JUVENILE SURVIVAL AND POPULATION REGULATION OF THE JACKSON ELK HERD

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Abstract: Elk (*Cervus elaphus nelsoni*) that summer in Grand Teton National Park (GTNP) are part of the migratory Jackson Elk Herd. They are fed in winter on the National Elk Refuge (NER) and have been hunted in portions of GTNP since 1950 to control population size. However, the number of elk in the Jackson Elk Herd has grown from about 8,000 in 1984 to >16,000 in 1997. We captured and radiocollared 164 newborn calves during 1990–92 to quantify juvenile mortality and its role in regulating the Jackson Elk Herd. Elk captured in GTNP (5.9 elk/km^2) and on adjacent national forest lands of lower elk densities (2.4 elk/km^2) were radiomonitored through May 1994. Mortality of calves was similar during summer (15.2%), fall (15.3%), and winter (16.5%) 1990–92. Most deaths resulted from predation, hunting, and winter mortality associated with increased precipitation, duration of winter, and epizootic disease. Survival of calves supplementally fed in winter exceeded survival of calves not fed ($P = 0.039$). All but 1 of 16 deaths of elk $\geq$1 year old ($n = 122$) resulted from hunting. Early-born calves experienced higher winter survival ($P = 0.02$) than late-born calves. Annual calf survival ($\bar{x} = 0.579$) was inversely related to birth date ($P < 0.01$) and winter precipitation ($P = 0.05$). Annual survival of female calves ($\bar{x} = 0.662$) exceeded survival of males ($\bar{x} = 0.502$; $P = 0.049$). Survival of juvenile elk born and summering in GTNP did not differ seasonally or annually from survival of juveniles outside the park ($P > 0.47$). Because much of the variation in juvenile survival was density independent, we recommend management that reduces the dependence of elk on supplemental feed and increases harvests of female elk.

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Since 1970, burgeoning populations of elk and white-tailed deer (*Odocoileus virginianus*) in a number of U.S. national parks have created concern about the consequences of policies that limit human intervention in ecosystem processes (Porter 1992, Wagner et al. 1995). During the early 1980s, approximately 35% of the Jackson Elk Herd in northwestern Wyoming and 50% of the elk that wintered on the NER spent summer and fall in GTNP (Smith and Robbins 1994). In 1950, federal legislation more than doubled the area of GTNP and provided for an elk hunt in portions of GTNP to assist with annual reductions of the Jackson Elk Herd. Elk hunts were also conducted on the north half of the NER to control elk numbers. Adult elk that summered in GTNP were harvested at lower rates and had higher survival than elk that summered outside the park (Smith and Robbins 1994). Accordingly, the number of elk that summered in the expanded park area increased from <1,000 elk in 1950 (Cole 1969) to nearly 4,000 in the early 1980s (Smith and Robbins 1994).

The annual hunt in GTNP, termed an elk reduction program, was controversial (Dexter 1984, Wood 1984). Subsequently, a 1986 natural resource management plan recommended investigating whether reduced or no hunting of elk in GTNP would be compatible with proper management of the elk herd (Grand Teton National Park 1986). This recommendation was predicated on hypotheses that numbers of elk in GTNP would be regulated by density-dependent mechanisms, as reported in some populations of elk (Knight 1970, Houston 1982, Sauer and Boyce 1983) and other ungulates (Fowler 1987).

To help clarify processes regulating the Jackson Elk Herd, we compared survival of juvenile elk that occupied GTNP and other summer ranges, and we compared survival of elk that were fed in winter versus elk not fed. We predicted the following:

(1) Male calves are more likely to die from natural causes of mortality than female calves (Clutton-Brock et al. 1985). Hunting-relat-

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ed deaths are not sex-biased in calves, but are male-biased among elk ≥1 year old where hunters are allowed to harvest either-sex elk.

(2) First-year survival of elk calves varies positively with birth mass (Clutton-Brock 1985, 1987).

(3) Survival of calves inversely varies with parturition date. Mortality of late-born calves is most pronounced in winter (Albon et al. 1987, Singer et al. 1997).

(4) Overwinter survival of juvenile elk does not vary with supplemental feeding regimen but instead varies with population density, winter severity, or both.

(5) Annual survival of juvenile elk that were born and summered in GTNP does not differ from juveniles that summered outside the park. Any increased natural mortality of GTNP elk is compensated by higher hunting mortality of elk that summered outside GTNP on national forest lands.

STUDY AREA

Cole (1969), Boyce (1989), and Smith and Robbins (1994) described the boundaries, topography, climate, and vegetation communities of the Jackson Elk Herd unit, which encompasses 5,195 km^2 in the Snake River watershed of northwest Wyoming. Elk of the Jackson herd migrate 10–90 km between seasonal ranges. The elk occupy 4 relatively distinct geographical areas during summer, which are referred to as herd segments: GTNP, southern Yellowstone National Park (YNP), the Teton Wilderness Area (TW), and the Gros Ventre drainage (GV; Cole 1969, Boyce 1989, Smith and Robbins 1994; Fig. 1). Nearly all the elk that summer in GTNP winter on or adjacent to the NER (Smith and Robbins 1994). In the early 1990s, densities of elk within GTNP's central valley (5.9 elk/km^2; Fig. 1) exceeded densities outside the park (2.4 elk/km^2; Smith 1994).

About 80% of the Jackson Elk Herd, and nearly all GTNP elk, are supplementally fed alfalfa hay for 2–3 months each winter (Boyce 1989). The number of elk in the Jackson herd and the number that winter on the NER have doubled since 1984 (Table 1).

METHODS

Calf Capture, Monitoring, and Forensics

Each year during 1990, 1991, and 1992, we captured 2 groups of calves within 1 week of birth: 1 group that would summer inside GTNP, and another group that would summer outside GTNP. Smith and Anderson (1996) described the capture and handling procedures. We followed animal welfare protocol as outlined by the University of Wyoming and the U.S. Fish and Wildlife Service at the time of the study

Calves were aged according to Johnson (1951). We categorized calves as late-born (greater than the median birth date of their cohort) or early-born to test if birth date influenced survival. We estimated birth mass from sex-specific daily growth rates of newborns (Smith et al. 1997). We categorized birth mass of calves as heavy-born (greater than the median birth mass of their cohort) or light-born to test if birth mass influenced survival.

We fitted an expandable 230-g radiocollar (Telonics, Mesa, Arizona, USA) on each calf. Collars were designed to last for ≥26 months (3 summers) and included a mortality switch (Smith et al. 1998).

We monitored radiocollared elk from May 1990 to May 1994. We monitored neonates twice daily from birth to 15 July from 4 fixed telemetry towers (Fig. 1; Smith and Anderson 1996). From 15 July to 1 December, elk were located 3 times weekly from towers or 2–3 times weekly from aircraft. Elk that wintered on the NER were located biweekly from the ground during 1 December–1 May. Elk that wintered elsewhere were located monthly from aircraft.

During winter 1992–93, we replaced radiocollars on 42 of the 69 (61%) surviving elk because batteries were due to fail or collar materials were deteriorating. Those elk were immobilized with powdered succinylcholine chloride injected via Cap-Chur guns.

The protocol for forensic examination and diagnostic testing of elk remains was previously described by Smith and Anderson (1996). Cause of death was not determined for most mortalities in winter, because of the longer intervals between monitoring sessions and the rapid scavenging of carcasses.

Population Size

Each February, observers riding on feeding vehicles counted the number of elk wintering on the NER and the 3 feedgrounds in the GV and classified them as calves, females, yearling males, and mature males (Fig. 1; Boyce 1989). Elk wintering at other locations were surveyed

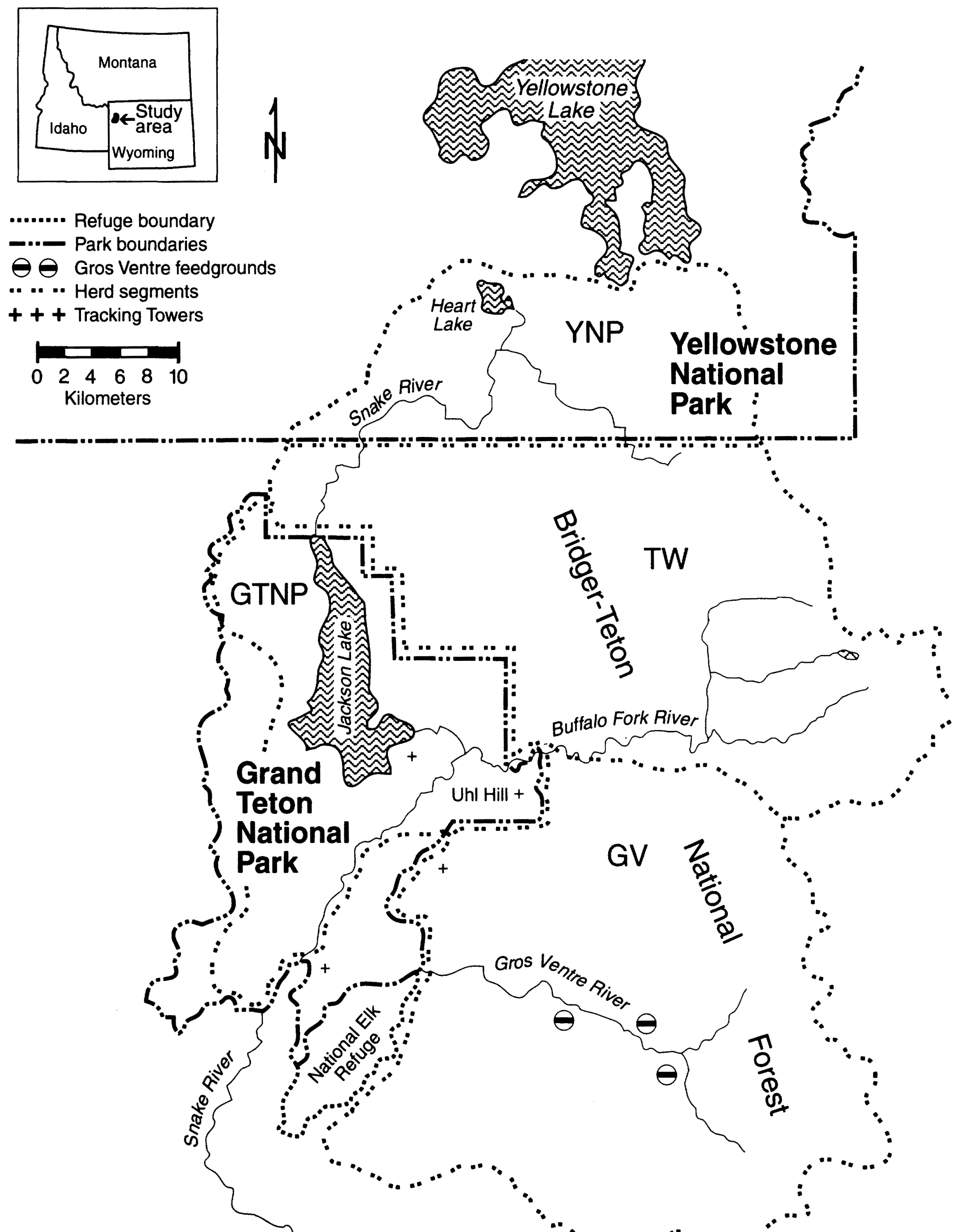

Fig. 1. Winter feedgrounds and summer distributions of the 4 herd segments of the Jackson Elk Herd: Grand Teton National Park (GTNP), Yellowstone National Park (YNP), Teton Wilderness (TW), and Gros Ventre Drainage (GV).

Table 1. Numbers of elk counted on the National Elk Refuge (NER), on the 3 Gros Ventre (GV) elk feedgrounds, and throughout the Jackson Elk Herd unit during February 1984–97. Elk counted and classified in the central valley of Grand Teton National Park (GTNP) were observed during helicopter surveys in August 1990–97.

	Elk in the Jackson herd			Elk counted in GTNP	
Year	NER	GV	Herd[a]	*n*	Calves: 100 cows
1984	5,010	1,574	7,581		
1985	5,758	1,328	8,500		
1986	6,430	1,665	9,593		
1987	7,820	1,227	11,276		
1988	7,753	1,567	12,443		
1989	9,486	2,334	14,919		
1990	8,131	1,778	13,992	673[b]	48.2
1991	8,314	1,469	12,095	1,486	47.4
1992	8,800	1,186	13,458	1,210	52.4
1993	8,295	1,688	14,220	1,628	44.7
1994	8,500	1,514	15,066	1,280	44.0
1995	9,436	1,970	14,899	1,633	38.4
1996	10,004	1,577	14,042	1,450	46.0
1997	10,736	1,947	16,218	1,224	36.5

[a] Includes elk counted from feed wagons at the NER and GV feedgrounds, and elk counted from aircraft at winter ranges where elk were not supplementally fed.

[b] A smaller area of GTNP was surveyed in 1990 than in succeeding years.

from helicopter (Smith and Robbins 1994). We used a helicopter to count and classify elk that summered in a portion of GTNP during each August (Smith and Anderson 1996).

Survival Estimates and Statistical Analysis

We used the Kaplan-Meier product limit estimator (Kaplan and Meier 1958, Cox and Oakes 1984) to estimate survival of calves during the 3 periods when we observed mortalities: (1) neonatal (birth–15 Jul), (2) fall (10 Sep–30 Nov), and (3) winter (1 Jan–15 May), and to estimate survival of elk ≥1 year old during the fall hunting season (10 Sep–30 Nov) and on an annualized basis. We estimated survival rates for animals that retained their radiocollars throughout a given time period or until they died. For calves that died during the neonatal and fall time periods, time of death was known to the day. Because radiomonitoring was less frequent in winter, we analyzed winter survival on a monthly basis.

We constructed pairwise log-rank tests to compare survival curves between the sexes and among years (Pollock et al. 1989). Neonatal survival was compared between elk born inside and outside GTNP (Smith and Anderson 1996). We also tested differences in fall and winter survival between calves that summered inside and outside GTNP, fall survival between elk ≥1 year old that summered inside and outside GTNP, and winter survival between calves that wintered on and off NER.

Survival (pairwise log-rank tests) did not differ among years. Consequently, we pooled the 1990–92 cohorts to estimate calf survival for each period and each sex. During 1992, only 2 of 49 (4%) calves we radiocollared summered outside GTNP. Therefore, we pooled only the 1990 and 1991 cohorts to test spatial differences in calf survival.

Hunting-related mortalities were censored to estimate annual survival of calves, exclusive of hunting. When testing differences in mortality and survival of elk ≥1 year old from different summer ranges, we pooled elk that summered in GTNP and the NER and compared them to all others.

We used likelihood ratio chi-square to test for differences in distributions of the sexes during winter (Sokal and Rohlf 1981). We used least squares linear regression to examine relations between cohort survival and various environmental and feeding variables. We used SYSTAT software (SYSTAT 1992) for all statistical tests and considered $P < 0.05$ as significant. All means are presented ± standard error.

RESULTS

We captured 164 calves (126 in GTNP, 38 in the Bridger-Teton National Forest) and radiocollared them when <1–7 days old ($\bar{x}$ for age = 3.6 ± 0.19 days). Twelve of 89 (13%) males and 7 of 75 (9%) females cast their collars prior to 15 July and were censored from mortality estimates (Table 2). An additional 19 elk, whose collars deteriorated and fell off before they could be replaced during winter 1992–93, were not included in all analyses.

Temporal Patterns of Mortality

All 56 deaths of radiocollared calves occurred in 1 of 3 time periods: 22 (39%) from birth to 15 July (neonatal; see Smith and Anderson 1996), 18 (32%) during fall, and 16 (29%) during winter. During fall, 14 calves were legally harvested, 2 were wounded by gunshots and were later found dead, and 2 were killed by mountain lions (*Felis concolor*) in GTNP in October of 1990 and 1991. Twelve of 16 deaths of calves during winter occurred in winter 1992–93. Carcasses of 15 winter mortalities were ex-

Table 2. Survival rates (*S*) of elk calves during the neonatal period (birth–15 Jul), fall hunt (10 Sep–30 Nov), and winter (1 Jan–15 May). The 1990–92 cohorts are pooled.

Period	Location	Sex	No. marked	No. deaths	Survival S	Survival SE	95% CI	P[a]
Neonatal	All	M	89	16	0.738	0.002	0.643–0.833	0.018
Neonatal	All	F	75	6	0.900	0.001	0.830–0.971	
Neonatal	All	Both	164	22	0.837	0.001	0.779–0.895	
Fall Hunt	All	M	61	9	0.848	0.002	0.757–0.940	0.74
Fall Hunt	All	F	57	7	0.874	0.002	0.787–0.961	
Fall Hunt	All	Both	118	16	0.862	0.001	0.799–0.925	
Winter	All	M	50	9	0.817	0.003	0.711–0.922	0.67
Winter	All	F	49	7	0.857	0.003	0.759–0.955	
Winter	All	Both	99	16	0.837	0.001	0.765–0.909	
Winter	On NER[b]	Both	71	8	0.886	0.001	0.812–0.960	0.039
Winter	Off NER	Both	28	8	0.714	0.007	0.551–0.878	
Annual	All	M	89	35	0.502	0.003	0.395–0.609	0.049
Annual	All	F	75	21	0.662	0.003	0.547–0.777	
Annual	All	Both	164	56	0.579	0.002	0.499–0.660	

[a] Differences in survival between the sexes were tested with a log-rank chi-square test.
[b] NER = National Elk Refuge.

tensively scavenged, but 1 intact carcass was recovered and necropsied in March 1993. Diagnostic tests confirmed septicemic pasteurellosis caused by the bacterium *Pasteurella multocida*, capsule B, serotype 3/4.

All deaths of elk ≥1 year old were related to hunting (17 legally harvested, 3 cripple losses, 1 probable illegal kill), except for a 12.5-month-old male killed by a mountain lion during June 1991. Survival during hunting season did not differ ($P > 0.53$) between calves (0.862) and elk ≥1 year old (0.835; Tables 2, 4). However, annual survival of elk ≥1 year old (0.826) exceeded ($P < 0.01$) annual survival of calves (0.579; Tables 2, 4).

Prediction 1—Survival Differences Between Sexes

Neonatal survival was higher among females (0.900) than males (0.738), and annual calf survival was also higher among females (0.662) than males (0.502; Table 2, Fig. 2). During the fall hunting season, survival of females ≥1 year old (0.890) exceeded survival of males (0.729; Table 4, Fig. 2). Only calves died during winter. Although winter survival of all radiocollared calves was not sex-biased (Table 2, Fig. 2), 7 of 8 calves that died off the NER were males, and 6 of 8 that died on the NER were females. Similarly, 20 of 28 radiocollared calves that wintered off the NER were males, and 41 of 71 calves that wintered on the NER were females ($G_1 = 7.01$, $P = 0.008$).

Predictions 2 and 3—Effect of Birth Mass and Birth Date

Light-born calves were no less likely than heavy-born calves to survive as neonates, ($\chi^2_1 = 0.21$, $P = 0.72$), during fall ($\chi^2_1 = 0.14$, $P = 0.79$) or during winter ($\chi^2_1 = 0.42$, $P = 0.44$).

Table 3. Survival rates (*S*) of radiocollared elk calves from the 1990 and 1991 cohorts that were born in and summered in Grand Teton National Park (GTNP) compared to calves from outside GTNP during the neonatal period (birth–15 Jul), fall (10 Sep–30 Nov), and winter (1 Jan–15 May).

Period	Location	No. marked	No. deaths	Survival S	Survival SE	95% CI	P[a]
Neonatal	GTNP	84	12	0.816	0.002	0.732–0.899	0.47
Neonatal	Outside GTNP	31	5	0.835	0.005	0.699–0.970	
Fall Hunt	GTNP	54	7	0.866	0.002	0.773–0.960	0.52
Fall Hunt	Outside GTNP	29	6	0.793	0.006	0.646–0.941	
Winter	GTNP	45	3	0.933	0.001	0.862–1.004	0.80
Winter	Outside GTNP	23	1	0.957	0.002	0.873–1.040	
Annual	GTNP	84	22	0.658	0.003	0.543–0.773	0.89
Annual	Outside GTNP	31	12	0.606	0.007	0.447–0.765	

[a] Differences in survival between geographic locations were tested with a log-rank chi-square test.

Table 4. Survival rates (*S*) of juvenile elk 1–4 years old that summered in Grand Teton National Park (GTNP) and outside GTNP during the fall hunting season (10 Sep–30 Nov 1991–93), and from June 1991 to June 1994.

Period	Location	Sex	No. elk[a]	No. deaths	Survival *S*	Survival SE	95% CI	*P*[b]
Fall	All	M	48	13	0.729	0.004	0.603–0.855	0.015
Fall	All	F	73	8	0.890	0.001	0.819–0.962	
Fall	GTNP	Both	78	14	0.833	0.002	0.750–0.917	0.84
Fall	Outside GTNP	Both	43	7	0.837	0.003	0.728–0.946	
Fall	All	Both	121	21	0.835	0.001	0.768–0.901	
Annual	All	Both	122	22	0.826	0.001	0.759–0.894	
June 1991–June 1994	All	Both	82	22	0.503	0.003	0.401–0.606	

[a] Includes every fall that each individual elk was alive.
[b] Differences in survival between the sexes and between geographic areas were tested with a log-rank chi-square test.

Birth date had no effect on neonatal survival ($\chi^2_1 = 0.38$, $P = 0.57$) or whether calves were harvested by hunters ($\chi^2_1 = 1.83$, $P = 0.29$). Winter survival was higher in early-born calves than in late-born calves ($\chi^2_1 = 4.48$, $P < 0.04$). The effect was reinforced for calves born in GTNP ($\chi^2_1 = 6.99$, $P < 0.01$).

Prediction 4—Annual Variation in Cohort Survival

Survival during winter 1992–93 (0.625) was lower than during the previous 2 winters (0.941; $\chi^2_1 = 17.1$, $P < 0.01$). Winter 1992–93 had warmer temperatures in December and January but more precipitation and deeper snow than the previous 2 winters (Table 5). Combined December and January precipitation ($r^2 = -0.99$, $P = 0.03$), the number of days elk were fed ($r^2 = -0.99$, $P < 0.03$), and mean cohort birth mass of calves entering each winter ($r^2 = 0.99$, $P < 0.01$) varied multicollinearly with cohort survival of radiocollared calves (Table 5).

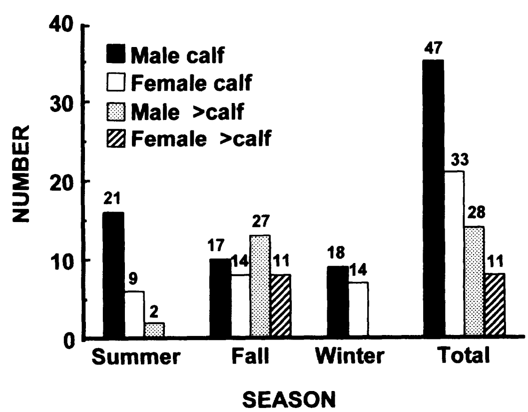

Fig. 2. Numbers of radiocollared calves and elk ≥1 year old that died during summer (15 May–15 Jul), during fall (10 Sep–30 Nov), and during winter (1 Jan–15 May) 1990–93. Numbers above bars indicate percentage of each age–sex group that died. Note that 1 elk ≥1 year old died between 15 May and 15 July as a yearling.

Prediction 5—Effects of Seasonal Distribution

We found no differences in seasonal or annual survival between calves from GTNP and calves from summer ranges outside GTNP ($P > 0.47$; Table 3). Annual survival for these 2 groups also did not differ when hunting mortalities were censored and only natural causes of mortality were considered (Table 3). Likewise, survival of elk ≥1 year old did not differ between GTNP and summer ranges outside the park (Table 4).

Winter survival of calves on the NER (0.886) was higher than survival of calves wintering off the NER (0.714; Table 2). Calves that summered in GTNP were more likely to winter on the NER than calves that summered elsewhere ($G_1 = 16.05$, $P < 0.01$).

DISCUSSION

Sex-Specific Calf Mortality

A ratio of 89 males:75 females at birth in year *x* declined to 41 males:42 females 1 year later. This male-biased mortality was due to 3 factors: (1) male-biased neonatal mortality (Smith and Anderson 1996); (2) sex-bias in winter range attendance; and (3) calf mortality off the NER exceeding mortality on the NER, suggesting an effect of supplemental feeding. More female calves died on the NER and more male calves died off the NER because of the relative abundance of each sex using those winter ranges. More female calves used the NER than expected because of neonatal mortality of calves born in GTNP, nearly all of which wintered on the NER, was male-biased. More male calves

Table 5. Cohort survival of radiocollared elk calves during winters 1990–91 through 1992–93 in relation to climatic variables, supplemental feeding regimen, and number of elk. Test results are of correlations between each variable and winter survival.

Independent variable	Cohort 1990	Cohort 1991	Cohort 1992	*r*	*P*
Winter survival[a]	0.919	0.968	0.625		
Mean December and January temperature (°C)	−22.9	−22.0	−19.5	0.84	0.26
December and January precipitation (cm)	3.4	1.6	9.2	−0.99	0.03
December and January snow depth (cm)	69	53	104	−0.98	0.09
Cohort birth mass (kg)	16.1	16.2	15.6	+0.99	<0.01
Cohort Julian birth date[a]	149.0	151.8	152.0	0.23	0.68
Number of days of supplemental feeding	65	57	97	−0.99	0.03
Daily ration (kg)	3.4	3.0	3.8	0.84	0.26
Julian ending date of feeding	83	83	107	−0.98	0.09
Julian starting date of feeding	15	22	11	0.75	0.34
Elk in the Jackson herd	12,905	13,457	14,220	0.83	0.28
Elk on the National Elk Refuge	8,314	8,800	8,295	0.28	0.65

[a] Winter survival of calves from each cohort that were alive on 1 January.

wintered off the NER than expected because females that summered outside GTNP were more likely to produce male calves (Smith et al. 1996), and calves that summered outside GTNP were more likely to winter off the NER.

Changes in sex ratios can significantly alter growth rates of ungulate populations (Medin and Anderson 1979). After 1 year of life, the male:female ratio of calves that summered in GTNP favored females (84:100), and the sex ratio of calves outside GTNP favored males (140:100). As these yearlings are recruited into the breeding population, the GTNP herd segment has the potential to add 29% more calves per 100 elk annually than the other herd segments, given that midsummer calf:cow ratios are similar throughout the Jackson herd (Smith and Anderson 1996).

Effects of Birth Mass and Birth Date on Survival

Contrary to our expectations, we found no correlation between birth mass of individual calves and their survival. However, survival was positively correlated with mean cohort birth mass. Cohort birth mass was a function of environmental conditions when calves were in utero (Smith et al. 1997), a density-independent relation also reported in red deer (*Cervus elaphus;* Albon et al. 1987).

Predation (n =15) and disease (n = 4) accounted for 19 of 22 (86%) neonatal deaths. Predators selected early-born calves, whereas late-born calves died from other causes (Smith and Anderson 1996).

As we predicted, late-born calves, which were presumably energetically disadvantaged (Clutton-Brock et al. 1982, 1987; Festa-Bianchet 1988), were more likely to die during winter than early-born calves. We have no evidence of differences in either birth mass or timing of parturition that may lead to differential survival of calves from the various herd segments of the Jackson herd.

Hunter Harvests and Herd Growth

Survival rates, particularly of adults, greatly influence the growth rate of an elk population (Nelson and Peek 1982). Whereas most calves died from causes unrelated to hunting, 21 of 22 deaths of animals ≥1 year old were related to hunting. Annual harvest of radiocollared elk of all age and sex classes was 13.4%, plus an additional 2.1% unretrieved wounding loss (2 calves, 3 cows). This wounding loss was 21% of the hunter take of antlerless elk and compares to wounding losses of 18% of cow elk in Colorado (Freddy 1987), 27% of females and 12% of males in northern Idaho (Leptich and Zager 1991), and 0% of females and 21% of males in northcentral Idaho (Unsworth et al. 1993). Responses to a 1967 questionnaire survey of guides and outfitters in western Wyoming indicated a 22% wounding loss (Straley 1968).

To help control numbers of elk in the national parks, elk are hunted in portions of the NER and GTNP (Boyce 1989; Wyoming Game and Fish Department. 1997. District 1 annual big game unit reports, 1996. Volume XX1, unpublished). Harvests were lower (17%) among GTNP elk than elk that summered outside GTNP (24%) from 1978–84 (Smith and Robbins 1994). Although the number of elk harvested annually in GTNP increased after 1987, the harvest rate remained at 17% (Table 4). Hunting seasons in some areas outside GTNP became more restrictive during the 1990s (Smith 1994; Wyoming Game and Fish Department. 1997. District 1 annual big game unit reports, 1996. Volume XX1, unpublished). Consequently, we measured lower hunting mortality of radiocollared elk that summered outside GTNP (16%) than occurred 10 years earlier (24%).

Reduced harvest rates contributed to higher annual survival of radiocollared elk ≥1 year old throughout the Jackson herd during this study (M = 0.729, F = 0.890) than during 1978–84 (M = 0.630, F = 0.778; Smith and Robbins 1994). Concomitantly, the size of the Jackson herd has grown from <8,000 elk in 1984 to >16,000 elk in 1997, or >5,000 in excess of the herd objective of 11,000 wintering elk (Table 1; Wyoming Game and Fish Department. 1997. District 1 annual big game unit reports, 1996. Volume XX1, unpublished).

Summer Recruitment of Calves

Densities of elk within GTNP's central valley (5.9 elk/km^2) were an estimated 2.5-fold higher in 1991 than densities outside the park (2.4 elk/km^2; Smith 1994). Despite this disparity, we found no difference in survival rates of elk that summered inside versus outside GTNP. Moreover, Smith and Anderson (1996) reported similar recruitment rates of calves inside versus outside GTNP during August helicopter classifications of elk. On the Isle of Rhum, Scotland, females in home ranges of the highest red deer densities produced later calves, lighter calves, and their calves had poorer survival, primarily during winter, than those from lower-density areas of the island (Clutton-Brock et al. 1982, 1987). Elk densities may not have been sufficiently different on summer ranges of the Jackson herd to produce differences in such demographics.

Boyce (1989) reported density-dependent summer calf:cow ratios (recruitment) in GTNP as a function of combined cow, calf, and yearling male numbers counted during 1970–82. Only 36% (SE = 3.3) of animals observed during those censuses could be classified (Smith and Robbins 1994). Consequently, ground classifications were abandoned, and replicated helicopter classifications were initiated in GTNP in 1990 to increase reliability of classifications. More than 99% of elk observed from helicopter were classified (S. L. Cain, Grand Teton National Park and B. L. Smith, unpublished data). During 1990–97, when elk numbers were higher in the Jackson herd than at any time since 1970, calf:cow ratios were not correlated with either total elk classified in GTNP ($F_{1,6} = 0.61$, $P = 0.47$) or with the combined number of cow, calf, and yearling male elk classified each year ($F_{1,6} = 0.70$, $P = 0.44$; Table 1).

Winter Survival and Calf Recruitment

Winter survival was reported to regulate, in a density-dependent fashion, both red deer on the Isle of Rhum, Scotland (Clutton-Brock et al. 1985), and northern YNP elk (Houston 1982, Singer et al. 1997). Unlike the nonmigratory red deer of Rhum, migration of Jackson and northern YNP elk between seasonal ranges may help alleviate resource competition. Houston (1982) identified effects of undernutrition on reproduction, birth mass, and survival of calves as paramount in the growth trajectory of YNP's northern herd. Elk that migrated down the Yellowstone River and were reduced in density by hunting tended to show higher calf:cow ratios in winter than elk that remained well within YNP (Houston 1982:44).

Elk are hunted throughout the Jackson herd, and about 80% are supplementally fed to reduce undernutrition and winter mortality. Consequently, Jackson calves that wintered off the NER (0.714; Table 2), like calves not food supplemented in northern YNP (0.719; Singer et al. 1997), had poorer overwinter survival than calves that were food supplemented on the NER (0.886). However, survival of calves on the NER declined as the number of days the elk were fed during winter increased. Feeding began earlier when December precipitation was heavy and more elk were on the NER, and feeding extended later into spring when cool March temperatures delayed new vegetation growth (Smith et al. 1997). Winter mortality was a significant component of annual mortality of radiocollared calves only during winter 1992–93, when above-average precipitation fell (National Oceanic and Atmospheric Administration 1992) and an estimated 160 elk, mostly calves, succumbed to an epizootic of septicemic pasteurellosis on the NER (T. J. Roffe, U.S. Geological Survey, and B. L. Smith, unpublished data). Outbreaks of pasteurellosis were detected at the NER during previous winters (Franson and Smith 1988). We are monitoring survival of additional cohorts of calves to clarify relations among calf survival, population demographics, and environmental factors.

MANAGEMENT IMPLICATIONS

Similar rates of midsummer calf recruitment (Smith and Anderson 1996), juvenile dispersal (Smith 1994), and juvenile survival of elk occupying summer ranges in GTNP and summer ranges outside GTNP suggest significant differences did not exist in the processes regulating numbers of elk in those 2 areas of differing elk densities. Winter food supplementation increased survival of elk <1 year old. Our findings suggest much of the variation in juvenile survival was density independent, varying inversely with winter precipitation, epizootic disease, and predation. Survival of elk ≥1 year old was high, with 80–95% of mortality resulting from hunting (Smith and Robbins 1994, this study). To stem the growth of the Jackson herd will require innovative management strategies. Implementing hunting seasons that harvest more female elk is 1 alternative. Reducing the proportion of the elk herd that is supplementally fed in winter may be another (Smith and Robbins 1994).

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