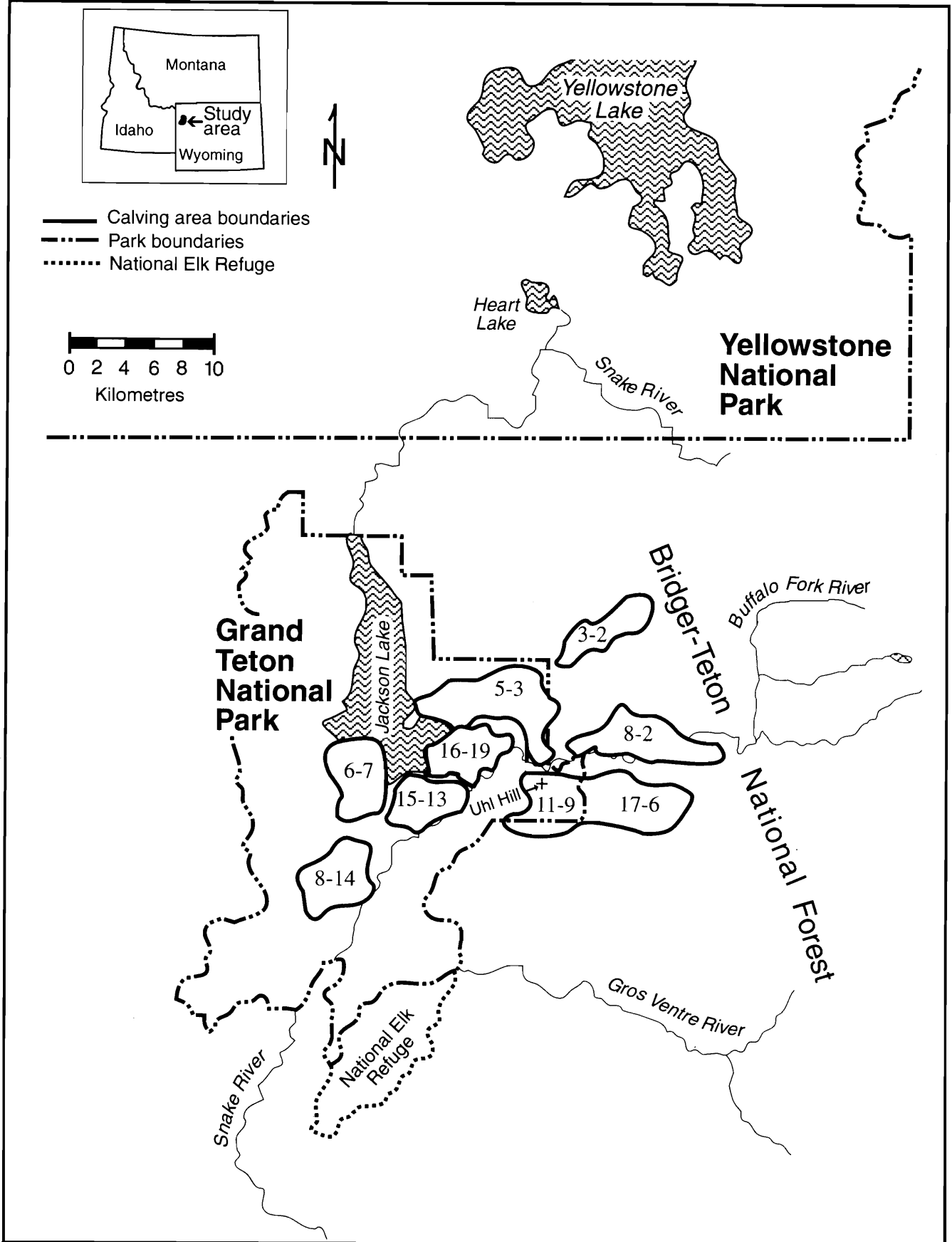


Table 1. Fate of newborn calves captured on calving areas in Grand Teton National Park (GTNP) and outside the park on the Bridger–Teton National Forest (BTNF).

Capture location	Sex	No. of cast collars	No. killed by predators	No. of deaths from other causes	No. surviving	Total
GTNP	M	9	7	4	41	61
	F	6	4	1	54	65
BTNF	M	3	4	1	20	28
	F	1	0	1	8	10
Total		19	15	7	123	164

that could not reliably be located from ground stations, were located from aircraft three times weekly to obtain visual locations.

Forensics

Radio collars on mortality mode were reached on foot or horseback, whichever was more efficient. We investigated locations of all but two mortality signals within 24 h of initial detection of the mortality signal. The other two were investigated within 48 h. Black bears and other large carnivores seldom find and scavenge carcasses of neonatal ungulates within 24 h of death (Franzmann et al. 1980; Ballard et al. 1981; Larsen and Gauthier 1989). Black bears were present at three mortality locations and a coyote at another.

The vicinity of each collar was thoroughly searched for signs of predation and scavenging, such as animal tracks, scat, bed sites, and guard hairs. Hair samples were sent to the Wyoming Game and Fish Laboratory and identified on the basis of color, texture, and scale patterns of the medulla and cuticle (Moore et al. 1974). Carcasses were skinned and examined for evidence of predation, including bruising, hemorrhaging and fresh blood around wounds. They were also examined for predator-specific wounds, canine spacing, and distinctive consumption patterns (Henne 1975; Wade and Bowns 1985).

Samples of organ tissues and lymph nodes were collected for diagnostic testing at the Wyoming State Veterinary Laboratory. However, in some cases bone fragments were the only remains.

Summer herd classifications

To measure recruitment of calves, three experienced observers in a Bell Jet Ranger helicopter classified elk (calves, yearling and older cows, yearling bulls, and mature bulls) on summer ranges during the first 2 weeks of August 1990–1993. Summer range in GTNP was divided into six survey units and parallel transects were flown from north to south across each unit. The means of three replicate classifications in 1991 and 1993 and two replicates in 1992 and 1994 were used to calculate calf:cow ratios.

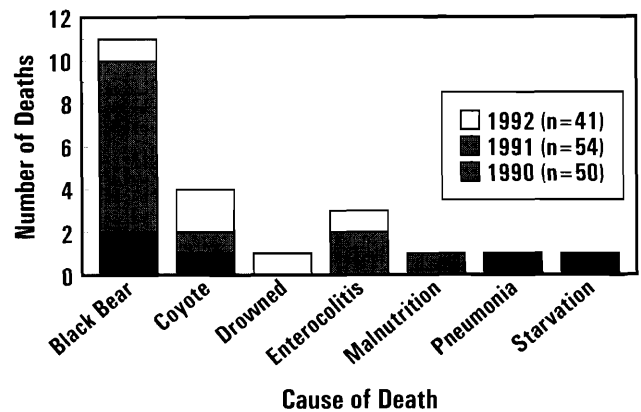
In 1990 and 1991, we flew unreplicated classification transects within six survey units of summer ranges in YNP, TW, and the GV. We surveyed one transect in the GV in 1992. We estimated sample size adequacy for each of GTNP, YNP, TW, and the GV according to Czaplowski et al. (1983). Calf:cow ratios were estimated according to Thompson (1992):

$$r = \frac{\sum_{i=1}^n Y_i}{\sum_{i=1}^n X_i}$$

where

r is the ratio of calves : 100 cows classified
n is the number of survey units

Fig. 3. Causes of neonatal mortality (birth to 15 July) of radio-collared elk calves during 1990–1992.



Y is the number of calves classified
X is the number of cows classified

and

$$\text{variance}(r) = \frac{1}{n\bar{X}^2} \left[\frac{1}{n-1} \sum_{i=1}^n (Y_i - rX_i)^2 \right]$$

Statistical treatment

We used Student’s *t* tests and Mann–Whitney *U* tests in the SYSTAT (SYSTAT, Inc., Evanston, Illinois) for Windows statistical software package to test whether mortality rates and ages and birth masses of mortalities differed among groups of elk. We used likelihood ratio χ^2 tests to test the goodness of fit of categorical data. For all statistical tests, $\alpha < 0.05$ was considered significant. Statements that two categories “tend” to differ indicate a test result approaching significance and instances where there were additional grounds for believing that a difference existed. The significance level of the three pairwise *t* tests comparing calf:cow ratios for summer ranges outside GTNP was set at 0.0167 to maintain an experimentwise critical level of 0.05 for the comparisons. Likewise, α was set at 0.01 for the five pairwise *t* tests comparing calf:cow ratios in GTNP during 1990–1994. All means are presented \pm standard error (SE).

Results

A total of 126 calves in GTNP and 38 in the Bridger–Teton National Forest were captured and radio-collared when < 1–7 days old (Table 1, Fig. 2). Twelve male and seven female calves cast their collars prior to 15 July and were removed from mortality estimates.

Proximate causes of mortality

Twenty-two of the 145 (15%) calves retaining their collars died prior to 15 July (Table 1). Mortality did not differ among years ($G = 3.3$, $df = 2$, $P = 0.19$). Fifteen (68%) calves were killed by predators: 4 by coyotes, 10 by black bears, and another likely by a black bear. Predation by black bears was greater in 1991 than in 1990 and 1992 combined ($G = 7.1$, $df = 1$, $P = 0.008$), but all deaths from predation were not significantly different among years ($G = 3.6$, $df = 2$, $P = 0.16$; Fig. 3). All four coyote predations and 8 of 11 black bear predations occurred in GTNP. No infectious agents or other predisposing factors were identified in any deaths by predation.

Table 2. Calf:cow ratios (r) obtained by classifying elk from a helicopter during the first 2 weeks of August 1990–1994.

Year	Area	No. of calves	No. of cows	r^a
1990	GTNP	173	359	0.48±0.02a
1990	Outside	546	1136	0.48±0.02a
1991	GTNP	241	606	0.40±0.01b
1991	Outside	747	1964	0.38±0.02b
1992	GTNP	333	690	0.48±0.01a
1992	Outside	86	186	0.46a
1993	GTNP	300	761	0.39±0.03b
1994	GTNP	398	932	0.43±0.01ab

Note: Southern Yellowstone National Park, the Teton Wilderness area, and the Gros Ventre drainage were surveyed outside Grand Teton National Park (GTNP) in 1990 and 1991. Only the Gros Ventre drainage was surveyed outside Grand Teton National Park in 1992.

^aValues are given as means ± SE. Values followed by a different letter are significantly different ($P < 0.01$); those followed by the same letter do not differ ($P > 0.1$).

Numbers of deaths from causes other than predation were similar among years (Fig. 3). One calf drowned in a swiftly moving stream in June 1992 while migrating north along the west side of Jackson Lake. The two deaths from enterocolitis in 1991 were associated with a coronavirus infection and the one in 1992 was due to a rotavirus infection. One calf died of bacterial pneumonia in 1990. The calves that died of starvation and malnutrition were observed with adult females shortly before their deaths (Fig. 3). No cases of abandonment of calves by their dams were documented.

Calves killed by predators were 2–23 days old ($\bar{x} = 7.0 \pm 1.4$ days) and were younger (Mann–Whitney test, $U = 15.5$, $P = 0.009$) than calves that died from all other causes ($\bar{x} = 18.9 \pm 2.8$ days). No calves >27 days old died until the fall hunting season.

Factors affecting mortality of individual animals

Sex

Significantly more radio-collared males than expected died before 15 July ($G = 4.2$, $P = 0.041$). More males than females died from predation (11 males, 4 females) and other causes of mortality (5 males, 2 females). Among calves born in GTNP, the interaction of sex and location of birth was significant ($G = 81.8$, $df = 1$, $P = 0.001$), with more males than expected and fewer females than expected dying in GTNP.

Birth mass

Neonatal mortality resulting from predation and all other causes was no greater for light-born than for heavy-born calves ($P > 0.29$). Likewise, calves in the lower quartile of all birth masses were no more likely to die than heavier calves ($G = 0.98$, $df = 1$, $P = 0.32$). Birth masses of calves that died as a result of predation did not differ from those of calves that died from all other causes ($t = 0.13$, $P = 0.73$).

Birth date

Neonatal mortality resulting from predation tended to be greater in early-born calves than in late-born calves ($G =$

3.7, $df = 1$, $P = 0.055$). This effect was significant for calves born in GTNP ($G = 4.1$, $df = 1$, $P = 0.042$). The susceptibility of early-born calves to predation was apparent for males ($G = 6.05$, $df = 1$, $P = 0.014$) but not for females ($G = 0.27$, $df = 1$, $P = 0.61$).

Neonatal deaths from all causes did not differ between early-born and late-born calves ($G = 0.3$, $df = 1$, $P = 0.59$). The higher predation rate among early-born calves was offset by a higher mortality rate of late-born calves from causes other than predation ($G = 4.3$, $df = 1$, $P = 0.04$). The mean birth date of calves that died from predation (29 May) was 9 days earlier ($t = 13.2$, $P = 0.002$) than that of calves which died from all other causes (7 June).

Spatial effects

Neither the predation rate ($G = 0.09$, $df = 1$, $P = 0.76$) nor the overall neonatal mortality rate ($G = 0.21$, $df = 1$, $P = 0.65$) differed between calves born in GTNP and those born outside the park. August calf:cow ratios, which indicate recruitment of elk calves into the population after neonatal mortality has occurred, did not differ ($P > 0.5$) between GTNP and the other summer ranges during any year (Table 2). Calf:cow ratios were correlated ($r = 0.93$, $df = 3$, $P = 0.01$) with mean monthly temperature in April.

Discussion

Causes of juvenile mortality

The neonatal loss in this study, 15%, was considerably less than the losses in YNP, 31% (Singer et al. 1996), and in Idaho, 66% (Schlegel 1976), but similar to the mortality of elk in Colorado (Bear 1989) and red deer in Scotland, where predation was minimal (Guinness et al. 1978; Blaxter and Hamilton 1980; Clutton-Brock et al. 1982, 1985b). Fifty percent of calves that died before 15 July were killed by black bears compared with at least 24 of 35 neonatal deaths due to black bear predation on Idaho elk (Schlegel 1976). Black bears killed 57 and 35% of radio-collared neonatal moose during 2 years in Alaska (Franzmann et al. 1980). Singer et al. (1995) reported that 75% of neonatal elk losses in Yellowstone National Park resulted from predation; 12–16 of 30 predations were by grizzly bears (*Ursus arctos*) and black bears and 11 others by coyotes. Predation in the Jackson elk herd may have been less than in Yellowstone because grizzly bears were uncommon in the calving areas where we captured calves.

Poor foraging conditions may have prompted bears to find alternative food sources in 1991, the year when the most calves were killed by bears, to meet nutritional requirements (Schwartz and Franzmann 1991). The spring of 1991 was unusually cool and growth of vegetation was delayed. However, without knowing the relative numbers, distributions, and food habits of bears each year, the cause of the higher calf predation in 1991 is equivocal.

The phenotypes of those animals that die can be important in regulating population size (Lomnicki 1980). In juvenile Scottish red deer, neonatal survival was density-independent and correlated with birth mass, which was largely a function of April temperatures during each cohort's gestation (Clutton-Brock et al. 1985b; Albon et al. 1987). In Jackson elk, mortality of individual calves was not related to birth mass.

However, the calf:cow ratio each August was correlated with mean temperature during April, the first full month of the third trimester of gestation and of new forage growth.

Early-born male calves were more often predated despite the fact that females were born earlier than males (Smith et al. in press). Twelve of 19 calves that cast their collars were also males. Male calves may be more active and rambunctious than females and thus fall prey to bears and coyotes more often than females. Geist (1982) noted that "in the hider strategy, unlike the swamping strategy, there is no premium on bearing a precocious calf, in fact a lively calf may endanger itself by making itself visible to predators." Bears may have hunted calves more actively early in the parturition period either because other protein sources were less abundant, or because the proportion of very young (i.e., vulnerable) calves, relative to all calves, was higher.

Male-biased mortality reduced the sex ratio of 77 male : 68 female calves at capture (excluding calves that cast collars) to 61 males : 62 females on 15 July. The sexes of dead calves were not reported by Schlegel (1976) or Singer et al. (1995), but black bears preyed more heavily on male white-tailed deer fawns (Ozoga and Clute 1988).

Viral enterocolitis, attributable to coronavirus and rotavirus infections, has been suspected but not reported in free-ranging elk (E.S. Williams, Wyoming State Veterinary Laboratory, personal communication, 1993). Both families of viruses cause enteritis and diarrhea in domestic bovine neonates (Mebus 1990a, 1990b) and neonatal diarrhea in farmed red deer, which may kill 50% of afflicted animals (Smits 1992). Coronaviral and rotaviral enterocolitis have caused neonatal mortality in wild Rocky Mountain elk at fenced research facilities in Wyoming (E.S. Williams, personal communication, 1992) and Oregon (J. Cook, Washington State University, personal communication, 1994).

Two radio-collared calves that succumbed to coronaviral enterocolitis were 16 and 18 days old. An unmarked calf 14–21 days old with lesions consistent with rotaviral or coronaviral enterocolitis was found dead <200 m from a dead 23-day-old radio-collared calf diagnosed with rotaviral enterocolitis. Three of these four cases of mortality due to enterocolitis occurred in an area grazed by domestic cattle. However, under field conditions there is no reported evidence that cross-species infection is important (Mebus 1990a, 1990b).

Herd productivity

Smith and Robbins (1994) estimated the fecundity of elk that wintered on the NER at 63 calves per 100 females ≥ 1 year old. Midsummer calf:cow ratios (after neonatal losses) averaged 42.5:100 during this study and 45.4:100 during 1978–1984 (Smith and Robbins 1994). This is a 28–33% difference between expected natality and observed midsummer recruitment. We documented only 15% mortality of radio-collared neonates. The additional 13–18% loss of expected production probably occurs for one or both of the following reasons. (1) Some barren cows may occupy habitats in midsummer in which they are less observable than calf–cow groups, thereby biasing recruitment estimates upward. (2) Estimates of neonatal mortality of free-ranging ungulates are probably downward-biased because of significant perinatal mortality. Still births, calves rejected and

abandoned by dams, and calf mortality immediately post partum are missing from samples of captured neonates. Over half of all preweaning mortality (including still births) of red deer calves occurred within 24 h of birth (Blaxter and Hamilton 1980) and of caribou fawns within 48 h of birth (Whitten et al. 1992). Similarly, Ozoga and Clute (1988) concluded that mortality of white-tailed deer fawns based on collared samples was underestimated because many died when <48 h old, before they could be captured.

Spatial patterns of mortality

Animal densities on summer–fall ranges have been inversely correlated with productivity of deer and elk herds (Julander et al. 1961; Verme 1967; Rudd et al. 1983). We found no difference in midsummer calf:cow ratios, which reflect a combination of natality and juvenile survival, between GTNP and summer ranges outside the park. Furthermore, the correlation of summer calf:cow ratios with mean annual April temperatures suggests a density-independent effect on natality and (or) neonatal survival.

On the Isle of Rhum, hinds with home ranges in the highest density areas produced calves that were born later, were lighter, and had poorer survival, primarily during winter, than those from lower density areas of the island (Clutton-Brock et al. 1982). However, densities of deer on Rhum were 4–5 times greater than those in GTNP (Clutton-Brock et al. 1982, p. 313). Houston (1982) identified undernutrition at high densities and its effects on reproduction, calf birth masses and survival of calves (both in summer and winter) as paramount in the growth trajectory of Yellowstone's migratory northern herd. Human predation on elk that migrated outside the park in winter dampened the effects of winter food limitations on the herd by reducing density. One might expect the migratory Jackson herd's response to density to mimic that of Yellowstone's northern herd. Elk that summer in GTNP are subject to human predation, albeit at rates equal to or less than those on elk that summer outside GTNP (Smith 1994; Smith and Robbins 1994). However, winter nutritional deprivation is mitigated by food supplementation of much of the herd, and calf recruitment has trended upward in GTNP (Boyce 1989, p. 54). The benefits of winter feeding on the condition of parous females and neonatal growth of offspring (Smith et al. 1996) apparently mask negative effects that current densities of elk on summer ranges may impose on offspring survival.

These aspects of the Jackson herd's population biology do not support the hypothesis that higher elk densities in GTNP are regulating elk numbers in the park differently from those outside the park. We concur with Boyce (1989) that hunting in GTNP is warranted to limit numbers of elk in GTNP that winter on NER.

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