

Early Development of Supplementally Fed, Free-Ranging Elk

Author(s): Bruce L. Smith, Russell L. Robbins, Stanley H. Anderson

Source: *The Journal of Wildlife Management*, Vol. 61, No. 1 (Jan., 1997), pp. 26-38

Published by: Allen Press

Stable URL: <http://www.jstor.org/stable/3802411>

Accessed: 26/07/2009 14:28

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=acg>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.



Allen Press is collaborating with JSTOR to digitize, preserve and extend access to *The Journal of Wildlife Management*.

EARLY DEVELOPMENT OF SUPPLEMENTALLY FED, FREE-RANGING ELK

BRUCE L. SMITH, National Elk Refuge, PO Box C, Jackson, WY 83001, USA

RUSSELL L. ROBBINS,¹ National Elk Refuge, PO Box C, Jackson, WY 83001, USA

STANLEY H. ANDERSON, Wyoming Cooperative Research Unit, University of Wyoming, Laramie, WY 82071, USA

Abstract: Early development of cervids has been correlated with juvenile survival and lifetime reproductive success. We investigated the contributions of elk (*Cervus elaphus*) densities, weather conditions, and supplemental feeding to birth weights, birthdates and weight gains of neonatal elk in northwest Wyoming during 1978–92. Male calves of free-ranging elk were born later ($P = 0.01$) and weighed more ($P < 0.03$) than females. Annual rates and duration of supplemental feeding had no measurable effect on birth weight of elk calves. Cohort birth weights varied independently of elk densities on winter and summer ranges, but correlated with December and January temperatures ($P < 0.001$) and with the onset of spring greenup ($P < 0.04$). Winter survival and cohort birth weight were correlated for those calves that entered each winter.

Nutritional benefits of winter feeding on maternal condition entering late gestation may have improved milk yields of dams thus producing weight gains through the first week of life that exceeded rates of gain previously reported for elk neonates.

J. WILDL. MANAGE. 61(1):26–38

Key words: birth weight, *Cervus elaphus*, elk, growth rate, reproduction, supplemental feeding, survival, weather, Wyoming.

Birth weight and parturition date influence survival of juvenile elk and red deer (Thorne et al. 1976, Clutton-Brock et al. 1982, 1987). Red deer hinds occupying ranges of relatively low population density (relative abundance of good grazing) produce calves of higher birth weights and earlier birthdates than hinds in high density habitats (Guinness et al. 1978a,b).

Density-independent effects on birth weights have also been demonstrated. Albon et al. (1987) found cohort birth weights of red deer calves were correlated positively with mean daily temperatures during the 2 months (Apr and May) immediately preceding birth. They suggested the timing of the first flush of spring growth influenced the nutritional status of pregnant females and fetal growth (Albon et al. 1983). Neonatal survival varied positively with cohort birth weights (Albon et al. 1987) as did lifetime reproductive success (Clutton-Brock et al. 1988).

In western Wyoming, some 23,000 elk are supplementally fed during winter, about 7,500 at the National Elk Refuge (NER), and the remainder on 22 feedgrounds operated by the State of Wyoming (Boyce 1989, Thorne et al. 1991). Winter feeding of elk also occurs in Washington, Oregon, Idaho, and Utah on an

annual or periodic basis. The influence of winter feeding on weight dynamics and reproduction has been studied in confined elk (Thorne and Butler 1976, Thorne et al. 1976, Oldemeyer et al. 1993), but the effects of winter supplementation on birth weight, growth, and survival of free-ranging elk are unknown.

We measured birth weights, birthdates, early neonatal growth, and monitored survival during 1990–92 of a free-ranging elk herd that was supplementally fed in winter at the NER. These data were collected from calves born in Grand Teton National Park (GTNP) and from calves born in the Bridger-Teton National Forest (BTNF). In addition, calves born to wild elk cows confined in pastures and supplementally fed at the NER during the winters of 1978, 1979, 1980, and 1982 (Oldemeyer et al. 1993) provided a comparative sample from elk held under controlled conditions.

We tested the following predictions of density effects on reproduction:

1. Birth weights of calves born in GTNP would be lower than birth weights of calves born outside GTNP, where elk densities were lower (Robinette et al. 1957, Julander et al. 1961, Clutton-Brock et al. 1982:261–262).

2. Cohort birth weights would not vary with winter population size because fetal growth is influenced more strongly by the onset of spring

¹ Present address: Rt. 2, Box 50, Elk Point, SD 57025, USA.

growth than by competition for food during winter months (Clutton-Brock et al. 1987). In addition, supplemental feeding alleviates winter forage limitations.

We also tested the following predictions of density-independent effects on reproduction:

1. Cohort birth weights would be positively correlated with spring (late gestation) temperatures and their influence on new forage growth (Albon et al. 1987).

2. Cohort birth weights would not be correlated with winter supplemental feeding rations or duration because feeding does not continue through late pregnancy when most fetal growth occurs (Verme 1963, Sadlier 1969, Smith and Wilbrecht 1990).

3. Male calves would be born earlier and heavier than females (Johnson 1951, Guinness et al. 1978a, Clutton-Brock et al. 1982:165).

4. Cohort fitness would correlate with cohort birth weight (Albon et al. 1987).

This research was supported financially by the Wyoming Game and Fish Department, Grand Teton National Park, U.S. Fish and Wildlife Service, Bridger-Teton National Forest, Wyoming Cooperative Wildlife Research Unit, Rocky Mountain Elk Foundation, National Rifle Association, and Safari Club International. S.L. Cain, M.A. Gingery, and R.L. Wallen of Grand Teton National Park; D.S. Moody and H.J. Harju of the Wyoming Game and Fish Department, and W.L. Noblitt of Bridger-Teton National Forest provided administrative assistance and aid in securing funding. Helicopter services were contracted from Hawkins and Powers Aviation of Greybull, Wyoming. Among those who assisted with the field research were: J.A. Dalton, M.J. Heisler, W.D. Helprin, D.D. Katnik, K.C. McFarland, K.E. McGinley, A.E. Parker, A.M. Strassler, and K.D. Ward. M. Festa-Bianchet, and J.G. Cook reviewed this manuscript.

STUDY AREA

The study was conducted in the Jackson elk herd unit, which encompassed 5,490 km² in the Snake River watershed of northwest Wyoming. Elevations ranged from 1,950 to >3,650 m. Cole (1969), Boyce (1989), and Smith and Robbins (1994) described the herd unit's boundaries, topography and vegetative communities. Summer ranges of the elk varied from sagebrush (*Artemisia* spp.) grasslands to subalpine coniferous forests of lodgepole pine (*Pinus contorta*) and subalpine fir (*Abies lasiocarpa*) to alpine tundra.

The National Elk Refuge encompassed 98 km² of irrigated grasslands, shrublands, and mixed conifer-aspen (*Populus tremuloides*) forest near the southern end of the Jackson Hole Valley (Fig. 1). Mean annual temperatures decreased, and precipitation and snowfall increased in the Jackson elk herd unit from the NER northward to Yellowstone National Park (YNP) (Smith and Robbins 1994). The Jackson reporting station, adjacent to the NER, received 420 mm precipitation annually. Mean January and July monthly temperatures were -9.3 and 16.2 C (Nat. Oceanic and Atmos. Adm. 1970-86; Fig. 1).

More than 80% of the elk herd is supplementally fed for about 3 months each winter at either the NER or 1 of 3 State of Wyoming feedgrounds. About half the elk that winter on the NER summer in GTNP, 28% in southern YNP, and the remainder in the Bridger-Teton National Forest (Smith and Robbins 1994), a significant increase in the proportion of elk summering in GTNP from the 1960s (Cole 1969). Cole's (1969) population estimates indicated the highest summer densities of elk in the herd unit occurred in the central and eastern portions of GTNP (Fig. 1)—about 3.8 elk/km².

In 1991, biologists of the Jackson Hole Cooperative Elk Studies Group (Wyo. Game and Fish Dep., Nat. Park Serv., U.S. Fish and Wildl. Serv., and U.S. For. Serv., cooperating) updated estimates of elk densities in the herd unit. Estimates were based on their collective knowledge of elk numbers from aerial censuses, telemetry data, migration patterns, track counts, and harvest data (Boyce 1989, Roby et al. 1991, Smith and Robbins 1994). Elk numbers within central and eastern GTNP averaged 5.9 elk/km² compared to 2.4 elk/km² outside GTNP.

METHODS

Calf Capture

During 1990-92, we captured 165 newborn calves within a week of birth. Six were captured on foot, 8 from horseback, and 151 from a Hillar 12-E helicopter. A stratified random sampling design called for capturing 2 groups of 25 neonates each year—1 group that would summer inside GTNP and another group that would summer outside the park. We allocated captures among 8 distinct calving areas (Fig. 1) based upon the proportion of adult cows that used each calving area and the probability that animals born in each area would summer inside or outside GTNP (Smith and Anderson 1996). These

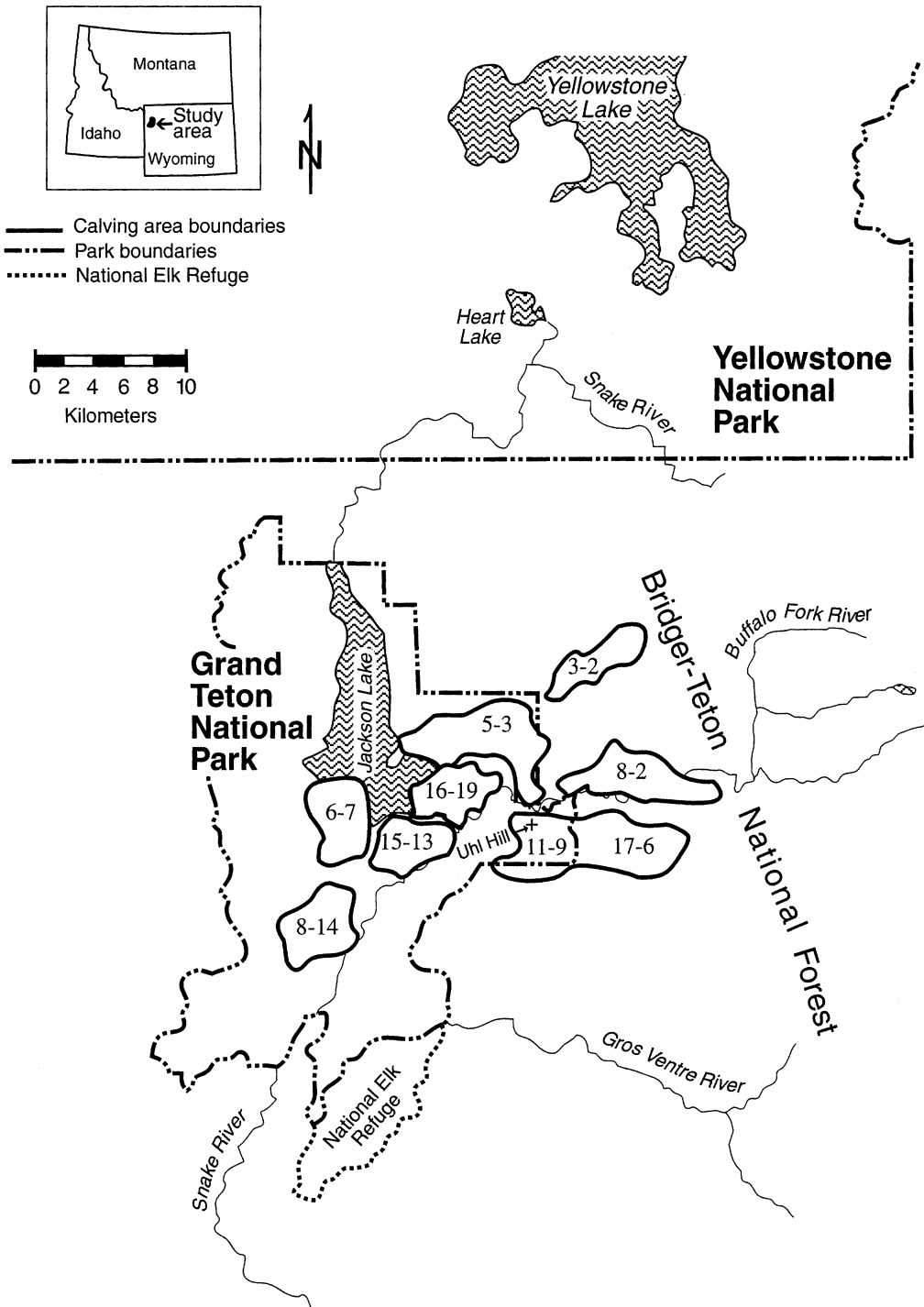


Fig. 1. Distribution of calves (M—F) captured and radiocollared during 1990–92 in the Jackson elk herd. Calves born to dams held in pastures on the National Elk Refuge from 1978 to 1982 were also captured to evaluate variation in birth weights.

Table 1. Quality of alfalfa hay fed to elk in winter from 1978 to 1992 and comparative quality of samples of new spring growth of grasses collected 25 March 1992 on the National Elk Refuge. Means are presented \pm standard errors.

Year	Forage type	No. of samples	% digestible dry matter	% digestible energy	% crude protein
1978	Alfalfa hay	2	58.5 \pm 0.58	No data	16.6 \pm 0.49
1979	Alfalfa hay	4	61.8 \pm 0.69	No data	17.5 \pm 0.41
1980	Alfalfa hay	2	60.3 \pm 1.61	No data	15.8 \pm 0.25
1982	Alfalfa hay	4	53.4 \pm 2.32	No data	15.5 \pm 0.68
1990	Alfalfa hay	9	62.7 \pm 0.68	2.43 \pm 0.22	17.4 \pm 0.72
1991	Alfalfa hay	5	62.8 \pm 0.95	2.66 \pm 0.04	17.5 \pm 0.42
1992	Alfalfa hay	3	61.4 \pm 0.41	2.60 \pm 0.02	15.8 \pm 0.18
Mean	Alfalfa hay	7 yr	60.1 \pm 1.27	2.56 \pm 0.07	16.6 \pm 0.34
1992	<i>Poa</i> spp., <i>Agropyron spicatum</i> , <i>A. smithii</i>	1	71.8	3.05	26.4
1992	<i>Agropyron cristatum</i> , <i>A. spicatum</i>	1	70.8	3.00	25.4
1992	<i>Elymus junceus</i>	1	69.2	2.94	28.3
1992	<i>Bromus inermis</i>	1	75.3	3.19	32.3
1992	<i>Bromus inermis</i>	1	75.0	3.19	25.9
Mean	Spring green-up	5	72.4	3.07 \pm 0.05	27.7 \pm 1.26
P^a			<0.001	0.001	<0.001

^a P = Significance of difference between means for alfalfa hay and spring green-up samples (Student t -test). For the alfalfa hay samples, there were no differences ($P > 0.05$) among years or between means for 1978–82 vs. 1990–92.

criteria were developed in a 7-year study of radiocollared adult elk of the Jackson elk herd (Smith and Robbins 1994). Calves were captured from helicopter during 27 May–8 June 1990, 26 May–9 June 1991, and 27 May–6 June, 1992. Each year we rotated capture efforts among the 8 calving areas. Efforts to capture calves from horseback and on foot were apportioned to those calving areas in which collars had been cast by calves previously captured from helicopter. No calves were captured after 30 June. Nearly all of the elk that frequent the calving areas where these 165 calves were captured winter on or adjacent to the NER (Boyce 1989, Smith and Robbins 1994).

We collected data from captive-born calves at the NER in 1978, 1979, 1980, and 1982. Oldemeyer et al. (1993) described the experimental design of those studies that evaluated weight dynamics and reproductive success of adult female elk supplementally fed in pastures during winter. We fed elk 2.3 kg/animal/day of pelleted alfalfa hay, averaging 58.5% digestibility and 16.4% crude protein content (Table 1). The same type of feed has also been provided to the free-ranging herd on the NER since 1975 for an average of 79 days annually (Smith and Wilbrecht 1990). Nine to 10 females were held in each of 3 4-ha pastures on the NER through birthing, and released with their calves approximately 1 August each year. Cessation of the 1978–82 feeding trials each winter coincided

with termination of supplemental feeding of the free-ranging herds of elk wintering on the NER. Thereafter, the elk foraged on native vegetation in the pastures.

During the parturition period, we searched pastures daily to locate newborn calves. A total of 86 calves were captured, marked, sexed and weighed within 24 hours of birth. Analyzing these data with the 1990–92 results helped separate the effects of feeding from other environmental variables.

Aging Criteria

Captured calves were manually restrained, blindfolded, hobbled, sexed, aged, and weighed to the nearest 0.25 kg. We considered weights of calves ≤ 1 day old as birth weights. To age neonates captured during 1990–92, we measured eruption of incisor 1 and diameter of the umbilicus with calipers, and categorized degree of healing of the umbilicus, hardening of the hooves, and stature/coordination of each animal according to Johnson (1951). Relation of these variables to age was modeled with stepwise multiple regression.

A daily rate of gain of 0.8 kg/day was reported for captive-raised, maternally nursed elk neonates during the first month postpartum in Washington (Robbins et al. 1981) and in Wyoming (Thorne et al. 1976). Johnson (1951) reported a 0.9 kg/day gain for free-ranging elk neonates in southwestern Montana. When cap-

ture weights of the 1990–92 calves were corrected with either of these reported rates of gain, estimated birth weights of calves ≥ 2 days old were significantly greater than capture weights of calves ≤ 1 day old ($P = 0.001$). Therefore we estimated birth weights of calves > 1 day old by regressing capture weight on age. The regression slopes provided the sex-specific daily rates of gain of males and females.

Survival of Calves

An expandable 230-g radiocollar (Telonics Inc., Mesa, Ariz.), was placed on each calf. A mortality switch with a 5-hour delay was integrated into the transmitter's circuitry.

Smith and Anderson (1996) reported the protocols for monitoring radiotransmitters and for conducting forensic investigations. Nineteen calves that cast their collars before 15 July and 5 additional calves that cast collars later in summer or fall were censured from calculations of survival.

Neonatal, winter, and annual survival was analyzed by cohort as a function of mean cohort birth weight during 1990–92 with least squares linear regression. We did not measure age, weight, condition, dominance rank, and other characteristics of dams that may influence birth weights of calves and subsequent survival. Dams of all calves born to a cohort were subject to a similar set of environmental variables, providing a sample size of 3 data points. Therefore, we did not use logistic regression to test maternal and environmental effects on individual offspring survival.

Forage Quality

Samples of the pelleted hay, weighing 2 kg each, were randomly collected from feed storage sheds and sent to Bar Diamond Inc. in Parma, Idaho for analyses of crude protein, digestible dry matter, and digestible energy content. On 25 March 1992, samples of new grass growth were collected from 5 locations on the NER. Fifty-g samples of plants consumed by the wintering elk herd were clipped to simulate the removal of leaves by the elk. These were air-dried and sent to Bar Diamond Inc. for analyses.

Statistical Treatment

Regression, ANOVA, Student's *t*-test, and Chi-square routines in the SYSTAT (SYSTAT, Inc., Evanston Ill.) for Windows statistical software

package were used to test hypotheses. We used 2-way ANOVA to test the relation of sex and year of birth to age of calves, and to test the effects of sex and whether birth weights were known (calves ≤ 1 day old) or estimated (calves > 1 day old) on birth weights. Tukey's HSD procedure was used to test pairwise differences of ANOVA results. Differences between sexes and among years of the non-normally distributed birthdates were tested with nonparametric tests. To examine whether births of either sex were more prevalent among late-born and early-born calves, Chi-square frequencies of the sexes among the earliest third of births were compared to frequencies among the last third.

Birth weights and growth rates of neonates may be indirectly affected by supplemental feeding of adult females. Relations between cohort birth weights and mean daily ration level, number of days fed annually, starting date of feeding, and ending date of feeding each winter were interactively examined with stepwise, multiple regression. We also examined the correlation of cohort birth weights with 2 measures of elk density on winter ranges collected annually: (1) numbers of elk counted on the NER feedgrounds, and (2) total herd size estimates derived from feedground counts plus helicopter censuses of elk not attending feedgrounds (Smith 1994b).

$\alpha < 0.05$ was considered significant for all statistical tests. Statements that 2 categories "tended" to differ indicate a result that approached significance with additional grounds for believing that a difference existed. All means are presented \pm standard errors (SE).

RESULTS

Ages of Calves 1990–92

Mean ages were 3.5 ± 0.19 days of 90 captured males and 3.7 ± 0.20 days of 75 captured females (range = 0–7 days, Table 2). Capture age did not differ among years ($F_{2,159} = 2.22$, $P = 0.11$), or between sexes ($F_{1,159} = 0.86$, $P = 0.36$). For females, the model $age = constant + capture\ weight + incisor\ eruption + umbilicus\ diameter$ explained 93% of the variance ($R^2 = 0.93$, $F_{3,67} = 312.8$, $P < 0.001$). The same model explained 87% of the variance in ages of males ($R^2 = 0.87$, $F_{3,86} = 98.2$, $P < 0.001$). Incisor eruption alone explained 76% ($F_{1,85} = 178.5$, $P < 0.001$ for males) and 87% ($F_{1,69} = 434.7$, $P < 0.001$ for females) of the variation in ages.

Table 2. Sex, Julian birth dates, age in days at capture, capture weights (kg) and estimated birth weights (kg) of confined elk calves born 1978–82 at the National Elk Refuge and free-ranging elk calves born 1990–92 in Grand Teton National Park and the Bridger-Teton National Forest of northwest Wyoming.

Year	Sex	n	Birthdate $\bar{x} \pm SE$	Age at capture ^a $\bar{x} \pm SE$	Capture wt $\bar{x} \pm SE$	Est. birth wt ^b $\bar{x} \pm SE$
1978	M	8	161.6 ± 2.4		16.0 ± 0.89	
1978	F	10	160.2 ± 2.5		16.7 ± 0.79	
1979	M	11	161.2 ± 2.1		14.9 ± 0.76	
1979	F	6	161.2 ± 3.3		14.6 ± 1.02	
1980	M	12	159.4 ± 2.0		16.2 ± 0.72	
1980	F	17	158.5 ± 1.9		15.6 ± 0.61	
1982	M	9	156.4 ± 2.3		15.9 ± 0.84	
1982	F	13	159.1 ± 2.2		15.2 ± 0.70	
1990	M	27	150.5 ± 1.3	3.9 ± 0.34	21.0 ± 0.74	16.2 ± 0.50
1990	F	26	148.8 ± 1.5	4.0 ± 0.35	19.7 ± 0.62	15.7 ± 0.51
1991	M	35	151.9 ± 1.2	3.1 ± 0.30	19.4 ± 0.65	15.9 ± 0.44
1991	F	28	149.6 ± 1.5	4.1 ± 0.33	19.3 ± 0.59	15.2 ± 0.49
1992	M	28	151.9 ± 1.3	3.4 ± 0.33	20.7 ± 0.73	16.8 ± 0.49
1992	F	21	151.5 ± 1.7	3.1 ± 0.38	18.1 ± 0.69	15.4 ± 0.57

^a All calves weighed from 1978 to 1982 were ≤ 1 day old.

^b Weights of calves captured from 1990 to 1992 corrected for a daily rate of gain (Fig. 2). Capture weights of all calves born from 1978 to 1982 were considered birth weights.

Capture Weights 1990–92

There were no significant differences in capture weights of males ($F_{2,87} = 1.50$, $P = 0.23$), females ($F_{2,72} = 0.50$, $P = 0.61$), and all calves ($F_{2,162} = 1.00$, $P = 0.37$) among the 3 years of the study. Capture weights were correlated ($P < 0.001$) with age at capture of males ($r = 0.88$) and females ($r = 0.72$).

Sex-Specific Birth Weights

Confined Elk 1978–82.—A total of 86 calves (40 M and 46 F) were weighed (Table 2). We found no differences in birth weights between sexes ($F_{1,78} = 0.66$, $P = 0.42$), nor among years ($F_{3,78} = 0.77$, $P = 0.52$).

All Years 1978–92.—For all calves ≤ 1 day old, there were no significant differences in birth weights due to sex ($F_{1,95} = 1.05$, $P = 0.31$) or year ($F_{6,95} = 0.62$, $P = 0.72$). Birth weights of 86 calves born 1978–82 and the 23 weights of calves ≤ 1 day old captured from 1990 to 1992 were similar ($t = 0.53$, 107 df, $P = 0.45$). However, when the estimated birth weights of all calves captured from 1990 to 1992 (adjusted with Johnson's [1951] 0.9 kg/day growth rate) were tested against the known birth weights of the 1978–82 calves, both males ($t = 4.54$, 128 df, $P < 0.001$) and females ($t = 2.29$, 119 df, $P = 0.024$) were heavier during 1990–92. Furthermore, the 1990–92 estimated birth weights (using Johnson (1951) 0.9 kg daily rate of gain) of male calves > 1 day old were heavier than

those of males ≤ 1 day old ($P < 0.02$); and the estimated birth weights of females > 1 day old tended to be heavier than females ≤ 1 day old ($P = 0.05$; Table 2). These results suggested that daily rate of gain of both sexes was greater than 0.9 kg/day.

Daily Rate of Gain

Regressing capture weights on ages of the 1990–92 neonates provided equations predicting rate of gain of male and female calves with different slopes ($F_{1,88} = 5.3$, $P = 0.024$; Fig. 2). The regression equations explained 60% of the variance in capture weights of males ($F_{1,88} = 133.9$, $P < 0.001$) and 51% of the variance in capture weights of females ($F_{1,73} = 76.6$, $P < 0.001$).

When birth weights of calves > 1 day old were adjusted for these estimated rates of gain, 1990–92 birth weights were heavier for males than for females ($t = -2.25$, 163 df, $P = 0.027$; males = 16.2 ± 0.26 ; females = 15.4 ± 0.25). The 1990–92 males weighed no more than the 1978–82 males ($P = 0.31$). The 1990–92 females weighed no more than the 1978–82 females ($P = 0.71$).

Age and Birth Dates of Calves

Confined Elk 1978–82.—There were no differences in Julian birthdates among years for all calves (Kruskal-Wallis test = 1.41, 3 df, $P = 0.70$), male calves ($P = 0.65$), or female calves

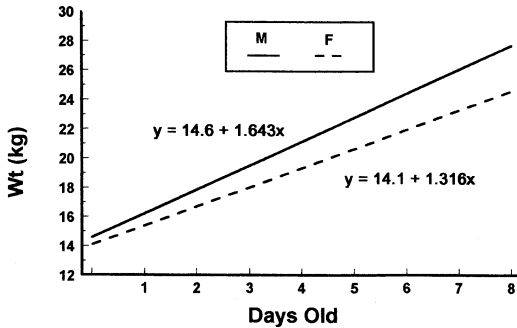


Fig. 2. Capture weights of elk calves regressed on age of the calves at capture. Slopes of the equations are estimated daily rates of gain for males and females during the first week of life.

($P = 0.63$). Neither sex was more prevalent among early or late births ($\chi^2 = 1.47$, 2 df, $P = 0.48$; Fig. 3).

Free-ranging Elk 1990–92.—Julian dates of birth of captured calves did not differ among years (Kruskal-Wallis test = 5.41, 2 df, $P = 0.16$). Male calves were born 1.6 days later than females (Mann-Whitney $U = 2,586$, 1 df, $P = 0.01$; Table 2) and tended to be more prevalent among late births ($\chi^2 = 3.43$, 1 df, $P = 0.064$; Fig. 3).

Mean annual birthdates of confined and free-ranging elk were not compared. During 1990–92, our sample of birthdates may not have been representative of all births in the population because intensive searching for calves was terminated before parturition was completed.

Relation of Birthdate and Birth Weight

Birth dates and birth weights from 1978 to 1982 were related for neither male ($r^2 = 0.05$, $P = 0.10$) nor female calves ($r^2 = 0.01$, $P = 0.79$). For all 251 calves (using the adjusted birth weights derived from the equations in Fig. 2 for the 1990–92 calves) the relations remained non-significant ($P = 0.28$ for males; $P = 0.44$ for females).

Annual Variation in Birth Weights

Density-Dependent Factors.—Neither numbers of elk in the herd unit the previous winter ($r = 0.09$, $P = 0.84$), nor numbers of elk counted on the NER the previous winter were correlated with cohort birth weights ($r = 0.48$, $P = 0.28$). During 1990–92, calves were captured in the

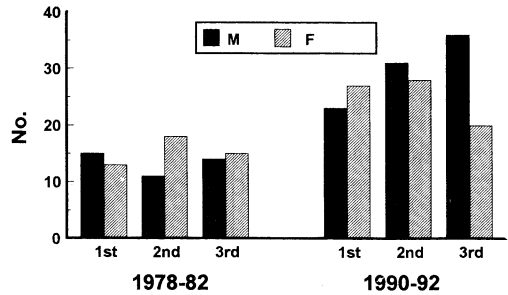


Fig. 3. Distributions of males and females among the first third, second third, and last third of births each year pooled for 1978–82 (elk calves born to confined dams) and 1990–92 (elk calves born to free-ranging dams).

relatively high density summer range of GTNP and another sample in lower density areas of BTNF. Birth weights of the 2 samples were not different for males ($P = 0.77$) or for females ($P = 0.53$).

Supplemental Feeding Levels and Duration.—Cohort birth weights were not correlated with feed rations ($P = 0.65$; Table 3). Rations fed to the confined elk in 1978–82 were held constant at 2.3 kg/day, to evaluate weight dynamics of females, but were no different than rations fed to the free-ranging herds those winters ($t = -1.69$, 6 df, $P = 0.14$). Larger daily rations were fed to elk during 1990–92 than 1978–82 primarily due to depletion of standing forage biomass by the larger numbers of elk during 1990–92 (Table 3).

Of those variables associated with the length and timing of feeding, starting date of feeding ($r = 0.71$, $P = 0.041$) and number of days fed ($r = -0.8$, $P = 0.03$) were each correlated with cohort birth weights, although in the opposite directions expected if winter feeding were to promote larger birth weights (Fig. 4). Larger cohort birth weights followed winters when feeding started later and extended over fewer days. Refuge managers began feeding earlier in years when larger numbers of elk wintered on the refuge and December snow cover was deeper ($R^2 = 96.5$, $P < 0.001$).

The number of days elk were fed each winter reflected winter duration, primarily the depth and duration of snow cover. In years when combined December and January snow depths were greater, the elk were fed for more days ($r = 0.95$, $P = 0.001$). The ending date of feeding varied inversely with March temperatures ($r = -0.82$, $P < 0.023$).

Table 3. Comparison of winter feeding variables, weather conditions^a, numbers of elk wintering on the National Elk Refuge, and calf birth weights and sex ratios. From 1978 to 1982 dams of the calves born in this study were confined to pastures on the NER. From 1990 to 1992 dams of calves were free-ranging on the NER. Data are presented as means \pm standard errors. Significance of differences between study periods (*P*) based upon Students *t*-tests.

Variable	Study period		<i>P</i>
	1978-82	1990-92	
Ration (kg/animal/day) ^b	5.0 \pm 0.8	7.3 \pm 0.3	<0.01
No. of days fed	79.8 \pm 10.3	63.0 \pm 2.6	0.24
Begin feeding (Julian)	18.3 \pm 5.9	20.0 \pm 6.8	0.87
End feeding (Julian)	100.5 \pm 2.3	85.0 \pm 2.4	<0.01
Dec snow depth (cm)	48.9 \pm 15.9	28.8 \pm 5.9	0.35
Dec and Jan snow depth (cm)	111.1 \pm 23.5	65.2 \pm 7.4	0.17
Dec and Jan temp (C)	-16.0 \pm 4.5	-20.3 \pm 1.8	0.47
Mar temp (C)	-3.5 \pm 0.8	-1.2 \pm 0.8	0.11
Elk on NER	7,630 \pm 319	8,479 \pm 368	0.14
Calf birth weights	15.7 \pm 0.3	15.9 \pm 0.2	0.49
Birth sex ratio (males : females)	40:46	90:75	

^a Data from National Climatic Data center 1977-92.

^b The free-ranging elk were fed 6.13 \pm 0.67 kg/animal/day in 1978-82 compared to 5.0 \pm 0.08 for the confined elk (*P* = 0.14).

Weather Effects.—Mean cohort birth weights from 1978 to 1992 correlated with mean daily March temperatures ($r = 0.78$, $P = 0.037$), but not with April ($P = 0.2$) or May ($P = 0.45$) mean daily temperatures, or combined March and April ($P = 0.09$) or April and May ($P = 0.55$) temperatures (Fig. 5). Combined monthly average temperatures for December and January accounted for 95% of the residual variance in birth weights not explained by March temperatures ($r = 0.975$, $P < 0.001$; Fig. 5). Birth weights were significantly lighter ($t = 3.05$, 5 df, $P = 0.029$) after the 3 winters (1979, 1982, 1991) with the coldest combined December, January, and March monthly temperatures than after the other 4 winters. Neither monthly precipitation nor snow depths from December through March were correlated with cohort birth weights.

When March temperatures were warmer, supplemental feeding was ended earlier ($r = -0.82$, $P < 0.023$), as elk foraged on new grass growth. Although elk were fed a diet of high quality alfalfa hay, the digestibility and the crude protein content of new grass were far superior to the hay (Table 1).

Survival of Calves

Mean birth weights of the 3 cohorts that were radiocollared were not correlated with neonatal survival ($r = 0.92$, $P = 0.26$), or annual survival ($r = 0.43$, $P = 0.72$; Table 4). However, the mean birth weight of those calves alive at the beginning of each winter was positively correlated with winter survival ($r = 0.99$, $P = 0.002$). Cohort winter survival was also correlated with

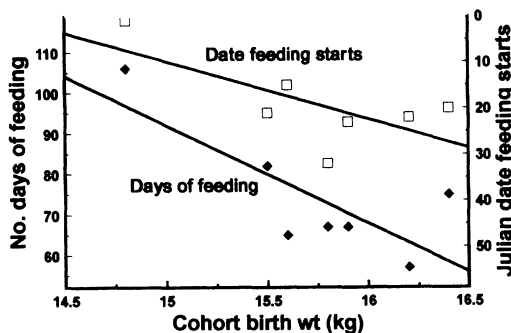


Fig. 4. Mean cohort birth weight (kg) of elk calves increased with later initiation of winter feeding and decreased with the number of days that elk were fed at the National Elk Refuge, 1978-82 and 1990-92.

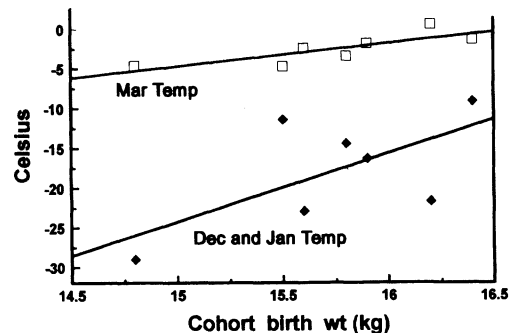


Fig. 5. Mean cohort birth weight (kg) of elk calves was positively correlated with combined mean monthly December and January temperatures and with mean March temperature in Jackson, Wyoming, 1978-82 and 1990-92.

Table 4. Cohort survival of elk calves captured from 1990 to 1992 as neonates (birth–15 Jul), winter (1 Jan–15 May), and annually (through 1 Jun) with fall hunting mortalities included and censured.

Cohort	Birth weight $\bar{x} \pm SE$	Neonatal survival	Winter survival ^a	Annual survival ^a	Hunting-censured annual survival ^a
1990	15.92 ± 0.33	45 of 50 (90%)	34 of 37 (92%)	34 of 47 (72%)	39 of 47 (83%)
1991	15.62 ± 0.32	42 of 54 (78%)	30 of 31 (97%)	30 of 53 (57%)	40 of 53 (75%)
1992	15.99 ± 0.37	36 of 41 (88%)	19 of 31 (61%)	20 of 40 (50%)	23 of 40 (58%)

^a Five calves that cast radiocollars after 15 Jul (3 in 1990, 1 in 1991, 1 in 1992) are censored from the sample.

mean March temperature of each cohort's year of birth ($r = 0.99$, $P = 0.015$).

DISCUSSION

Dates of Birth

The distribution of calving dates of the confined animals agreed closely with parturition dates reported elsewhere. Eighty percent of births occurred before 15 June compared to 75% in Colorado (Bear 1989) and 80% for Roosevelt elk in Oregon (Hines and Lemos 1979). The earliest birth over the 7 years of this investigation was 20 May and the latest was 13 July. Nelson and Leege (1982) stated that in central Washington state, elk cows producing calves after 15 June would not find sufficient protein in available forage for optimal milk production when lactation demands peak—about 48 days postpartum. High mortality in late-born young, as a consequence of insufficient milk production and shortened time to feed on high quality forage, was reported for red deer (Guinness et al. 1971) and bighorn sheep (Festa-Bianchet 1988). However, late births and out-of-season births may be relatively common in the Jackson herd as a consequence of winter feeding effects on physiological condition of females (Smith 1994a).

Birth Weights and Growth Rates

Free-ranging male calves outweighed females by 0.8 kg during 1990–92, compared to 1.5 kg in Idaho (Schlegel 1976). Clutton-Brock et al. (1982:164–165) attributed a male-biased 0.5 kg birth weight differential in red deer to greater maternal investment in sons than daughters.

We found higher growth rates of male than female calves, as did Blaxter and Hamilton (1980) for red deer. Data presented in Robbins et al. (1981; Table 2) indicated no difference in

rates of gain during the first month for 4 female and 3 male elk calves. Clutton-Brock et al. (1982:167–168; 1983) suggested the immediate cause of the increased postpartum cost of rearing male calves was that their more frequent demands stimulated their mothers to produce more milk. Male caribou calves have a higher milk intake and grow faster than females (McEwan 1968, McEwan and Whitehead 1971). In several species of domestic animals, a relation between demands of offspring and milk yields of mothers has been shown (Arnold and Dudzinski 1969).

Selective pressures of predation, hypothermia, seasonal food shortages, and the need to attain a minimal necessary size for winter survival have produced relatively high neonatal growth rates in ungulates, particularly those inhabiting temperate and arctic climates (Robbins and Robbins 1979). Maternal condition, as measured by kidney fat index, body weight, and mammary gland weight, was considered an important influence on growth rates of red deer calves on Rhum (Clutton-Brock et al. 1982:90), and captive red deer (Blaxter and Hamilton 1980). When supplementally fed, elk may require a smaller allocation of their dietary intake in spring for recovery of body condition lost in winter to catabolism of lean body tissue and fat. Although supplemental feeding of mothers does not produce larger birth weight calves than reported elsewhere, it may enhance neonatal rates of gain.

Our estimate of growth rate likely exceeded that reported for free-ranging Montana elk calves (Johnson 1951) because of (1) the beneficial effects of winter feeding on post-winter condition of adult females, as discussed above, and (2) potential bias stemming from recapture of calves in the Montana study. Recaptured calves were as much as 14 days old (Johnson 1951). As noted by Murie (1951:137) and Bear (1989), we found

that calves >4–5 days old were less likely to remain bedded and were difficult to capture. Calves captured at >1 week old may be weaker, smaller animals due to poor nutrition or health. Thus Johnson (1951) may have underestimated daily rates of gain.

Free-ranging Jackson elk may have achieved higher neonatal rates of gain than pen-raised calves for 2 reasons:

1. Free-ranging Jackson elk on free choice diets may have produced superior milk yields. In other deer species and in domestic ruminants, food availability or quality have been correlated with milk yields of females and growth in juveniles (Thomson and Thomson 1953, Kitts et al. 1956, Verme 1963, Grubb 1974). Analyses of spring growth of a variety of grasses collected in April from the NER showed higher digestibility and crude protein levels than hay diets fed to captive elk (Thorne et al. 1976, Robbins et al. 1981). Robbins et al. (1981) noted that food intake of dams increased markedly as lactation began. Increased passage rates of highly digestible spring green-up may promote conversion of forage to milk to calf growth (Nelson and Leege 1982:328).

2. Thorne et al. (1976) and Robbins et al. (1981) reported weight gains as averages for the first month postpartum, whereas our estimates are for the first week postpartum. Robbins and Moen (1975) reported a linear growth pattern over time for white-tailed deer fawns. Cowan and Wood (1955) concluded, from repeated weighings of black-tailed deer fawns, that there were 3 relatively distinct phases of growth. The first lasted for about 1 week, when the instantaneous growth rate approached 10%/day. Growth rate slowed in each of the subsequent 2 phases measured from 7 to 21 days and 22 to \approx 100 days postpartum. A 10% postpartum growth rate for a 16-kg elk calf approximates the daily growth rate for males (1.6 kg/day) and exceeds the growth rate for female elk (1.3 kg/day) estimated in this study. Caribou calves also experienced much higher rates of gain during the first week postpartum than thereafter (Parker et al. 1990).

Just as the hider strategy in neonatal calves minimizes encounters between young elk and predators, it also minimizes energy expenditures and maximizes growth (Geist 1982). Rapid growth rates during the hider period are certainly adaptive. As calves grow, they become

stronger and fleet enough to join herd life and to flee from predators (Altmann 1963, Geist 1982).

Density Effects

Supplemental feeding maintains artificially high densities of elk on the NER, and promotes high survival rates (Murie 1951, Boyce 1989: 143–145, Smith 1994b). Approximately 125 elk/km² wintered on the southern 6,000 ha of the NER during this investigation. However, cohort birth weights were not correlated with elk densities in winter, which concurs with studies of red deer (Clutton-Brock et al. 1987).

Clutton-Brock et al. (1982:261–262) found that hinds calving on ranges with high red deer densities tended to produce smaller calves. Females leave the NER and arrive at calving areas in and adjacent to GTNP during the last trimester of pregnancy (Smith and Robbins 1994). We found no difference in birth weights of elk captured inside and outside GTNP, suggesting that densities of elk on calving areas were not sufficiently high or different to affect birth weights, or that elk densities in spring were not a significant variable controlling birth weights.

Effects of Supplemental Feeding

Duration of winter feeding at the NER has varied annually (0–146 days) to compensate for natural forage depletion and to reduce winter mortality (Robbins et al. 1982, Boyce 1989:129–130). As expected, supplemental feeding did not significantly influence annual variation in birth weights, probably because serious demands on parous females do not occur during the first 170 days of gestation (Moen 1973, Nelson and Leege 1982). The average ending date of feeding during the 7 years of this study was 4 April. That date preceded the mean birthdate (7 Jun) of elk born from 1978 to 1982 by 64 days, and was about 186 days into gestation.

Larger cohort birth weights followed winters when feeding started later and extended over fewer days. Feeding began later and elk were fed fewer days when December snow depths were shallower and animals were presumably less nutritionally stressed. Once feeding began, the energetic costs of foraging in deep snow (Parker et al. 1984) were offset by the ease of meeting maintenance requirements on supplemental feed. However, temperate cervids lower activity, metabolism and food intake in winter

(Mautz 1978a, Nelson and Leege 1982) which lowers the potential benefit on reproduction of feeding the high quality alfalfa hay provided at the NER.

Weather Effects

Winter feeding of Jackson elk apparently does not mitigate the effects of adverse winter conditions on female elk and birth weights of their offspring. Our results suggest that fetal growth was negatively affected by (1) the dam's condition entering late pregnancy related to temperatures in December and January (largely before supplemental feeding began), and (2) delayed conversion of dams to a diet of green forage in spring.

During winter a complex of variables affect energy balance of cervids, many of which are correlated with critically low temperatures (Nelson and Leege 1982, Hobbs 1989). We do not know the specific component processes of energy balance of dams that affected offspring birth weights. Robinson's (1977) review of nutritional effects on birth weights of domestic sheep indicated that undernutrition during mid- and late gestation has a more dramatic effect on weight dynamics of the maternal body than on the fetus. Increased costs of thermoregulation and foraging dynamics, and reduced energy intake all draw on energy reserves (Hobbs 1989). Most elk lose weight during Wyoming winters, even when supplementally-fed during mid gestation (Thorne and Butler 1976, Oldemeyer et al. 1993). As a consequence they catabolize fat and endogenous protein for maintenance and lose body condition that must be recovered later for fetal growth, lactation, and survival next winter (Mitchell et al. 1976, Mautz 1978b).

Elk and other northern latitude cervids begin recovering body condition after spring green-up becomes available (Mitchell et al. 1976, Mautz 1978a,b; Nelson and Leege 1982, DelGuidice et al. 1990). Presumably less dietary energy and protein is allocated to fetal growth in spring and more to recovery of body condition following cold winters when females experience greater weight losses. We found that mean monthly March temperatures accounted for most variation in birth weights of Jackson elk, suggesting that when green-up occurs early, dams are not only able to recover their body condition but can allocate more energy to fetal growth. Jackson elk clearly preferred green grass over pelleted hay, and they exploited areas of the youn-

gest, most digestible growth across the refuge as snow melted. Preference of green grass in spring has previously been reported for elk (Gruell 1980), mule deer and bighorn sheep (Hobbs and Spowart 1984).

Cohort birth weight of red deer and their adult survival varied with annual spring temperatures and consequent growth of new grass during their birth year (Albon et al. 1987). Because most fetal growth occurs during the last 2 months of gestation, differences in spring nutrition have a marked effect on birth weights (Sadler 1969, Thorne et al. 1976, Albon et al. 1987). We also found spring (Mar) temperatures to be a major component of variation in cohort birth weight. Cohort birth weight and consequent cohort survival were significantly related only during winter, although the probability of Type II errors was high with survival of only 3 cohorts measured. Winter survival and cohort birth weight were correlated when the analysis was limited to those calves that entered each winter, but not when all calves born into each cohort were included. This finding is intuitively reassuring and should be considered when survival is evaluated seasonally in future studies. Additional years of data are needed to reliably evaluate the influence of spring temperatures and birth weights on survival of Jackson elk.

MANAGEMENT IMPLICATIONS

The influence of supplemental feeding on the early development of elk was apparently limited to the greater first week weight gains of Jackson calves than reported elsewhere. The overriding density-independent effects on birth weights have important implications for managers faced with public pressures to feed elk. Although emergency feeding may be warranted under the worst of conditions to reduce winter mortality, our findings suggest that at levels of food supplementation at the NER, winter feeding is not justified as a means of reducing low birth weights and increasing calf survival.

Calving areas with twofold differences in elk densities did not produce calves of differing birth weight. Density-dependent effects are highly non-linear, with substantial effects on population productivity occurring only as population density nears ecological carrying capacity (Sinclair 1977, Fowler 1981). Therefore, declines in birth weights and offspring survival, as a consequence of crowding on parturition areas and summer ranges within sanctuaries such as GTNP,

may not occur until very high densities are reached.

LITERATURE CITED

- ALBON, S. D., T. H. CLUTTON-BROCK, AND F. E. GUINNESS. 1983. Influence of climatic variation on the birth weights of red deer. *J. Zool. (Lond.)* 200:295-298.
- , ———, AND ———. 1987. Early development and population dynamics in red deer. Density-independent effects and cohort variation. *J. Anim. Ecol.* 56:69-81.
- ALTMANN, M. 1963. Naturalistic studies of maternal care in moose and elk. Pages 233-253 in H. L. Rheingold, ed. *Maternal behavior in mammals*. John Wiley and Sons, New York, N.Y.
- ARNOLD, G. W., AND M. L. DUDZINSKI. 1969. The effect of pasture density and structure on what the grazing animal eats and animal productivity. Pages 42-48 in B. J. F. James, ed. *Grazing in terrestrial and marine environments*. Angus and Robertson, Sydney, Australia.
- BEAR, G. D. 1989. Seasonal distribution and population characteristics of elk in Estes Valley, Colorado. *Colo. Div. Wildl. Spec. Rep.* 65, Fort Collins. 14pp.
- BLAXTER, K. L., AND W. J. HAMILTON. 1980. Reproduction in farmed red deer. Calf growth and mortality. *J. Agric. Sci., (Camb.)* 95:275-284.
- BOYCE, M. S. 1989. *The Jackson elk herd: intensive wildlife management in North America*. Cambridge Univ. Press, Cambridge, U.K. 306pp.
- CLUTTON-BROCK, T. H., F. E. GUINNESS, AND S. D. ALBON. 1982. Red deer: behavior and ecology of two sexes. Univ. Chicago Press, Chicago, Ill. 378pp.
- , M. MAJOR, S. D. ALBON, AND F. E. GUINNESS. 1987. Early development and population dynamics in red deer. Density-dependent effects on juvenile survival. *J. Anim. Ecol.* 56:53-67.
- , S. D. ALBON, AND F. E. GUINNESS. 1988. Reproductive success in male and female red deer. Pages 325-343 in T. H. Clutton-Brock, ed. *Reproductive success*. Univ. Chicago Press, Chicago, Ill.
- COLE, G. F. 1969. *The elk of Grand Teton and Southern Yellowstone National Parks*. Natl. Park Serv. Res. Rep. GRTE-N-1. Washington, D.C. 80pp.
- COWAN, I. MCT., AND A. J. WOOD. 1955. The growth rate of black-tailed deer. *J. Wildl. Manage.* 19:331-336.
- DELGUIDICE, G. D., L. D. MECH, AND U. S. SEAL. 1990. Effects of winter undernutrition on body composition and physiological profiles of white-tailed deer. *J. Wildl. Manage.* 54:539-550.
- FESTA-BIANCHET, M. 1988. Nursing behavior of bighorn sheep: correlates of ewe age, parasitism, lamb age, birth date and sex. *Anim. Behav.* 36:1445-1454.
- FOWLER, C. W. 1981. Comparative population dynamics in large mammals. Pages 437-455 in C. W. Fowler and T. D. Smith, eds. *Dynamics of large mammal populations*. John Wiley and Sons, New York, N.Y.
- GEIST, V. 1982. Adaptive behavioral strategies. Pages 219-278 in J. W. Thomas and D. E. Towell, eds. *North American elk: ecology and management*. Stackpole Books, Harrisburg, Pa.
- GRUBB, P. 1974. Population dynamics of the Soay sheep. Pages 242-272 in P. A. Jewell, C. Milner, and J. M. Boyd, eds. *The ecology of Soay sheep on St. Kilda*. Athlone Press, London, U.K.
- GRUELL, G. E. 1980. Fire's influence on wildlife habitat on the Bridger-Teton National Forest, Wyoming. Vol. 2. Changes and causes, management implications. U.S. Dep. Agric. For. Serv. Res. Pap. INT-252. 35pp.
- GUINNESS, F. E., G. A. LINCOLN, AND R. V. SHORT. 1971. The reproductive cycle of the female red deer. *J. Reprod. Fert.* 27:427-438.
- , S. D. ALBON, AND T. H. CLUTTON-BROCK. 1978a. Factors affecting reproduction in red deer (*Cervus elaphus*) hinds on Rhum. *J. Reprod. Fert.* 54:325-334.
- , ———, AND ———. 1978b. Factors affecting calf mortality in red deer. *J. Anim. Ecol.* 47:817-832.
- HINES, W. W., AND J. C. LEMOS. 1979. Reproductive performance by two age-classes of male Roosevelt elk in southwestern Oregon. *Oreg. Dep. Fish and Wildl. Res. Rep.* 8. 54pp.
- HOBBS, N. T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. *Wildl. Monogr.* 101. 39pp.
- , AND R. A. SPOWART. 1984. Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. *J. Wildl. Manage.* 48:551-559.
- JOHNSON, D. E. 1951. Biology of the elk calf, *Cervus canadensis*. *J. Wildl. Manage.* 15:396-410.
- JULANDER, O., W. L. ROBINETTE, AND D. A. JONES. 1961. Relation of summer range condition to mule deer herd productivity. *J. Wildl. Manage.* 25:54-60.
- KITTS, W. D., I. MCT. COWAN, P. J. BANDY, AND A. J. WOOD. 1956. The immediate post-natal growth in Columbian black-tailed deer in relation to the composition of the milk of the doe. *J. Wildl. Manage.* 20:212-214.
- MAUTZ, W. W. 1978a. Nutrition and carrying capacity. Pages 321-348 in J. L. Schmidt and D. L. Gilbert, eds. *Big game of North America: ecology and management*. Stackpole Books, Harrisburg, Pa.
- . 1978b. Sledding on a brushy hillside: the fat cycle in deer. *Wildl. Soc. Bull.* 6:88-90.
- MCEWAN, E. H. 1968. Growth and development of barren ground caribou. Postnatal growth rates. *Can. J. Zool.* 46:1023-1029.
- , AND P. E. WHITEHEAD. 1971. Seasonal changes in energy and intake in reindeer and caribou. *Can. J. Zool.* 49:443-447.
- MITCHELL, B., D. MCCOWAN, AND I. A. NICHOLSON. 1976. Annual cycles of body weight and condition in Scottish red deer. *J. Zool. (Lond.)* 180:107-127.
- MOEN, A. N. 1973. *Wildlife ecology*. W. H. Freeman and Co., San Francisco, Calif. 458pp.
- MURIE, O. J. 1951. *The elk of North America*. Stackpole Books, Harrisburg, Pa. 376pp.

- NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 1970-1986. Climatological data, Wyoming. Vol. 79-95. Natl. Climatic Data Cent., Asheville, N.C.
- NELSON, J. R., AND T. A. LEEGE. 1982. Nutritional requirements and food habits. Pages 323-368 in J. W. Thomas and D. E. Toweill, eds. *Elk of North America: ecology and management*. Stackpole Books, Harrisburg, Pa.
- OLDEMEYER, J. L., R. L. ROBBINS, AND B. L. SMITH. 1993. Effect of feeding level on elk weights and reproductive success at the National Elk Refuge. Pages 64-68 in R. Callas, D. Koch, and E. Loft, eds. *Western states and provinces elk workshop*. Calif. Fish and Game Dep., Eureka.
- PARKER, K. L., C. T. ROBBINS, AND T. A. HANLEY. 1984. Energy expenditures for locomotion by mule deer and elk. *J. Wildl. Manage.* 48:474-488.
- , R. G. WHITE, M. P. GILLINGHAM, AND D. F. HOLLEMAN. 1990. Comparison of energy metabolism in relation to daily activity and milk consumption by caribou and muskox neonates. *Can. J. Zool.* 68:106-114.
- ROBBINS, C. T., AND A. N. MOEN. 1975. Milk consumption and weight gain of white-tailed deer. *J. Wildl. Manage.* 39:355-360.
- , AND B. L. ROBBINS. 1979. Fetal and neonatal growth patterns and maternal reproductive effort in ungulates and subungulates. *Am. Nat.* 114:101-116.
- , R. S. PODBIELANCIK-NORMAN, D. L. WILSON, AND E. D. MOULD. 1981. Growth and nutrient consumption of elk calves compared to other ungulate species. *J. Wildl. Manage.* 45:172-186.
- ROBBINS, R. L., D. E. REDFEARN, AND C. P. STONE. 1982. Refuges and elk management. Pages 479-507 in J. W. Thomas and D. E. Toweill, eds. *Elk of North America: ecology and management*. Stackpole Books, Harrisburg, Pa.
- ROBINETTE, W. L., J. S. GASHWILER, J. B. LOW, AND D. A. JONES. 1957. Differential mortality by sex and age among mule deer. *J. Wildl. Manage.* 21:1-16.
- ROBINSON, J. J. 1977. The influence of maternal nutrition on ovine foetal growth. *Proc. Nutr. Soc.* 36:9-16.
- ROBY, G., J. BOHNE, AND D. MCWHIRTER. 1991. District 1 annual big game herd unit reports, 1991. Vol. 16. 1. Wyo. Game and Fish Dep., Cheyenne. 406pp.
- SADLER, R. M. F. S. 1969. The ecology of reproduction in wild and domestic mammals. Methuen, London, U.K. 321pp.
- SCHLEGEL, M. 1976. Factors affecting calf elk survival in northcentral Idaho—a progress report. *West. Assoc. State Game and Fish Comm.* 56:342-355.
- SINCLAIR, A. R. E. 1977. The African buffalo—a study of resource limitation of populations. Univ. Chicago Press, Chicago Ill. 355pp.
- SMITH, B. L. 1994a. Out-of-season births of elk calves in Wyoming. *Prairie Nat.* 26:131-136.
- . 1994b. Population regulation of the Jackson elk herd. Ph.D. Thesis, Univ. Wyoming, Laramie. 265pp.
- , AND S. H. ANDERSON. 1996. Patterns of neonatal mortality of elk in northwest Wyoming. *Can. J. Zool.* 74:1229-1237.
- , AND R. L. ROBBINS. 1994. Migrations and management of the Jackson elk herd. *U.S. Natl. Biol. Serv. Resour. Pap.* 199. 62pp.
- , AND J. W. WILBRECHT. 1990. Supplemental winter feeding of elk on the National Elk Refuge, Wyoming. Pages 30-41 in M. Zahn, J. Pierce and R. Johnson, eds. *Proc. western states and provinces elk workshop*. Wash. Dep. Wildl., Olympia.
- THOMSON, A. M., AND W. THOMSON. 1953. Effect of diet on milk yield of the ewe and growth of her lamb. *Br. J. Nutr.* 2:290-305.
- THORNE, E. T., AND G. BUTLER. 1976. Comparison of pelleted, cubed, and baled alfalfa hay as winter feed for elk. *Wyo. Game and Fish Dep. Tech. Rep.* 6, Cheyenne. 38pp.
- , R. E. DEAN, AND W. G. HEPWORTH. 1976. Nutrition during gestation in relation to successful reproduction in elk. *J. Wildl. Manage.* 40:330-335.
- , J. D. HERRIGES, AND A. D. REESE. 1991. Bovine brucellosis in elk: conflicts in the Greater Yellowstone Area. Pages 296-303 in A. G. Christensen, L. J. Lyon, and T. N. Lonner, eds. *Proc. elk vulnerability symposium*. Mont. State Univ., Bozeman.
- VERME, L. J. 1963. Effect of nutrition on growth of white-tailed deer fawns. *Trans. North Am. Wildl. Nat. Resour. Conf.* 20:431-443.

Received 1 June 1995.

Accepted 8 December 1995.

Associate Editor: Hobbs.