EFFECTS OF SUMMER-AUTUMN NUTRITION AND PARTURITION DATE ON REPRODUCTION AND SURVIVAL OF ELK

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Abstract: Recent declines in numbers and juvenile recruitment in many elk (*Cervus elaphus*) herds in the western U.S. has sparked interest in factors that may cause these declines. Inadequate nutrition or delayed parturition, the latter of which may be caused by inadequate numbers of mature bulls (i.e., highly skewed sex ratios), may have separate or synergistic effects on population dynamics and productivity. We evaluated the implications of late parturition and summer-autumn nutrition on reproduction and survival of Rocky Mountain elk (*C. e. nelsoni*) using a captive herd of 57 cow elk.

We induced early (Sep) and late breeding (Oct) and 3 levels of summer-autumn nutrition on the cows. Food was offered ad libitum at 3 levels of digestible energy (DE): high = 2.9–3.0 kcal of DE/g of diets, medium = 2.6–3.0 kcal/g, and low = 2.3–3.0 kcal/g. Within these ranges, DE content was gradually reduced from late June through early November to mimic seasonal changes in the wild. During summer and autumn, we measured calf growth; body mass, nutritional condition, and breeding dynamics of cows; and growth and pregnancy of yearlings. We also measured carry-over (i.e., time-lag) responses including over-winter calf and cow survival and parturition date and birth mass, as functions of previous summer-autumn nutrition and previous parturition date. Between autumn 1995 and spring 1998, we conducted 2 years of parturition-date, summer-autumn nutrition experiments, 2 winters of calf survival experiments, and 1 winter of cow survival experiments.

Early birth provided calves with more time to grow before onset of winter. This "head-start" advantage was maintained through late autumn, but its magnitude was diluted in some instances due to faster growth of some late-born calves. Body mass, body fat, and timing and probability of conception by cows in autumn were little influenced by parturition date the previous spring.

Summer-autumn nutrition significantly affected calves and their mothers. Growth of calves in the low and medium nutrition groups ceased by mid-September and late October. By December, calves in the high nutrition group were 40% and 70% heavier than calves in the medium and low groups, respectively. Cows in the high nutrition group accumulated about 75% and 300% more fat than cows in the medium and low groups by mid-October. Eighty percent of cows in the low nutrition group failed to conceive, and those in the medium group bred 10–14

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days later than cows in the high group. Summer-autumn nutrition of calves influenced their probability of becoming pregnant as yearlings. Probability of pregnancy approached 100% for those yearlings that had high summer-autumn nutrition as calves and yearlings, despite near starvation their first winter of life.

Winter survival of calves was related to their size at the onset of winter. Smaller calves lost more body mass daily than did large calves, and thus they survived fewer days through winter. Summer-autumn nutrition largely determined calf body size at the start of winter and, consequently, determined the proportion of winter survived. Survival of cows over winter was as related to body fat at the onset of winter as it was to nutrition during winter.

Carry-over effects of summer-autumn nutrition and parturition date on birth characteristics the following spring were minor. We detected no significant carry-over effect of summer-autumn nutrition or autumn condition on birth mass, although reduced condition in autumn delayed subsequent parturition date. Extent of body fat depletion in cows during the winter-survival experiments in 1998 accounted for 45% of the variation in parturition date. Ninety percent depletion delayed parturition an average of 34 days.

Delayed parturition, of a magnitude expected due to highly skewed sex ratios (≤3 weeks under extreme conditions), probably has only a weak influence on vital rates of free-ranging elk. In contrast, fat accretion and probability of pregnancy of cows, and growth and overwinter survival of calves, were sensitive to small (10–20%) differences in DE content of food. Digestible energy levels of our 2 lower nutrition levels reflect DE ranges reported for large ungulate herds during summer and autumn in western North America. Thus, our data suggest that limiting effects of summer-autumn nutrition on populations may be greater than often assumed, perhaps greater than those during winter in some ecosystems, and consequently indicate a need for greater understanding of nutrition's influence on population dynamics and how this influence varies across space and time. To enhance future research, we present animal- and vegetation-based guidelines for evaluating nutritional influences on elk populations.

WILDLIFE MONOGRAPHS 155:1–61

Key words: *Cervus elaphus*, digestible energy, dry-matter intake, elk, gestation, growth, habitat, lactation, nutrition, nutritional condition, Oregon, population dynamics, pregnancy, reproduction, survival.

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INTRODUCTION

Management and conservation have increased elk numbers from an estimated 100,000 to nearly 1 million over the last century in the United States (Christensen et al. 1999). Nevertheless, what may be perceived as a "golden" era may be coming to a close in some areas of the country. Like mule deer (*Odocoileus hemionus*) herds across much of the West (Carpenter 1998), productivity and population size of many elk herds in Idaho, Washington, and Oregon are declining, in some cases precipitously (Irwin et al. 1994, Gratson and Zager 1999, Ferry et al. 2001). The economic and social values of elk are enormous, and their declines threaten operating revenues of several state wildlife management agencies.

Declining ungulate populations in the western United States present important new challenges to wildlife biologists. These challenges are particularly intractable because causes of the declines are not well understood. Increasing predation, highly skewed sex ratios (i.e., a preponderance of yearling bulls and few mature bulls), inadequate habitat, and interactions among these and other factors are often cited as causes (Cook et al. 1995, Noyes et al. 1996, Carpenter 1998). This ambiguity probably is caused by scientist's failure to identify influences of limiting factors that regulate populations (Morrison 2001). Whatever the case, if the changing demographics are to be understood and managed, greater understanding is required of population regulation, particularly regarding top-down versus bottom-up influences.

Bottom-up influences on productivity of herds result from habitat's capability to provide food and thermal protection from harsh weather. For elk in many ecosystems, contributions of thermal cover probably are minor (Cook et al. 1998), suggesting in turn that habitat's contribution to elk productivity is largely a function of its nutritional adequacy and production of forage. Nutrition influences herbivores through density-dependent mechanisms (Fowler 1987), can limit productivity via density-independent effects (nutritional inadequacy may occur regardless of herbivore density), or perhaps indirectly by complex interactions with such top-down factors as predation. Considerable livestock research has established nutrition's influence on a variety of life processes, and substantial work with selected wild ungulates such as white-tailed deer (*O. virginianus*) and red deer (*C. elaphus elaphus*) also have advanced our knowledge. Nevertheless, the nature and extent to which nutrition regulates free-ranging populations of even these oft-studied species remain poorly understood.

Research of nutritional influences on elk is particularly rare. Canadian efforts have provided useful insights in recent years (e.g., Haigh and Hudson 1993). However, research focused on effects of nutrition during summer and autumn on reproductive performance of lactating elk and their calves is virtually absent (exceptions include Hudson and Adamczewski 1990, Cook et al. 1996). This apparent lack of interest undoubtedly stems from perceptions that forage on summer ranges is adequately abundant and nutritious so as to preclude important limiting affects on reproduction, survival, and population dynamics (Wallmo et al. 1977, Marcum 1975, Lyon 1980, Nelson and Leege 1982, Leege 1984, Christensen et al. 1993, Unsworth et al. 1998).

Forage quality and quantity certainly are greatest during the growing season. Nevertheless, nutritional requirements for lactation and juvenile growth place considerable demands on large herbivores (Verme and Ullrey 1984, Oftedal 1985, Cook et al. 1996) that limit reproduction if unsatisfied. Nutritional deficiencies in summer and autumn have been reported (Julander et al. 1961, Pederson and Harper 1978, Verme and Ullrey 1984, Merrill and Boyce 1991, Parker et al. 1996, Parker et al. 1999, Alldredge et al. 2002), and these may reduce pregnancy rates, delay sexual maturity and breeding, and reduce overwinter survival of adults and juveniles. Moreover, forest management is the primary land management activity on most summer-autumn ranges of elk in the western U.S., and forestry can have appreciable effects on forage quantity and quality available on these ranges (Hett et al. 1978, Cook 2002). The potential effect of this activity on productivity of elk herds may depend on the extent to which summer-autumn forage conditions affect reproduction and survival.

Selective hunting of bulls has appreciably reduced abundance of mature bulls in many elk populations (Schommer 1991, Leckenby et al. 1991). Low mature bull:cow ratios can delay breeding (Noyes et al. 1996), suggesting that inadequate numbers of mature bulls might reduce herd productivity by delaying parturition and, in turn, by reducing calf survival. This hypothesis depends on at least 4 assumptions: (1) breeding delays result in similar delays in parturition; (2) late-born calves are unable to "catch-up" with their early-born counterparts; (3) breeding delays are of sufficient magnitude to be relevant to calf survival; and (4) differences in body size of juveniles at the onset of winter influence probability of winter survival.

Validity of these assumptions may depend to some extent on limitations imposed by nutrition. During summer and autumn, nutrition may influence potential for late-born calves to catch-up or may influence the probability that late-born calves fall further behind. During winter, differences in juvenile body size may affect survival if winter weather and nutritional conditions are harsh, but have little or no influence if winter conditions are mild (Hobbs 1989). Hence, influences of adult sex ratios on herd productivity may be mediated by nutrition.

This study was designed to simultaneously compare effects of summer-autumn nutrition and breeding and birth dates on a host of reproduction and survival variables of elk. We conducted a series of experiments from summer 1995 through spring 1998 using a captive herd of 57 cow elk to achieve 3 primary goals:

1. estimate the main and interactive influences of summer-autumn nutrition and parturition date on reproduction and survival;
2. quantify nutritional requirements of lactating cows and their calves in summer and autumn; and
3. quantify the relation between magnitude of nutritional restriction and magnitude of reduction in reproduction and survival.

We tested specific hypotheses regarding influences of summer-autumn nutrition and parturition date. The first 4 hypotheses pertain to direct effects of summer-autumn nutrition and parturition date on reproduction; the final 3 pertain to carry-over effects of nutrition and birth date on subsequent reproduction and survival:

1. Nutritional condition (i.e., as defined by Harder and Kirkpatrick [1994]), timing and probability of becoming pregnant (breeding dynamics), summer-autumn calf growth and body size in late autumn, and yearling growth and pregnancy probability are sensitive to summer-autumn nutrition.
2. These variables (nutritional condition and so forth) are sensitive to variation in parturition date (and by extension, timing of breeding) that can be attributed to marked differences in bull age (e.g., $\leq$21-day delay in average conception date in herds in which most breeding is by yearling bulls [Noyes et al. 1996]).
3. These variables are influenced by interactions between parturition date and summer-autumn nutrition (i.e., the combination of late parturition and low nutrition or early parturition and high nutrition has greater influence on reproduction than would be expected based on the separate effects of these 2 factors).
4. Nutritional condition of lactating and nonlactating cows in summer and autumn is differentially influenced by different levels of nutrition.
5. Winter survival of pregnant cows and their fetuses is influenced by nutrition of the cow during the previous summer and autumn, across varying levels of winter nutrition.
6. Calf mass at birth and timing of parturition is influenced by the mother's nutrition during the previous summer and autumn, and her timing of parturition the previous spring (i.e., there is a carry-over effect of summer-autumn nutrition and parturition date from one year to the next).
7. Probability of winter survival of calves maintained on low winter nutrition is sensitive to levels of nutrition the previous summer and autumn and their birth date.

Acknowledgments.—This study was supported by the Oregon Department of Fish and

Wildlife with funds from Federal Aid for Wildlife Restoration (Project W-87-R), Northwest Forest Resource Council, Pacific Northwest Research Station of the U.S. Forest Service, Boise Cascade Corporation, Rocky Mountain Elk Foundation, National Council for Air and Stream Improvement, and the Eastern Oregon Agriculture Research Center. We thank B. L. Dick, R. O. Kennedy, J. C. Nothwang, and P. Kennington of the U.S. Forest Service for fence construction and other tasks. C. W. Bowers, K. A. Brown, S. Cerini, M. Dial, S. E. and T. E. George, S. Han, D. A. Hengel, G. D. Jacobs, O. D. Lay, S. Shuckle, and B. Spicer served as field assistants. T. M. McCoy, DVM, treated sick animals. T. R. Stephenson introduced us to ultrasonography for measuring nutritional condition. C. T. Robbins provided valuable guidance on raising and training elk calves. B. B. Davitt provided nutrient analysis of elk food. J. W. Thomas and other U.S. Forest Service employees established the research infrastructure that supported this study. The managers and employees of Boise Cascade Corporation, particularly R. Messinger, S. Wilde, T. Lovlien, M. Gooderham, and R. Weinberger provided materials and logistical support to do the study on Boise Cascade Corporation timberlands. This research was conducted in accordance with approved animal welfare protocol (approval #92-F004) (Wisdom et al. 1993).

STUDY AREA

The study site was located on private timberlands 30 km west of La Grande in the Blue Mountains of northeast Oregon. It was on traditional summer range of elk in the grand fir (*Abies grandis*) zone on a northeast-facing aspect at 1,300–1,350 m. Average annual precipitation was 87 cm, most falling in winter and spring. Average minimum and maximum temperature was –5.8 and 0.1°C in January and 11.0 and 24.7°C in July (National Oceanic and Atmospheric Administration 1966–75). The study site received about 10 cm of precipitation each month during the winter, most falling as snow. During this study, snow began to accumulate in mid-November, attained a depth of about 1 m by mid-winter, and melted from most of the study area by early April (see Cook et al. 1998 for more details).

Facilities consisted of 2 pen complexes (Fig. 1). The primary complex was rectangular and built to enclose a 3-ha clearcut,

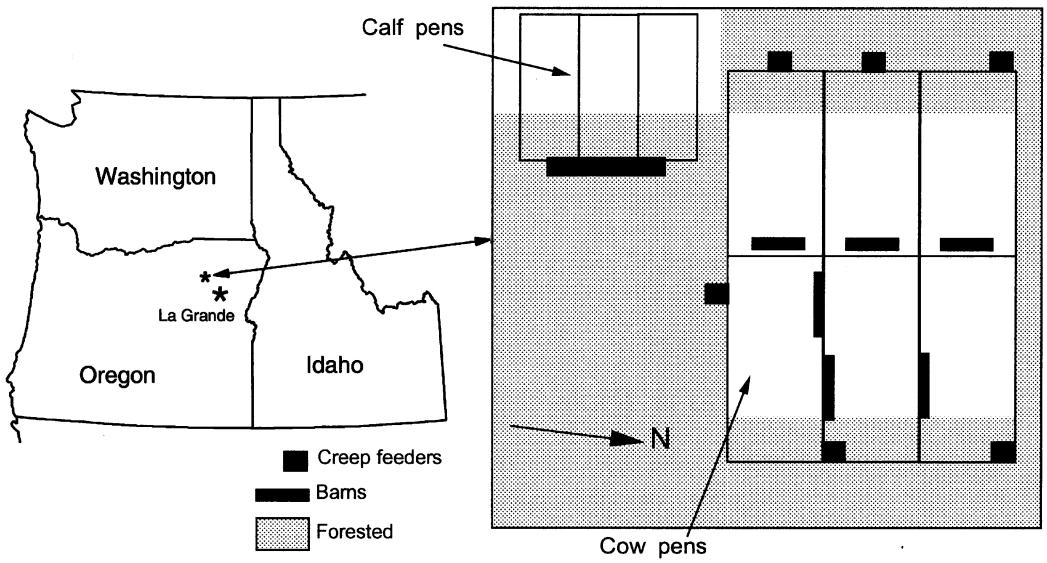

Figure 1. Layout of calf and cow elk pen complexes used for nutrition-reproduction studies in northeastern Oregon, 1995–1998. Each of the 6 pens for cows was 0.75 ha, and each of the calf pens was 0.3 ha. Both were constructed in clearcuts and contained mature forest. The barns were used for individually feeding food, weighing, and collecting physiological samples. Creep feeders attached to the cow pens were used to feed solid food to calves and were inaccessible to their mothers. All pens were interconnected to facilitate frequent rotation of elk among pens, to reduce potential microsite influences on elk performance. All forage was eliminated from all pens.

plus a small amount of adjacent forests. An access road running north-south split the complex in half, and each half was subdivided into 3 pens, providing a total of 6 pens 0.75 ha in size. Each pen contained similar amounts of forest (20%) and clearcut (80%) habitats. Small, 9-stall barns were built in each pen and used for individualized feeding, weighing, and handling as described by Cook et al. (1998). We held adult cows in this complex year-round, including during the breeding season when bulls were introduced to them.

A smaller complex about 1 ha in size held calves after weaning each year (Fig. 1). This complex consisted of 3 rectangular pens of equal size, each of which extended 20–30 m into forested habitat. A barn consisting of 55 stalls adjacent to the pens provided for individualized feeding and handling during winter survival experiments with the calves.

We also used five smaller pens built for previous studies (Cook et al. 1998) during the study. These were 0.1 ha in size, occurred with a feeding-handling barn, and were located in forested habitat. Feed storage facilities, an automated weather station, and technician housing also were present on the site (see Cook et al. 1998).

Elk were used during the summer of 1995 to eliminate vegetation within the pens by grazing and trampling. Pens remained unvegetated throughout the study.

METHODS AND DATA ANALYSIS

Experimental Animals

We used 2 cohorts of bottle-raised female elk, the first born in 1991 and the second in 1993 (Cook et al. 1996). The calves were captured when 1–4 days of age from the Starkey Experimental Forest and Range and adjacent areas in northeast Oregon. We used 22 4-year-old and 35 2-year-old cows at the beginning of the study. All bulls used for breeding during all 3 years were at least 3 years old; they were captured from wild stock held in the Starkey Experimental Forest and Range. They were transferred to the site each year at the start of the rut.

Overview

Preparation for the study started in early summer 1995, when all cows were fed a high quality diet so that they were in good to excellent nutritional condition at the start of the study (Fig. 2). In autumn 1995, cows were bred for the first time during 2 breeding

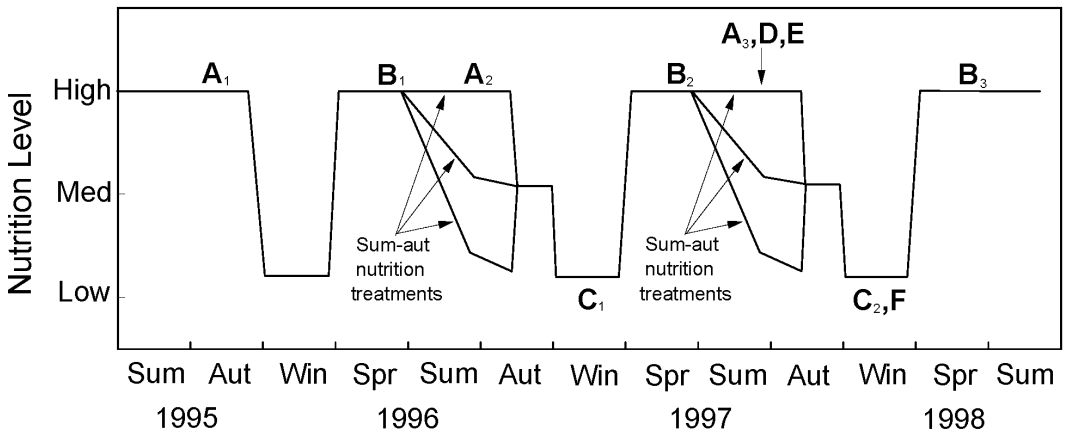

Figure 2. Chronological sequence of key events and experiments, and associated nutrition levels of calf and cow elk, northeastern Oregon, summer 1995 through summer 1998. The nutrition levels refer to relative differences in digestible energy intake: high corresponds to levels that supported a positive energy balance, medium roughly corresponds to maintenance levels, and low corresponds to levels that induced a negative energy balance. Large bolded letters identify timing of events and experiments: A = breeding times, B = birthing times, C = the experiments of calf winter survival, D = the experiment of lactating versus nonlactating cow performance, E = the experiment of yearling nutrition, breeding, F = the experiment of adult cow winter survival. At A_1, early and late breeding dates were induced in 2 groups of cows; at A_2 and A_3, timing of breeding was uncontrolled. Calves used in the C_1 and C_2 calf survival experiments were born at B_1 and B_2, respectively. Yearlings used in the experiment of summer nutrition-breeding (E) were born at B_1. The nutrition levels relate only to cows and calves in the experiments of summer-autumn nutrition (nutrition levels for experiments of calf winter survival, yearling nutrition-breeding, and cow winter nutrition are not presented in this figure).

periods to induce different parturition dates. We conducted experiments of direct effects of summer-autumn nutrition and parturition date on reproduction in 1996 and 1997. We compared nutritional effects on fat accretion of lactating and nonlactating cows in summer 1997. We also evaluated effects of summer-autumn nutrition on breeding dynamics of yearling cows this second summer using the cohort of calves born in spring 1996 (Fig. 2). We conducted experiments of carry-over effects of summer-autumn nutrition and parturition date on (1) adult cow and fetal survival in winter 1998, (2) survival of calves in winter 1997 and 1998, and (3) timing of birth and birth mass of calves in spring of 1997 and 1998 (Fig. 2).

Nutritional treatments were implemented only during summer and autumn; cows were offered identical diets the rest of the year (except for a subgroup during the winter survival experiment of 1998).

All pen complexes were constructed so that we could routinely rotate calves and cows among pens. This was intended to eliminate potential effects of microsite characteristics in each pen on elk responses to treatments. We rotated elk among pens twice per month, except during the parturition period to avoid disrupting mother-calf bonds. We emphasized varying digestible energy (DE) rather than protein or minerals. This was based on the assumption that energy, rather than protein or minerals, is most limiting to anabolic processes (Holter and Hayes 1977, Lyford and Huber 1988, Parker et al. 1999). We had insufficient elk for simultaneous examination of 2 or more nutritional constituents.

We conducted all statistical analyses with Statistical Analysis Systems (SAS Institute 1988), usually with the general linear models procedure (PROC GLM), except where noted.

Weather

We used an automated weather station, centrally located in a clearcut, to monitor weather conditions during the study. The station included probes to measure wind speed (Met-one 014A wind-speed sensor) and temperature (HMP 356 temperature-relative humidity probe). A CR10 control module accumulated and stored data on a SM192/716 storage module in a PC compatible format (Cook et al. 1998). All equipment was obtained from Campbell Scientific, Inc., Logan, Utah, USA. We calculated average, maximum, and minimum daily temperature and wind speed by month for the entire study.

Autumn Through Spring Feeding Regimes

Winter-spring feeding of cows used in the summer-autumn nutrition experiments was intended to be identical each winter of the study. We fed these cows submaintenance diets in winter to induce about 10% mass loss over winter. They received ad libitum, high quality diets during spring, to simulate natural seasonal cycles in forage conditions (see Cook 2002) and to eliminate nutritional restriction on fetal growth during the third trimester. During the breeding season until mid-December 1995, we fed all cows identical diets consisting of a mix of high quality pellets and alfalfa hay (Table 1) fed ad libitum. During the second (1996) and third (1997) years, we set feeding levels from the end of the rut (5 Nov) until the beginning of the winter mass loss period (mid-Dec) to hold body condition of the cows constant until early winter (Fig. 2). The purpose for this was to determine carry-over effects of parturition date and summer-fall nutrition on cow responses during winter and the following spring-summer period (i.e., prevent compensation by poor-condition cows in autumn).

Starting in mid-December of 1995, we fed cows a lower quality pellet and lower quantity of food to induce mass loss of 10% during winter. We occasionally adjusted feeding levels to ensure meeting our mass-loss goal. We monitored mass loss of non-pregnant cows to determine the need for adjusting feeding levels of pregnant cows, because fetal growth masked mass changes in pregnant cows. We terminated restricted feeding by the second week of March, re-acclimated the cows to the high quality rations and ad libitum feeding over a 2-week period, and then maintained this feeding regime through parturition, when the summer-autumn nutrition treatments were initiated. The feeding regimes of the subsequent winters and spring were

Table 1. Crude protein (CP), gross energy (GE), in vitro digestible dry matter (DDM), digestible energy (DE), and primary ingredients of rations fed to elk cows and calves, northeastern Oregon, 1995-1998.

Season	Year	Ration[a]	CP	GE	DDM	DE	Primary ingredients[b]
Sep-Nov	95	Pel-h	14.0	4.314	74.0	3.19	Oats, wheat, alf
		Hay-h	18.0	4.458	57.0	2.54	Alf
Dec-Feb	96	Pel-m	15.9	4.282	65.4	2.80	Feeder alf, ryegr, wheat middens
		Hay-h	17.9	4.363	64.4	2.81	Alf
Mar-Jun	96	Pel-h	15.7	4.315	79.4	3.43	Oats, wheat, alf
		Hay-h	16.7	4.340	63.2	2.74	Alf
Jul-Nov	96	Pel-h	15.7	4.315	79.4	3.43	Oats, wheat, alf
		Pel-l	13.8	4.062	56.5	2.30	Ryegr, straw, feeder alf, bent
		Hay-h	15.5	4.316	61.9	2.67	Alf
		Hay-m	13.6	4.337	56.7	2.46	Alf, orchard grass
		Hay-l	8.0	4.333	54.2	2.35	Fescue, mixed meadow grasses
Dec-Feb	97	Pel-m	14.3	4.291	67.1	2.88	Feeder alf, ryegr, wheat middens
		Hay-h	15.5	4.316	61.9	2.67	Alf
Mar-Jun	97	Pel-h	15.8	4.345	79.7	3.46	Oats, wheat, alf
		Hay-h	15.5	4.316	61.9	2.67	Alf
Jul-Nov	97	Pel-h	15.9	4.380	83.6	3.66	Corn, wheat middens, 19% alf
		Pel-l	14.2	3.997	56.3	2.25	Ryegr, straw, feeder alf, bent
		Hay-h	15.3	4.350	59.1	2.57	Alf
		Hay-m	8.3	4.361	57.7	2.52	Alf, orchard grass
		Hay-l	7.8	4.427	51.6	2.28	Fescue, mixed meadow grasses
Dec-Feb	98	Pel-m[c]	14.8	4.093	53.5	2.19	Feeder alf, ryegr, wheat middens
		Hay-h	15.3	4.350	59.1	2.57	Alf
Mar-Jun	98	Pel-h	15.9	4.371	79.9	3.49	Oats, wheat, alf
		Hay-h	15.3	4.350	59.1	2.57	Alf

[a] Ration codes are Pel = pellet and h, m, and l indicate relative level of DE content (i.e., high, medium, low). Units of nutritional constituents are percent CP, kcal of GE/g of food, percent DDM, and kcal of DE/g of food.

[b] Abbreviations are: alf = alfalfa hay; bent = bentonite (added to lower gross energy content); and ryegr = ryegrass screenings.

[c] Both the gross energy and DDM content of this pellet suggests the manufacturer inadvertently substituted the low-energy pellet for the medium-energy pellet formulation. The lower DE content of this pellet would account for the greater mass loss of cows in winter 1998 compared to the previous 2 winters.

intended to be identical (but see footnote "c" in Table 1).

For the first 2 winters of the study, we graphically illustrate body mass (BM) patterns, differences in mass loss between pregnant and open cows, and increases in mass during spring through the end of parturition.

Direct Effects of Summer-Autumn Nutrition and Parturition Date

Cow-calf performance.—In August 1995, the 57 cows were randomly assigned to 6 treatment groups in a 2 × 3 factorial design with 2 levels of breeding date and 3 levels of nutrition. We restricted randomization such that 2.5- and 4.5-year-old cows were equally distributed among each of the 6 groups. All cows assigned to the early breeding group were moved to the eastern 3 pens (Fig. 1), gates were opened so that cows could travel among these pens, and a bull was introduced on 5 September. We introduced the bull to the other cows on 5 October in the western 3 pens, and removed him from the study area on 5 November. This provided breeding dates expected of mature bulls (Sep breeding) and yearling bulls (Oct breeding) as described by Noyes et al. (1996).

Our objectives included evaluating effects of the treatments on probability and timing of breeding during the second and third (1996 and 1997) breeding seasons, so we provided cows with equal access to bulls during the entire rut of 1996 and 1997 and made no effort to induce different breeding dates. For this, we combined the 6 pens into 3 pens by opening gates to allow comingling of cows, within nutrition groups. We held wild-caught bulls in the pens, 1 in each pen, from about 5 September through 5 November both years. Thus, the early- and late-breeding treatments during the second

breeding season (1996) resulted from post-hoc segregation of cows based on observed parturition dates the following spring, rather than from random assignment to breeding-date categories as in the first year.

We formulated the summer-autumn nutritional treatments to meet 3 criteria. First, we selected DE levels with biological relevance to free-ranging elk on summer ranges of the Blue Mountains Ecoregion of eastern Oregon and southeastern Washington. Our "high" nutrition treatment was formulated to avoid restriction of reproductive performance, without being substantially greater in DE content than wild elk might obtain on native range. We based the DE level (Fig. 3A) on beef cattle requirements (National Research Council 1984) and earlier experiments with these elk (e.g., Cook et al. 1996). The "low" nutrition treatment was selected to represent DE levels that elk might encounter in xeric coniferous forest zones (e.g., ponderosa pine [*Pinus ponderosa*], Douglas fir [*Pseudotsuga menziesii*], and grand fir [*Abies grandis*]) of the Blue Mountains during relatively dry years (Holechek et al. 1981, J.G. Cook, unpublished data). We used time-specific averages from these data as the target DE level for cows in the low nutrition group. Target DE levels for the "medium" nutrition group were the average of those fed to the low and high groups (Fig. 3A).

Second, we based the summer-autumn nutrition treatments solely on food quality (quantity offered was unrestricted), because we wanted to evaluate effects of quality on amount of food consumed. Further, we had no criteria on which to select biologically relevant feeding levels (i.e., quantity). The DE targets also were used for calves when they began consuming solid food.

Third, we emphasized using hay rather than pelleted rations to implement the nutrition treatments, particularly in the second year of the study. Pelleted rations simplify such studies (e.g., enhance individualized feeding), but pellet formulation renders fibrous tissue into small particles that can increase passage rates and food intake (Minson and Wilson 1994, Grey and Servello 1995). During the first summer of the study, we fed pellets and hay in a 45:55 ratio. We reduced this ratio the second summer: the high nutrition group received a 30:70 ratio, the medium group received a 20:80 ratio, and the low group received a 10:90 ratio. The low group received just enough pellets to entice elk into their barn stalls. The higher levels were required for the other groups to achieve target DE levels (i.e., hay DE levels needed augmentation).

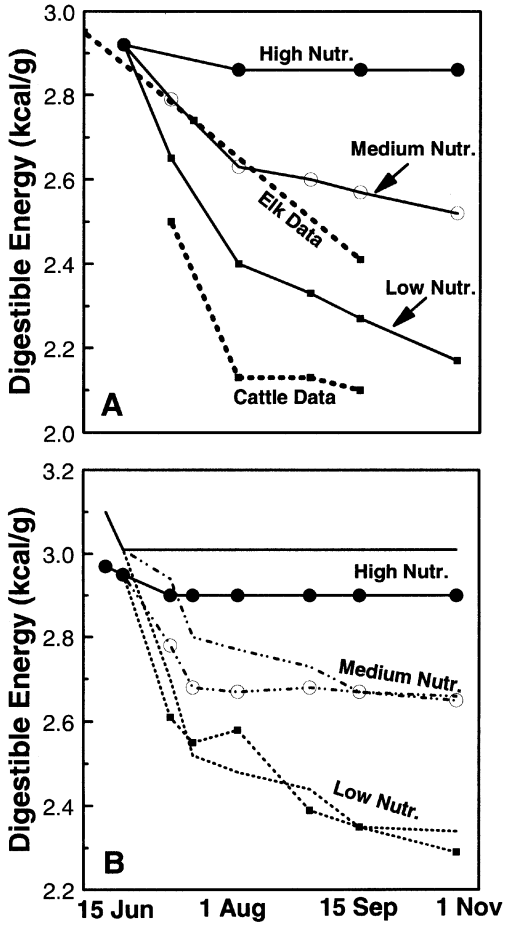

Figure 3. In graph A, target digestible energy (DE) content of food offered to cow elk and calves from late June through early November, 1996 and 1997, northeastern Oregon. Dashed lines labeled "elk" and "cattle" are dietary DE levels of elk (J.G. Cook, unpublished data) and cattle (Holechek et al. 1981) determined during drought years at moderate to low elevations in forest zones in the Blue Mountains Ecoregion of northeast Oregon. The average of these 2 DE levels set the target for the low nutrition treatment group. In graph B, actual DE content of food consumed by cows and calves from late June through early November, 1996 (lines without circles and squares) and 1997 (lines with circles and squares).

Attaining target DE levels across treatments involved combining foods of different quality. We used 2 pellet formulations and 3

different hays with varying levels of DE (Table 1). We formulated pelleted rations to provide required mineral concentrations based on beef cattle (National Research Council 1984). Mineral blocks were provided in pens. Type of hay offered at any given time over summer and autumn was that which most closely matched the target DE levels for the treatment group for that period, and the 2 pellet types were mixed in ratios so that the overall DE actually consumed by the elk matched the target for their nutrition group. This approach required monitoring of intake, because required pellet ratios reflected amount of hay eaten. We adjusted rations weekly to comply with desired DE levels and desired pellet:hay ratios. We increased DE in the high energy pellet formulation in 1997, compared to 1996, to compensate for the lower pellet:hay ratio of that year (Table 1).

We fed cows twice daily (typically at 0800 and 1300 hr). They were fed pelleted food individually in the barns in the mornings. Amount of pellets fed to each elk was based on metabolic body mass ($BM^{0.75}$). They generally consumed their pellets within 1–2 hours and were then released back to their calves. We fed hay communally within treatment groups in the hay mangers outside of the barns at the second feeding. All orts were collected and measured individually for pellets and communally for hay. We fed hay ad libitum, and the amount was adjusted each day such that cows in aggregate generally left no more than a few kg uneaten. This minimized selective feeding and waste. Thus, cows had access to food 24 hours each day, thereby ensuring our estimates reflected true voluntary intake (Minson 1990). However, we could estimate total daily intake of food only for treatment groups, not for cows individually within groups, thereby precluding variance estimates of daily intake by individuals.

We fed hay and pellets to calves in creep feeders (i.e., small pens that allowed calves to have continuous access to food while excluding cows [Fig. 1]). Hay was fed ad libitum to all calves. We offered calves about 1 kg more hay each day than was consumed the previous day, to provide ad libitum amounts while minimizing selection. We adjusted the ratio of high energy to low energy pellets such that the overall target dietary quality was achieved. Orts were removed from the feeders and weighed each day. Just after the rut, calves were weaned from their mothers and moved to the calf-pen complex (5 Nov in 1996, 15 Nov in 1997), where they remained segregated by nutrition level through late November. For experiments of winter calf survival, described below, we trained calves to enter the barns for feeding. Weaning, and this training, initiated a period of disrupted feeding that lasted 1–2 weeks.

Estimates of DE levels of each of the pellet and hay types were known sufficiently to formulate mixes of hay and pellet rations. More exact estimates of DE and crude protein were determined from samples of each collected over the feeding period. The Habitat Analysis Laboratory at Washington State University, Pullman, Washington, USA, conducted quality assays—crude protein by macro-Kjeldahl analysis, gross energy by bomb calorimetry, and dry-matter digestibility by 2-stage in vitro trials (Association of Official Agricultural Chemists 1980). We estimated DE content as the product of gross energy and in vitro digestibility (Hobbs et al. 1982).

Treatment responses included BM dynamics of cows and calves, nutritional condition of cows, and timing of breeding and pregnancy rates of cows. We weighed cows twice weekly on electronic scales in weighing chutes as they entered and exited the feeding barns (Cook et al. 1998). We weighed neonates with hand-held spring scales and older calves in the weighing chutes.

We estimated nutritional condition using 2 techniques developed in a companion study (Cook et al. 2001*a*,*b*). We developed a body condition score (BCS) in autumn 1996 and used it for the duration of the study. Our BCS, derived from the caribou (*Rangifer tarandus*) BCS by Gerhardt et al. (1996), relied on palpation of the withers, ribs, and rump (Cook et al. 2001*a*,*b*). Beginning in autumn 1997, we combined subcutaneous rump fat thickness, measured using ultrasound (Stephenson et al. 1998), and BCS into an index, referred to as LIVINDEX, that is superior to either measure used separately (Cook et al. 2001*a*,*b*). We used BCS solely from autumn through summer 1996–97 and

LIVINDEX thereafter. We also used ultrasound to measure thickness of the longissimus dorsi (loin) muscle between the twelfth and thirteenth rib. This provided an index to catabolism of lean mass that was particularly useful for cows in poor condition (Cook 2000). We sedated cows to measure condition using xylazine hydrochloride (0.5 mg/kg BM) administered intramuscularly by hand-injection with syringes. We reversed sedation by intravenous injection of yohimbine hydrochloride (0.1 mg/kg).

We converted BCS estimates to estimates of body fat (%) and gross energy (GE: Mcal/kg) of the ingesta-free body using the following equations (Cook et al. 2001*a*,*b*):

$$\text{FAT} = -5.53 + 4.78(\text{BCS}),$$

and

$$\text{GE} = 0.842 + 0.381(\text{BCS}).$$

We calculated LIVINDEX from estimates of BCS and rump fat thickness and, in turn, converted LIVINDEX estimates to ingesta-free body fat and GE. Fat and GE were calculated from LIVINDEX using the following equations (Cook et al. 2001*a*,*b*):

$$\text{FAT} = -9.9 + 9.187(\text{LIVINDEX}) - 1.383175(\text{LIVINDEX}^2) + 0.0839512(\text{LIVINDEX}^3),$$

and

$$\text{GE} = -0.37 + 0.823(\text{LIVINDEX}) - 0.128536(\text{LIVINDEX}^2) + 0.0077629(\text{LIVINDEX}^3).$$

We determined pregnancy status in all years of the study using pregnancy-specific protein B (PSPB) (Noyes et al. 1997) in serum collected in late autumn. Timing of conception in 1996 was determined also with PSPB, by sampling in selected windows such that conception during the first (5–24 Sep), second (25 Sep–15 Oct), and third (16 Oct–5 Nov) 3-week periods of the 9-week rut could be determined. Based on the assumption that PSPB could reliably identify pregnancy at about 30 days post-conception (it is now recognized that accuracy may increase up to about 40 days post-conception [G. Sasser, personal communication.]), we collected serum from all cows on 21 October, again on 12 November for cows found nonpregnant in October, and all cows again in mid-December. From this we assigned conception dates to each of the 3 periods. In 1997, timing of breeding was determined by direct observation. We collected feces daily and assayed them for progesterone metabolites, providing indications of estrus that confirmed field observations (Cook et al. 2001*c*).

These experiments evaluated effects of nutrition and parturition date on cow and calf performance from the end of parturition, when nutrition treatments were initiated, until early November, when calves were weaned. We used percent fat and GE of the ingesta-free body and BM changes to examine nutritional condition responses of cows. We averaged the 2 estimates of mass collected each week and converted them to change-in-mass (%) for statistical analysis. Change-in-mass was calculated as the difference between starting mass and mass each subsequent week, divided by starting mass, and converted to percent.

Effects of parturition date and summer-fall nutrition on BM dynamics were analyzed with fixed-effects, repeated measures 2-way ANOVA, using the multivariate mode of PROC GLM. The key effects for these analyses were the following interactions: week × nutrition, week × parturition date, and week × nutrition × parturition date effects. In an experiment of this type, only the interactions are of interest because effects appear after the experiment commences, if indeed the treatments influence the dependent variable (e.g., BM). We identified differences among treatments each week using least squares means. The assumption of sphericity (SAS Institute 1988: 605) was routinely violated, and we used the Huynh-Feldt adjustment to account for it (SAS Institute 1988: 605).

Before analyzing parturition date and nutrition effects, we identified potential confounding from calf gender, cow age, and, in the second year, the influence of previous-year nutrition (carry-over effect). For the first year, we conducted the repeated measures ANOVA with all variables included (e.g., parturition date, nutrition, gender, and cow age), plus interactions, to identify

calf gender and cow age effects. For the second year, insufficient df precluded repeated measures ANOVA with all independent variables (plus previous-year nutrition level). Hence, we conducted a sequential approach: (1) all main effects and highest order interactions (4- and 5-way interactions), (2) main effects and 3-way interactions, and (3) main effects and 2-way interactions. Although this was not an optimal analysis, it helped identify the nature and extent of influences of the potentially confounding variables.

We removed influences of significant confounding variables from the data set via the following. Within each of the 6 treatment groups, percent change-in-mass of cows of the first level of the potentially "confounding" factor (e.g., mean change-in-mass of mothers of female calves) was subtracted from that of the second level (e.g., mean change-in-mass of mothers of male calves) for each week of the data stream. The resulting difference should reflect the effect of the potentially confounding factor (e.g., calf gender effect). Next, we regressed these differences with time using linear and nonlinear (PROC NLIN) techniques. The models then were used to remove their confounding influences from the data set, providing a less confounded data set to illustrate parturition date and nutrition effects on cow performance.

We measured body fat and GE content of cows during the rut in late-October in 1996 and 1997, providing a single end-point estimate of summer-fall nutrition and parturition-date influences. Effects of nutrition and parturition date on body fat and GE content were identified using 2-factor, fixed-effects ANOVA, one for each attribute.

Influences of parturition date and nutrition on pregnancy rates were identified using logistic regression (PROC CATMOD) with pregnancy status as the dependent variable and parturition date and nutrition as the independent variables. We used a chi-square test as a supplemental analysis to compare influences of parturition date and nutrition (PROC FREQ). Then, we used logistic regression (PROC CATMOD) to provide equations of pregnancy probability as a function of nutritional condition during autumn.

We identified influences of parturition and nutrition on timing of conception (early, middle, and late) during the rut of 1996 using a chi-square test (PROC FREQ). Because actual breeding dates of cows were known in 1997, and thus the dependent variable was continuous, we conducted a fixed effects, 2-factor ANOVA for the second year of data, to identify influences of parturition date and nutrition.

Influences of birth date and summer-autumn nutrition on calf growth were evaluated in 3 stages. First, calf growth from birth until initiation of nutrition treatments in late June was evaluated as a function of birth date, birth mass, calf gender, cow age, in the first year, and previous-year nutrition of the mother, in the second year. We used fixed-effects analysis of covariance (ANCOVA), using all variables, and multiple regression (PROC GLM), using continuous variables, to compare effects of these factors on BM at the end of this period. To more thoroughly illustrate the contribution of birth mass to growth of neonates, we reran the ANCOVAs with birth mass excluded, generated residuals from the model, thereby removing the effects of all other variables, and regressed these residuals with birth mass. All potential interactions were included.

Second, we subtracted calf weights obtained when nutrition treatments were implemented from all subsequent calf weights. This removed the effects of birth date and other potential influences occurring soon after parturition on calf mass dynamics after the nutrition treatments were implemented. This permitted evaluation of a second potential effect of birth date: a lingering effect of birth date on growth rates later in summer and autumn (e.g., evidence of reduced or accelerated growth of late-born calves). We used fixed-effects, repeated measures ANOVA to identify influences of birth date, summer-autumn nutrition, and the potential for confounding due to calf gender and cow age. Because adjusted mass of all calves was zero at the start of the period, only the interaction terms with time were of interest. An initial run was conducted with all interactions included to provide initial indications of calf gender and cow age effects. We removed these effects if they were important as described above for cows.

Then, we re-ran the ANOVA to test for birth date and nutritional influences on calf growth over summer and autumn.

Third, we conducted a final 5-factor ANCOVA to determine effects of gender, nutrition, birth mass, cow age for the first year's experiment, previous-year nutrition of the mother for the second year's experiment, and actual birth date (rather than the early-late levels of the repeated measures ANOVA) on unadjusted BM of these calves at the time of their weaning by mid-November. To thoroughly examine the individual effects of these variables on BM at weaning, we reran the ANCOVA with 1 independent variable removed, calculated the residuals, then evaluated the relation between the removed independent variable with weaning mass, using simple linear regression, once for each independent variable. This provided a better illustration of each variable's effect on calf weaning mass with effects of all other independent variables removed.

Lactating versus nonlactating cow performance.—During the second summer, we compared differences in the effects of nutrition treatments between lactating and nonlactating cows over the summer-fall period. We used 12 nonlactating cows for this experiment. Six received a diet identical to that offered to the lactating cows in the high nutrition group, and 6 received the diet fed to the lactating cows in the low nutrition group. We monitored food intake and nutritional condition of these cows as described for their lactating counterparts.

We compared nutritional condition (LIVINDEX) estimated in mid-October using 2-factor ANOVA, with 2 levels of summer-autumn nutrition (low and high) and 2 levels of lactation status. Body condition scores collected the previous March and June were used to identify differences in condition, prior to the summer nutrition treatments, that might have accounted for differences in condition observed at the end of the summer-autumn nutrition period. We tested for differences in condition at each sampling time using 1-way ANOVA with 4 levels of the single factor: (1) summer lactating, high summer nutrition; (2) summer lactating, low summer nutrition; (3) summer nonlactating, high summer nutrition; and (4) summer nonlactating, low summer nutrition. Condition of 1/4 of the cows in this analysis was not determined in June, precluding a single, repeated-measures ANOVA in place of 3, 1-way ANOVAs.

Cow-calf food intake dynamics.—Our system of feeding provided direct, separate measures of pellets that cows and calves consumed each day. But it imperfectly segregated hay consumption by calves from that by cows, because calves were able to consume hay that was intended for the cows. We attempted to segregate hay consumption by cows and calves by constructing hay mangers for the cows that calves could not access. These were elevated above the reach of the calves, and a woven wire frame was built into the mangers to cover the hay and prevent cows from dropping flakes of hay out of the mangers. Casual observations indicated this approach worked when calves were small but was less effective as calves grew, particularly by late September.

Therefore, we conducted a 4-day trial at the end of the second summer-autumn season (10–14 Nov 1997), just after nutrition treatments for the cows were ended, to estimate how much hay intended for cows was consumed by their calves. During this trial, all food for cows was offered in the barn, such that all food consumed by calves was from their creep feeders and therefore could be estimated accurately.

In 1996 and 1997, cow-calf pairs within nutrition treatments were separated according to breeding group (i.e., early and late) through summer until the rut. Thus, we were able to measure food intake for each of the 6 treatment combinations during summer. However, when the rut began, we combined cows across breeding groups such that all cows within a nutrition treatment had access to the same bull (this was necessary because we had insufficient bulls for all 6 treatment combinations). Independent estimates of food intake for each parturition-date group therefore were obtained only through early September of both years.

Because elk within treatment groups were fed hay communally, we could not calculate variances of dry-matter intake, so we illustrated treatment effects on intake graphically. We first estimated intake for cow-calf pairs, simply because we were unable to completely

segregate hay consumption by cows and their calves. Such a presentation of intake data is atypical and precludes comparisons to published estimates of requirements. Hence, we also estimated intake by cows and their calves using the following approach. For cows, we calculated an initial estimate of total dry-matter intake based on pellet consumption in barn stalls and hay consumption from mangers. We next plotted with time, on an age and $BM^{0.75}$ basis, (1) estimates of dry-matter intake from 5 published studies of elk calves, red deer calves, and white-tailed deer fawns (reviewed by Cook et al. 1996) and (2) dry-matter intake of our calves, estimated from food consumed in the creep feeders, in the high nutrition group. We assumed that the time of divergence between the published estimates of intake versus that measured from the creep feeders in our study would indicate when in summer our calves began taking appreciable amounts of hay from the cow mangers. At the end of the experiment in early November, differences in hay intake by calves immediately prior to versus during the 4-day trial (where all hay fed to cows was provided in the barns and thus inaccessible to calves) indicated the amount of hay intended for cows that was actually consumed by calves. From these beginning and ending points, we calculated an adjustment to account for the hay calves stole from their mothers. We expressed all intake data on a daily basis averaged across weekly time intervals.

Yearling growth, intake, and breeding.—We evaluated carryover effects of summer-autumn nutrition/birth date of the first cohort of female calves on their pregnancy status as yearlings (n = 19). In early April 1997, we placed the 19 female calves from the winter calf survival experiment of 1996–97 on an ad libitum, high-quality feeding regime. The ration consisted of the high quality pellet (Table 1), fed in a ratio of 60:40 with alfalfa hay. This ration provided an overall DE level in the diet of 3.2 kcal/gram of dry-matter. Also in April, the 19 elk were ranked by BM and randomly assigned to 1 of 2 nutrition groups, such that the distribution of BM was similar in each. We fed elk in the high nutrition group the high quality ration through early September. We fed those in the medium nutrition group this ration until 1 August, then reduced their pellet:hay ratio to implement a DE feeding level of 2.9 kcal/g of food. Hay fed to both groups remained identical and was offered ad libitum. We maintained this feeding regime through 8 September.

These 19 females, now yearlings, along with 21 adult, nonlactating cows, were placed with a bull from 9 September through 7 November 1997. We fed all cows alfalfa hay (2.6 kcal of DE/g; Table 1) ad libitum during this time (intake was not measured). After the rut, we fed the yearlings only alfalfa hay through winter until parturition. They were closely monitored during parturition, and birth date, birth mass, and calf gender were determined for calves born to these cows.

We determined differences in total growth over summer between the high and medium nutrition levels using a t-test on BM at the end of summer. We also compared differences in BM between pregnant and nonpregnant yearlings for this cohort at 4 time periods: when these cows were 6-month-old calves (late Nov 1996), 10-month-old calves (Mar 1997), yearlings just prior to rut (Sep 1997), and yearlings just after the rut (Nov 1997). We used logistic regression (PROC CATMOD) to model probability of pregnancy as yearlings as a function of BM for each of these 4 time periods. These analyses provided insights particularly regarding influences of summer and autumn nutrition of calves on their probability of pregnancy as yearlings. We included the summer nutrition factor in these regressions to evaluate the combined influences of summer nutrition and BM.

Carry-over Effects of Summer-Autumn Nutrition and Parturition Date

Winter survival of cows and fetuses.—During the final winter of the study (1997–98), we evaluated influences of summer-autumn nutrition, autumn condition, and winter nutrition of cows on probability of winter survival of cows and their fetus. Our original intent with this experiment was to bolster understanding of carry-over effects of summer-autumn nutrition on fetal survival, but it provided data more useful for identifying carry-over effects on cow survival.

Lactating cows used in the summer-autumn experiment of 1997 that re-bred during the rut (1997), and all cows that were nonlactating but became pregnant over the same period, were used for this experiment. We placed cows that were lactating the previous summer-autumn on the same winter diet fed the previous 2 winters, which we hereafter refer to as the "winter-high" nutrition level. Pregnant cows that were not lactating the previous summer-autumn ($n = 21$) were randomly assigned to 2 winter nutrition groups, a low nutrition level designed to induce rapid weight loss and a medium nutrition level that was intermediate between the low and high levels (Table 2). This provided 4 treatment groups: (1) lactating and fed high nutrition in summer-autumn and fed high nutrition in winter (SHWH); (2) lactating and fed medium nutrition in summer-autumn and fed high nutrition in winter (SMWH); (3) nonlactating in summer-autumn and fed medium nutrition in winter (SNWM); and (4) nonlactating in summer-autumn and fed low nutrition in winter (SNWL) (the latter 2 groups of cows were fed alfalfa hay ad libitum through summer and autumn). We chose not to randomly assign summer-lactating cows to the winter nutrition groups, so that feeding of the cows lactating in the previous autumn was identical each winter of the study.

We analyzed in 2 stages effects of winter and summer nutrition on winter survival of cows during the final winter of the study. First, 1-way, repeated measures ANOVA was used to identify differences in rates of declining condition, loin thickness, and BM from early, mid-, to late winter (thus the interaction between each of these factors and time was of interest) among the 4 treatment groups identified above. Least squares means were used to identify when these groups differed. Second, because 1 cow died and 5 more were removed from the study to prevent death, we were able to model probability of winter survival based on winter nutrition level and beginning nutritional condition. We used logistic regression to predict (1) probability of surviving from mid-December through early March as a function of late-autumn nutritional condition and winter nutrition and (2) probability of surviving from mid-February through early March as a function of mid-February condition and winter nutrition.

Table 2. Dry matter (g of DM/kg $BM^{0.75}$) and digestible energy (kcal of DE/kg $BM^{0.75}$) feeding levels and strategies for 3 nutrition treatment groups (high, medium, and low) of cow elk, northeastern Oregon, winter 1997–98.

Date	Feeding strategy	High		Medium		Low	
		DM	DE	DM	DE	DM	DE
13 Nov	Maintenance	82	195	82	195	82	195
27 Dec	Begin treatment	51	121	44	105	36	84
28 Jan	Adjust treatment	47	112	40	95	33	79
19 Feb	Adjust treatment	37	87	31	74	26	61
27 Feb	Adjust treatment	47	112	40	95	33	79
06 Mar	End treatment	67	159	67	159	67	159
18 Mar	Ad libitum	90	212	90	212	90	212
05 Apr	Ad libitum	100	308	100	308	100	308
13 Apr	Ad libitum	105	325	105	325	105	325

Calf winter survival.—Our intention for this work was to evaluate the influences of birth date and summer-autumn nutrition on the ability of calves to survive during winter (i.e., test the hypothesis that larger calves have a greater probability of surviving winter). We conducted 2 of these experiments, 1 each winter of the study.

We simulated harsh winter conditions by feeding calves diets markedly below levels required for maintenance from mid-December until mid-March. In early December, all calves were individually fed identical diets of moderate quality that initiated a period of transition from the summer-autumn nutrition treatments to the overwinter submaintenance diets. At the end of the transition, we reduced feeding level to induce BM loss at a level that would guarantee virtually 100% "mortality" of the calves at winter's end. We based this level on experience gained during submaintenance feeding experiments in other studies (Cook et al. 1998). We used 2 variations of this approach (Table 3). In the first winter (1996–97), feeding level was stepped down gradually, mimicking winters in which harshest conditions occur relatively late in winter (i.e., late Feb and early Mar). In the second winter (1997–98), feeding level was dropped more abruptly early, thereby mimicking winters in which harsh conditions occur early and persist throughout winter. We fed calves all food individually in the barns, so that the

Table 3. Daily levels of pellet and hay dry matter, digestible energy (DE), and crude protein (CP) fed to elk calves in winter survival experiments of 1996–97 and 1997–98, northeastern Oregon. All values are expressed on a dry-matter basis per kg of $BM^{0.75}$.

	Dry matter (g)				
Year/Date	Total	Pellets	Hay	DE (kcal)	CP (g)
1996–97					
4 Dec	61.0	33.6	27.4	170	9.2
10 Dec	50.0	30.0	20.0	140	7.5
27 Dec	45.0	26.5	18.5	126	6.8
17 Jan	40.0	23.7	16.3	112	6.0
10 Feb	35.0	20.7	14.3	98	5.3
18 Feb	30.0	17.7	12.3	84	4.5
9 Mar	25.0	14.8	10.3	43	3.8
1997–98					
7 Dec	61.0	24.4	36.6	148	9.2
11 Dec	45.0	26.9	18.1	106	6.8
19 Dec	40.0	20.0	20.0	95	6.0
30 Dec	35.0	17.5	17.5	83	5.3
15 Jan	30.0	15.0	15.0	72	4.5

complete diet of each calf was strictly controlled. We fed each calf identical dry-matter and DE/kg $BM^{0.75}$. Calves typically required 4 hours in the barn to consume all food offered (once-per-day feeding).

The primary response variable used to judge the influence of prior birth date and nutrition on winter survival was the number of days of winter "survived." We retained calves in the experiment to the point where death was imminent, proclaimed "dead" for the purposes of the study, and then moved to different pens to allow recovery.

Identifying this point was somewhat subjective, but we found in earlier studies (Cook et al. 1998) that elk calves become lethargic, hypoglycemic, and hypothermic near death, and that these signs generally occur at about 20% BM loss. To prevent unwarranted mortality, we developed the following criteria to identify the point at which death was imminent:

1. Any calf was removed if mass loss was ≥25% (we found that calves rarely reached this level and so continuing with them was pointless).
2. For mass loss ≥22%, calves were removed if (a) rectal temperature was ≤38.3°C (~38.8–38.9° is normal), or (b) any evidence of weakness was evident (reluctance to stand when approached, unsteady or wobbly gait, or "glazed" appearance in eyes).
3. For mass loss of 19–21%, calves were removed if (a) temperature was ≤38.1°C, or (b) weakness was clearly evident.
4. For mass loss of 15–18%, they were removed if there was clear evidence of weakness, particularly if temperature was ≤38.6°C and rectal temperature could be obtained with little or no resistance from the calf. (Nearly all of these dam-reared calves stridently resisted handling when in good physical condition; thus we considered lack of resistance a good indication that the calf was seriously debilitated).

We weighed calves once each week and once each day as status became more critical. We measured rectal temperature in the morning; temperature later in the day was less indicative of susceptibility to nocturnal hypothermia.

We began the winter submaintenance diets on 11 December and terminated them 100 days later on 20 March, even if all calves had not been removed from the study. Rate of mass loss, calculated from the time the experiments began until calves were removed from the study, also provided useful insights regarding calf tolerance to winter conditions. We first calculated average total percent mass loss, rate of mass loss (percent per day), and number of days of winter survived by gender, to look for potential confounding by calf gender. We evaluated rate of mass loss as a function of beginning BM and calf gender using ANCOVA, and eliminated gender as a variable in the analysis if no significant influences were found. We used polynomial regression to model nonlinear relations. Finally, we identified effects of summer-autumn nutrition and birth date of the calves using 2-factor ANOVA. Data for each winter were analyzed separately, because the nutritional regimes were markedly different (Table 3).

Calf birth characteristics and gestation length.—We evaluated birth date, birth mass, and gestation length as a function of summer-autumn nutrition and parturition date of the cow the previous year, winter nutrition (final winter only), and nutritional condition of autumn and winter the previous year.

We determined birth date by close observation. Neonates were first captured and weighed the second day after birth, when 1 day old, to facilitate bonding between mother and calf. For the first 2 cohorts of calves, exact gestation length was unknown because exact conception dates were unknown. Direct observations of breeding, which we assumed to be analogous to date of conception, during the final breeding season of the study provided a basis to calculate gestation length for the third cohort.

We conducted analyses to identify variables that influenced birth mass, parturition date, and gestation length. We evaluated birth mass of spring 1997 and 1998 as a function of (1) previous-year summer-autumn nutrition and previous-year parturition date, and (2) nutritional condition the previous autumn. The former, plus calf gender, was evaluated with 3-factor ANOVA and the latter, again with gender, was evaluated using ANCOVA. We also used ANCOVA to evaluate relations between birth mass and change-in-condition during the cow-fetal winter survival experiment. We conducted this analysis using data from the 21 cows in the cow-fetal winter survival experiment that were fed the medium and low winter nutrition treatments during winter 1998. Because these cows were not lactating the previous autumn, we could not examine carry-over effects of previous-year summer-autumn nutrition and previous-year parturition date. Calf gender, and the interaction between gender and condition-change, also were included in this ANCOVA.

Influences on parturition date and gestation length were identified in 3 steps. First, we used 3-factor ANOVA to evaluate relations between parturition date and previous-year summer-autumn nutrition and previous-year parturition date. We included "year" as the third factor, because we combined data from the parturition period of 1997 and 1998 in this analysis. Second, for those cows in which gestation length could be directly calculated (1998 data only), we identified effects of previous-year summer-autumn nutrition and previous-year parturition date using 2-factor ANOVA. All possible interactions were included in both ANOVAs. Third, for those cows not lactating in autumn of 1997, included in the cow-fetal winter survival experiment of 1998, and for which conception dates were not determined, we used parturition date (of spring 1998) as a surrogate of gestation length based on the assumption that conception dates were approximately equal (all these cows were in good condition and nonlactating during the rut). We regressed parturition date with the overwinter decline in body condition.

RESULTS

Weather

We collected weather data from October 1995 through January 1998 (Table 4). We intended to collect data through spring 1998, but technical difficulty with the recording equipment, not evident at the time, prevented data collection after January.

Table 4. Monthly means ± SE of daily average, maximum, and minimum temperature (°C) for elk study area, northeastern Oregon, October 1995 to January 1998.

	1995			1996			1997			1998		
Month	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min
Jan				–3.3±1.1	0.0±1.0	–6.3±1.3	–2.9±0.8	0.7±0.7	–6.2±1.0	–4.1±1.0	–1.2±1.2	–6.4±1.0
Feb				–2.0±1.3	3.7±1.3	–6.4±1.4	–1.7±0.7	3.3±0.6	–5.7±0.8			
Mar				1.6±0.6	6.9±0.8	–2.5±0.7	1.4±0.7	6.2±0.9	–2.6±0.6			
Apr				5.0±0.7	10.8±0.9	0.2±0.6	3.0±0.7	8.5±0.9	–1.7±0.7			
May				6.4±0.6	11.4±0.6	1.9±0.7	9.4±0.8	14.8±1.0	4.0±0.7			
Jun				12.2±0.3	18.1±0.8	5.7±0.6	11.6±0.5	17.3±0.6	6.1±0.5			
Jul				18.6±0.8	25.2±0.8	11.4±0.8	15.9±0.6	22.4±0.7	9.1±0.5			
Aug				17.7±0.8	24.8±1.0	10.6±0.7	18.0±0.5	24.6±0.6	11.0±0.4			
Sep				11.1±0.8	17.8±1.0	5.1±0.7	13.5±0.8	19.6±0.9	8.4±0.8			
Oct	4.7±0.7	9.8±0.9	0.5±0.6	8.0±1.5	14.5±2.0	3.1±1.2	5.3±0.6	10.7±0.8	1.1±0.5			
Nov	3.2±0.7	7.1±0.7	0.2±0.8	–0.6±0.6	1.3±0.5	–2.3±0.9	2.2±0.5	6.7±0.7	–0.8±0.5			
Dec	–1.9±0.6	1.4±0.6	–4.8±0.7	–1.8±0.6	1.3±0.7	–4.6±0.7	–2.4±0.5	0.5±0.6	–5.1±0.6			

Temperature during June through October averaged 13.5°C in 1996 versus 12.9°C in 1997, indicating similar regimes during both summer-autumn experiments. Temperature during December through February of 1995–96, 1996–97, and 1997–98 averaged –2.4, –2.1, and –3.3°C. Average daily and minimum temperatures were similar during both calf survival experiments of the latter 2 winters (Table 4). Moreover, temperatures during summer and winter throughout the entire study were within ranges typical for this area (see Cook et al. 1998).

Harsh winds were infrequent during all seasons. During both summer-autumn periods, average wind speed was 1.3 m/s and average maximum wind speed was 2.8 m/s.

Autumn-Spring Body Mass Dynamics

During the first fall and winter of the study (1995–96), BM of cows varied among early- and late-bred and pregnant and non-pregnant cows, despite identical rations offered to all (Fig. 4A). Before feeding was restricted in late December, non-pregnant cows tended to lose mass, whereas pregnant cows tended to gain mass, particularly in late autumn. Early-bred cows tended to gain more mass than did late-bred cows. Both patterns probably reflected accretion dynamics of uterine and fetal tissues.

Initiation of restricted feeding in December (1995) induced mass loss among all groups by early January, and mass loss continued to differ among groups (Fig. 4A). Pregnant cows lost 5–7% whereas open cows lost 9–11% of their mass between December and March, and early-bred cows tended to be heavier than late-bred cows during winter, despite being fed the same amount of identical rations. Accretion patterns of uterine and fetal tissues probably accounted for these differences. During the second winter of the study, there was little evidence of an effect of early and late breeding on mass dynamics, but a difference between pregnant and non-pregnant cows was evident (Fig. 4B). Non-pregnant cows lost 3–4% of their mass by mid-December and lost 10–11% by early March, approximately twice that of pregnant cows.

The third trimester in springs of 1996 and 1997 was marked by pronounced increases in BM as fetal mass increased (Fig. 5).

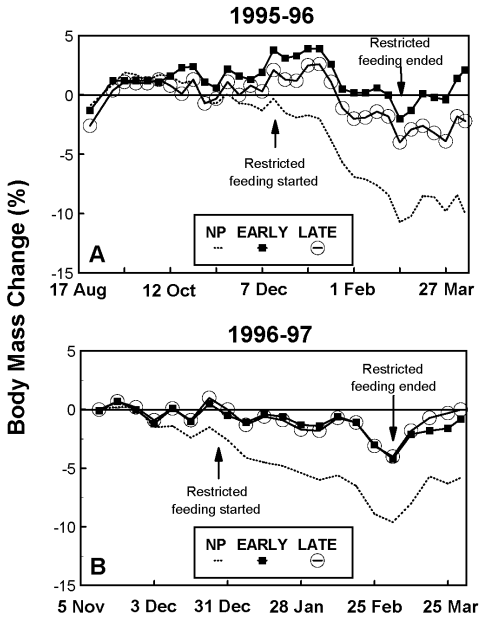

Figure 4. Body mass dynamics of elk cows during autumn through winter of 1995–96 (A) and during late autumn through winter 1996–1997 (B), northeastern Oregon. Category codes are: NP = nonpregnant; EARLY = early-bred treatment group; LATE = late-bred treatment group. Restricted feeding was set to reduce body mass 10% during winter; dry matter and digestible energy levels were as described for the "high" winter nutrition treatment presented in Table 2.

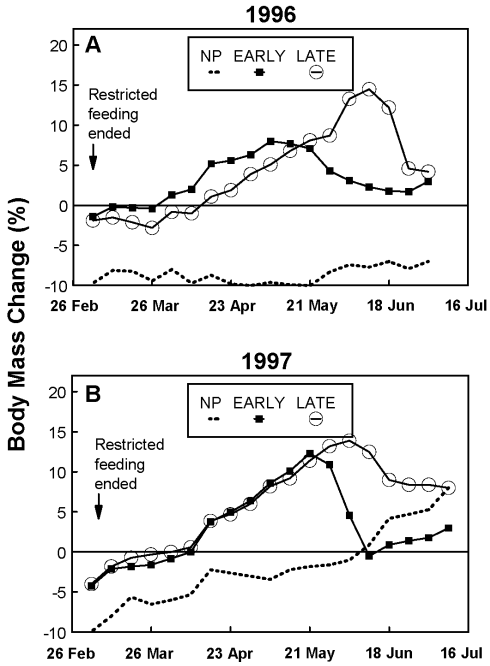

Figure 5. Body mass dynamics of elk cows during spring 1996 (A) and 1997 (B), northeastern Oregon. Category codes are: NP = nonpregnant; EARLY = early-bred treatment group; LATE = late-bred treatment group.

Differences were apparent between early- and late-bred cows in 1996, but not in 1997. Both groups increased mass 10–15% between early March and the birthing period, indicating rapid increases in fetal and uterine mass. In 1997, late-bred cows ended the parturition period several percentage points of mass higher than early-bred cows (Fig. 5B), perhaps suggesting some compensation for late parturition. Non-pregnant cows increased BM during spring in 1997, but failed to do so in spring 1996, reflecting a different feeding strategy (maintenance in 1996, ad libitum feeding in 1997) between the 2 years.

Direct Effects of Summer-Autumn Nutrition and Parturition Date

Breeding in fall 1995 produced 44 pregnant cows of the 57 placed with the bull; 31 2.5-year-old and 13 4.5-year-old cows bred. The 13 failures perhaps were due to lingering effects of porcine zona pellucida in previous experiments (Garrott et al. 1998), obesity in few cases, and permanent infertility in 2 cases. The subsequent spring, 2 small calves (<10 kg) were too weak to stand and nurse and were abandoned by their mothers 4–6 hours after birth, probably a function of low birth mass (Thorne et al. 1976). Another calf developed an umbilicus infection and was removed for veterinary care. Thus, 41 cows and calves were available for the experiment (Table 5). The induced breeding dates produced 2 parturition periods, ranging from 12 May through 10 June ($\bar{x}$ = 26 May ± 1.8 days [SE]) for the early-bred group, and 11 June through 29 June ($\bar{x}$ = 19 Jun ± 1.2 days) for the late-bred group.

Breeding during fall of 1996 produced 36 pregnant cows. Most of the cows in the low nutrition group of the previous autumn failed to breed, leaving a smaller sample size to evaluate summer-autumn nutrition influences in 1997 compared to that in 1996. Of the calves born in spring, 1997, 3 were abandoned and 3 died due to disease. Cows were split 50:50 into the early and late parturition-date categories at the end of parturition and randomly assigned to high, medium, and low nutrition levels. Of the cow-calf pairs used for the 1997 summer-nutrition experiment, parturition date of the early-bred group ranged from 20 May-9 June ($\bar{x}$ = 1 Jun ± 2.5 days) and 10 June through 8 July ($\bar{x}$ = 20 Jun ± 3.5 days) for the late-bred group (Table 5).

In both years, food was of higher quality than we anticipated, and fed diets averaged slightly higher in DE content than our targets (Fig. 3B). In 1996, all elk began the experiments consuming diets of 3.0 kcal of DE/g of food. The high nutrition level was held constant at 3.0 kcal/g until the end of the experiment (early Nov), the medium level was reduced to 2.7, and the low level to 2.3 (Fig. 3B). In 1997, elk began experiments consuming diets of 3.0 and then were reduced to 2.9 kcal of DE/g. The high nutrition group was fed this level until the end of the experiment, the medium group was reduced from 2.9 to 2.7 kcal of DE/g, and the low group from 2.9 to 2.3 kcal of DE/g.

Body mass dynamics of cows.—Nutrition treatments were initiated on 21 June; we analyzed BM dynamics of cows starting 25 June. Change-in-mass estimates indicated considerable influences of nutrition on BM dynamics of cows over summer (Fig. 6A). The initial repeated measures ANOVA indicated influences of calf gender ($P = 0.062$ [time × gender interaction effect]) and cow age ($P = 0.063$); no higher order interactions approached significance ($P \geq 0.54$). Mass gain of younger cows and cows with female calves was greater, or declined more slowly, than cows with male calves. Calf gender was an important confounding influence on parturition date and nutrition effects, because gender ratios varied markedly among the 6 treatment groups (Table 5). We therefore adjusted the data to remove effects of calf gender using the equation of Fig. 7A. This equation provided a time-specific adjustment (reflecting the time × gender interaction) that was equal across all treatment groups (reflecting no significant higher order interaction with gender) such that gender effects were removed (i.e., BM of cows with male calves was adjusted "up" as though they had given birth to female calves). We did not further complicate the data set by removing the cow age effect (Fig. 7B), because distribution of cow ages among the treatment groups was approximately equal (our initial randomization was designed to do this).

Table 5. Characteristics of elk cows and calves within treatment groups at the start of the 1996 and 1997 summer-autumn nutrition and parturition-date experiments, northeastern Oregon. Means of calf birth mass and birth date are presented for each treatment group.

		Number[b] of cows by birth year		Cow body[c] mass (kg)		Calf characteristics				
						Gender		Birth mass (kg)		
Year	Treatment[a]	1991	1993	Mean	SE	Male	Female	Mean	SE	Birth date
1996	EPHN	2	6	206.0	7.0	5	3	15.3	0.8	30 May
	EPMN	2	5	207.6	8.3	2	5	14.9	0.7	23 May
	EPLN	1	6	207.4	3.3	0	7	14.7	0.6	25 May
	LPHN	2	4	212.8	5.3	4	2	16.0	0.3	21 Jun
	LPMN	1	5	217.9	9.6	4	2	16.0	1.0	21 Jun
	LPLN	2	5	219.1	4.7	5	2	16.1	0.7	16 Jun
1997	EPHN	2	4	221.8	5.6	1	5	15.4	0.4	01 Jun
	EPMN	3	3	216.9	8.6	4	2	17.1	0.7	02 Jun
	EPLN	1	5	231.2	10.6	2	4	15.8	0.9	31 May
	LPHN	1	3	240.3	7.8	1	3	16.9	0.6	18 Jun
	LPMN	2	2	213.4	8.5	2	2	16.1	1.2	18 Jun
	LPLN	2	2	230.5	13.4	2	2	15.3	1.6	25 Jun

[a] Treatment groups are: EPHN = early parturition, high nutrition; EPMN = early parturition, medium nutrition; EPLN = early parturition, low nutrition; LPHN = late parturition, high nutrition; LPMN = late parturition, medium nutrition; and LPLN = late parturition, low nutrition.

[b] Birth year of cows.

[c] Body mass within 4 days after parturition.

With adjustments for calf gender, both nutrition and parturition date significantly influenced cow BM dynamics over summer and fall ($P < 0.001$ and $P = 0.010$, time × factor interactions). The 3-way interaction was not significant ($P = 0.304$), indicating that the relative influences of parturition date and nutrition were constant across time. Higher nutritional quality and earlier parturition date enhanced mass gain by cows; the magnitude of the nutrition effect was considerably greater than that of the parturition date effect (Fig. 6B). Body mass of cows on different nutritional treatments diverged within several weeks of implementing the nutrition treatments, when relatively small differences occurred in dietary quality. Divergence continued through August among treatment groups. After September, differences among treatment groups remained approximately constant through October.

In 1997, similar patterns emerged despite the smaller sample size (Fig. 8A). The initial analysis indicated no evidence of confounding by cow age and calf gender ($P \geq 0.25$ for interaction terms that included these 2 variables). However, potential confounding was evident for previous-year nutrition ($P = 0.025$, time × previous-year nutrition). Its effect was independent of nutrition and parturition date because there were no significant higher-order interactions. Cows in the previous-year medium and low nutrition groups gained more mass or lost less mass than cows fed the high nutrition level the previous year, suggesting accelerated anabolism to compensate for greater mass loss the previous year. Because cows with differing nutrition levels in 1996 were unequally distributed among the parturition date-summer nutrition treatment groups of 1997, we adjusted the 1997 data to remove the effects of previous-year summer nutrition using the equation of Fig. 9.

With adjustments for previous-year nutrition level, cow BM dynamics in 1997 were significantly related to summer-autumn nutrition ($P = 0.001$) and parturition date ($P = 0.001$) (Fig. 8B). Magnitude of the nutrition effect was greater than that of the parturition date effect, except that cows in the late parturition, high nutrition group gained no more mass than either medium nutrition group much of the summer (but see the nutritional condition data presented below).

Nutritional condition of cows.—Condition, based solely on BCS in autumn of 1996,

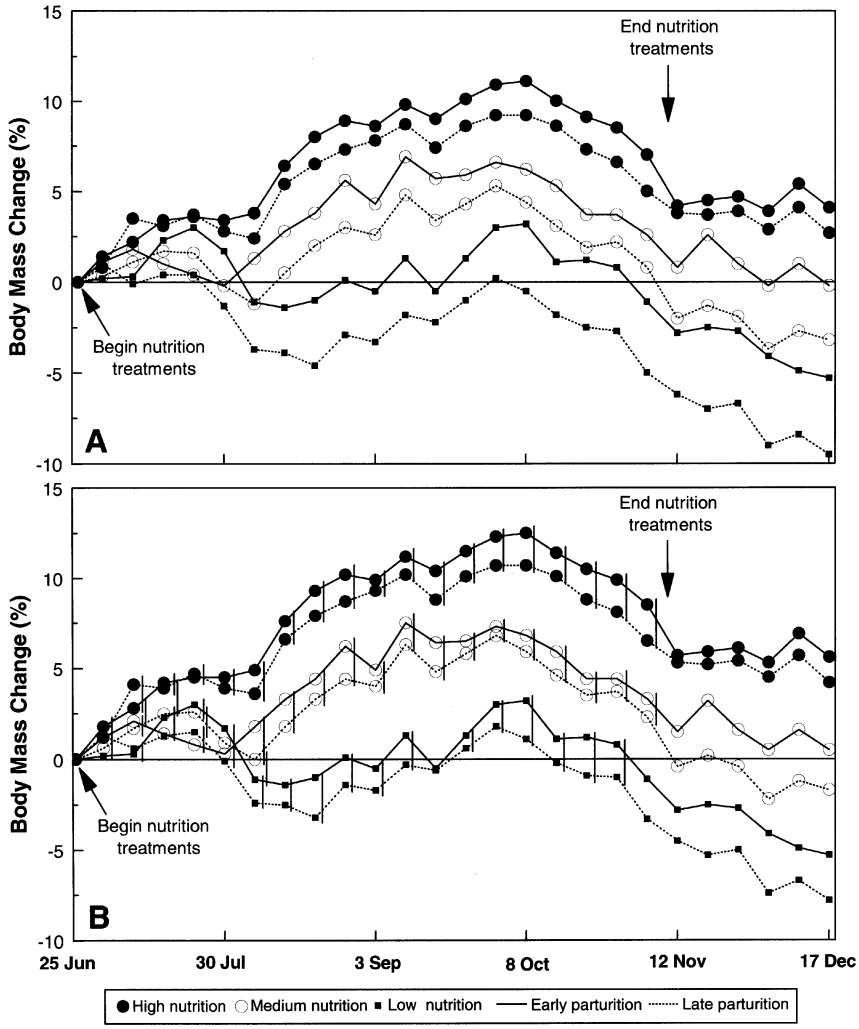

Figure 6. Body-mass dynamics of lactating elk during summer and autumn 1996, northeastern Oregon, across 3 levels of summer-autumn nutrition and 2 levels of parturition date. Graph A presents original data with no correction to remove effect of calf gender; data in graph B were adjusted to remove this effect. In graph B, percent changes in body mass not connected by vertical lines differ significantly ($P \leq 0.05$) within weekly periods.

varied markedly among nutrition groups ($P < 0.001$) and tended to vary among parturition date groups ($P = 0.058$) (Fig. 10). Cows in the high nutrition group averaged 14–15% body fat, compared to 10% in the medium group and 6–8% in the low group. Cows giving birth early had 1–3% more body fat than those giving birth late.

Condition in autumn 1997, based on ultrasound and BCS (Fig. 11) also was significantly influenced by summer-autumn nutrition ($P < 0.001$), but was unaffected by parturition date ($P = 0.46$). The magnitude of nutrition's influence evidently was greater the second year than the first (Fig. 11).

Breeding dynamics.—Our ability to simultaneously test influences of parturition date and summer-autumn nutrition on pregnancy was hindered by small sample sizes, yet analyses indicated important trends. In 1996, nearly all cows in the high and medium nutrition groups but only 25% of those in the low nutrition group became pregnant (Fig. 12). Logistic regression indicated that nutrition affected pregnancy probability ($P < 0.001$), but parturition date did not ($P = 0.92$). However, conducting this analysis required combining the high and medium

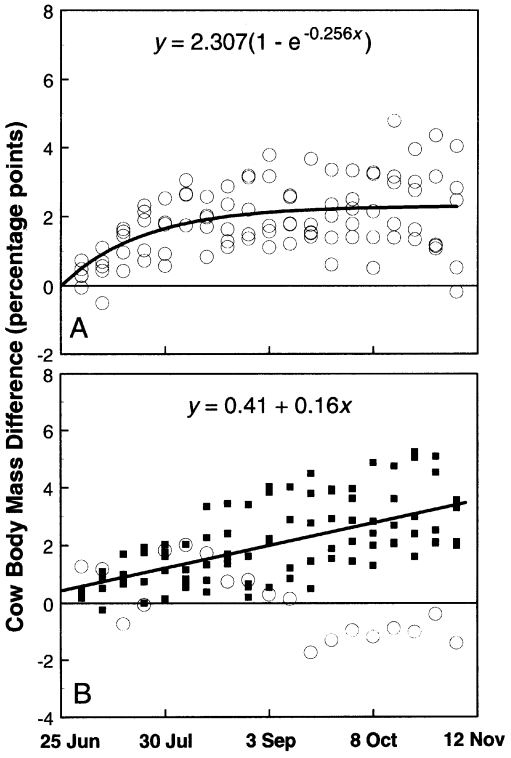

Figure 7. In graph A, observed differences in percent body mass of cow elk with female calves and those with male calves during summer and autumn 1996, northeastern Oregon. Data points were calculated as percent change in body mass of cows with females minus percent change in body mass of cows with males, within the nutrition-parturition date groups each week of the experiment. Thus, positive values indicate cows with female calves gained more, or lost less mass, than cows with male calves. The nonlinear equation describes this gender effect; the independent variable is number of weeks past 25 June. In graph B, observed differences in percent body mass change of 3-year-old and 5-year-old cows. Positive values indicate younger cows gained more, or lost less mass, than older cows, within nutrition-parturition date groups each week of the experiment. The linear equation describes the effect of cow age on their body mass changes; x is the number of weeks past 25 June. This equation was developed using data indicated by solid squares; data indicated by the open circles are from a treatment group (high nutrition, late parturition) that appeared anomalous and thus were treated as outliers for developing the equation.

nutrition groups, because the number of response functions was greater than the number of responses (1) in the high nutrition group (e.g., all cows bred). The chi-square test for each effect provided similar results (nutrition: $\chi^2 = 19.0$, df = 2, $P < 0.001$; parturition date: $\chi^2 = 0.09$, df = 1, $P = 0.76$) (conducted independently rather than simultaneously because of inadequate sample sizes). Because of the smaller sample size in 1997 ($n = 30$) than in 1996 ($n = 41$), we conducted only chi-square tests of each factor (Fig. 13). Summer-autumn nutrition affected pregnancy probability ($\chi^2 = 21.03$, df = 1, $P < 0.001$) whereas parturition date did not ($\chi^2 = 0.944$, df = 1, $P = 0.33$).

Probability of pregnancy increased as nutritional condition increased during both years ($P < 0.008$) (Fig. 14). Elk showed a threshold of condition (8–10% body fat, 1.9–2.1 Mcal/kg of GE), below which probability of pregnancy declined rapidly. Cows with <5% body fat or <1.6 Mcal/kg of GE had little probability of pregnancy (Fig. 14).

Timing of conception was similarly affected. In autumn 1996, all cows in the high nutrition group were pregnant by mid-October, compared to about 70% in the medium nutrition group.

The few cows that successfully bred in the low nutrition group did so even later than cows in the medium group (Figs. 12 and 13). Summer-autumn nutrition significantly influenced date of conception ($\chi^2 = 14.95$, df = 4, $P = 0.005$), but parturition date did not ($\chi^2 = 1.57$, df = 2, $P = 0.46$), although there was a trend of earlier conception of cows in the high and medium nutrition groups that gave birth early.

Observed breeding of individual cows in autumn 1997 allowed simultaneous comparison of nutrition versus parturition date on breeding date using ANOVA. As in 1996, summer-autumn nutrition significantly influenced breeding date ($P < 0.001$) whereas parturition date did not ($P = 0.22$), nor was the interaction between parturition date and nutrition significant ($P = 0.67$). Breeding date was nonlinearly related to both our measures of body condition. Above about 13% body fat, breeding date was insensitive to fat (Fig. 15).

Summer-autumn performance of lactating versus nonlactating cows.—Before the summer-autumn nutrition treatments began, nutritional condition of nonlactating and lactating treatment groups were similar (Fig. 16A). Nevertheless, considerable divergence occurred by mid-autumn ($P < 0.001$), but the differences occurred only among nutrition treatment groups of lactating cows. Both the low and high nutrition groups of nonlactating cows achieved a high level of condition equivalent to that of the high

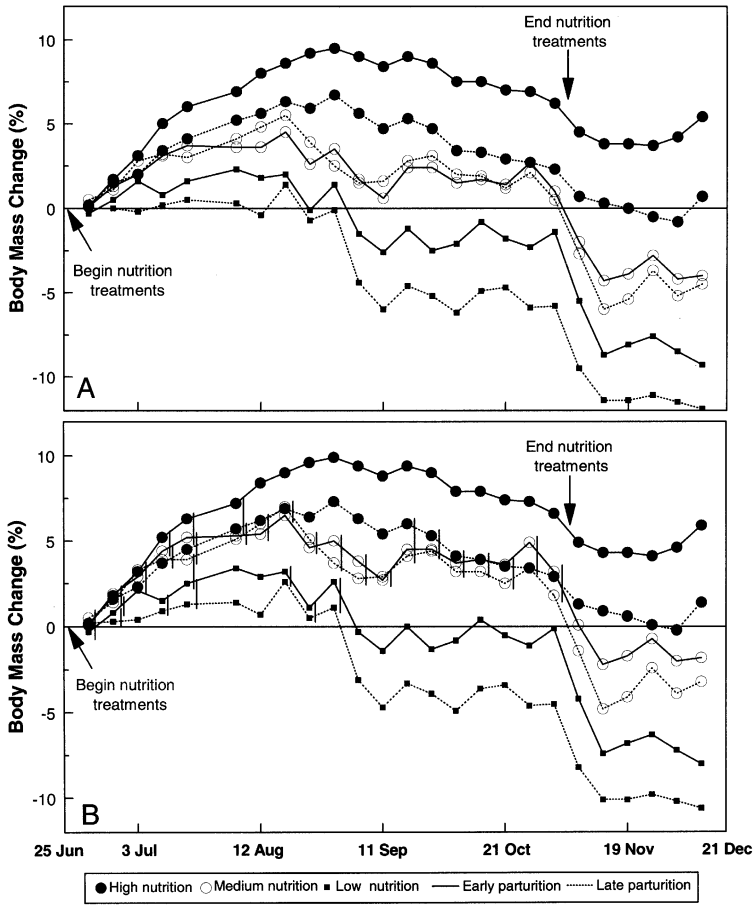

Figure 8. Body-mass dynamics of lactating elk during summer and autumn 1997, northeastern Oregon, across 3 levels of summer-autumn nutrition and 2 levels of parturition date. Graph A presents original data with no correction to remove effect of previous-year's nutrition treatment; data in graph B were adjusted to remove this effect. In graph B, percent changes in body mass not connected by vertical lines differ significantly ($P \leq 0.05$) within weekly periods.

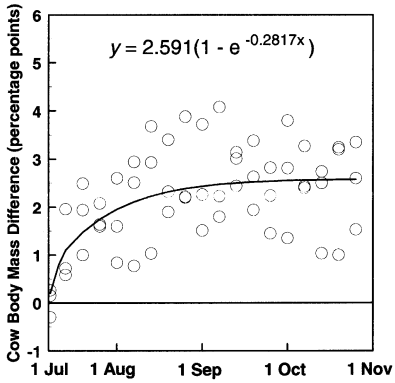

Figure 9. Observed differences in percent body mass change of cow elk during summer and autumn 1997 caused by previous year's (1996) summer-autumn nutrition treatment, northeastern Oregon. Data points were calculated as percent body mass change of elk in 1997 that were in the medium nutrition group of 1996 minus percent body mass change of elk in 1997 that were in the high group in 1996, within the nutrition-parturition date groups of 1997 for each week of the experiment. Thus, positive values indicate those cows in the medium nutrition group during summer-autumn in 1996 gained more mass, or lost less mass in 1997, than did those cows in the high nutrition group during summer-autumn in 1996. Values of the independent variable in the equation are number of weeks past 1 July.

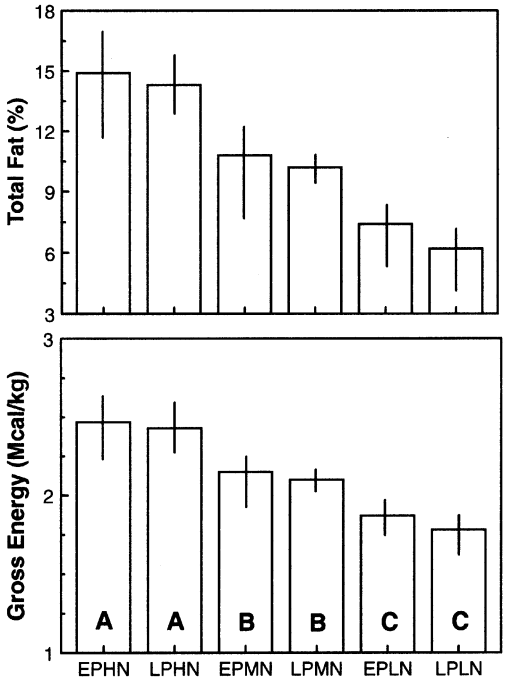

Figure 10. Nutritional condition of lactating elk near the end of the breeding season of 1996 across 3 levels of summer-autumn nutrition and 2 levels of parturition date, northeastern Oregon. Vertical lines indicate ranges of the data. Vertical bars with different letters differ ($P \leq 0.05$) and apply to both graphs. Total fat and gross energy content of the ingesta-free body were calculated from body condition scores using equations of Cook et al. (2001*a*). Parturition date-nutrition treatment codes are: EPHN = early parturition, high nutrition; EPMN = early parturition, medium nutrition; EPLN = early parturition, low nutrition; LPHN = late parturition, high nutrition; LPMN = late parturition, medium nutrition; LPLN = late parturition, low nutrition.

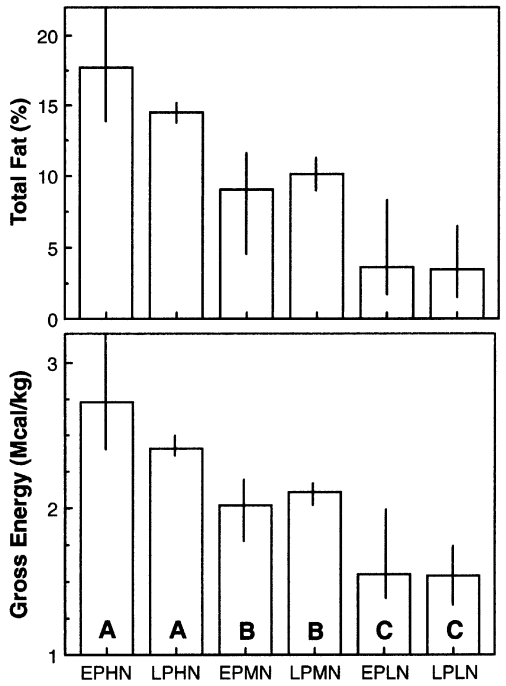

Figure 11. Nutritional condition of lactating elk near the end of the breeding season of 1997 across 3 levels of summer-autumn nutrition and 2 levels of parturition date, northeastern Oregon. Vertical lines indicate ranges of the data. Vertical bars with different letters differ ($P \leq 0.05$) and apply to both graphs. Total fat and gross energy content of the ingesta-free body were calculated from LIVINDEX scores (Cook et al. 2001*a*). Parturition date-nutrition treatment codes are: EPHN = early parturition, high nutrition; EPMN = early parturition, medium nutrition; EPLN = early parturition, low nutrition; LPHN = late parturition, high nutrition; LPMN = late parturition, medium nutrition; LPLN = late parturition, low nutrition.

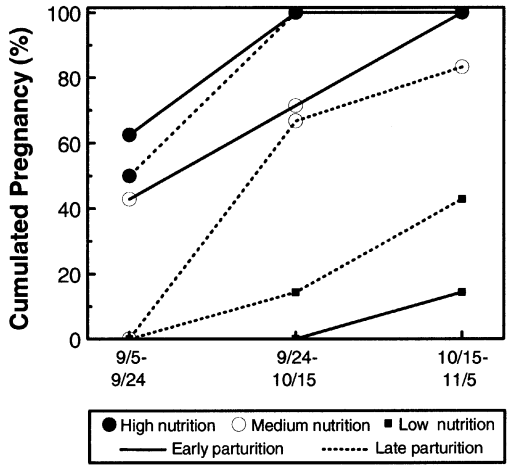

Figure 12. Cumulated pregnancy of lactating elk during the breeding season of 1996 across 3 levels of summer-autumn nutrition and 2 levels of parturition date, northeastern Oregon. Pregnancy status was determined with pregnancy-specific protein B (Noyes et al. 1997).

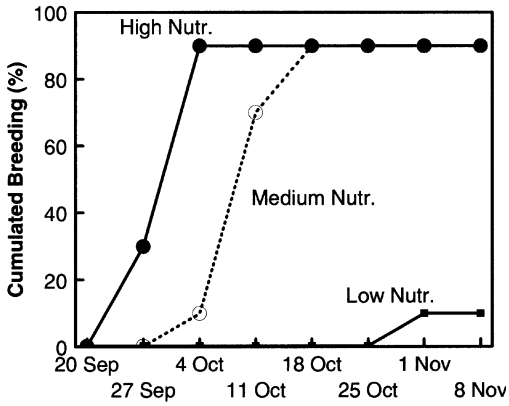

Figure 13. Cumulated breeding status of lactating elk during 1997 across 3 levels of summer-autumn nutrition, northeastern Oregon. Breeding dates were determined by direct observation.

nutrition group of lactating cows (>15% fat), based on both the BCS and LIVINDEX scoring systems (Fig. 16A,B,C).

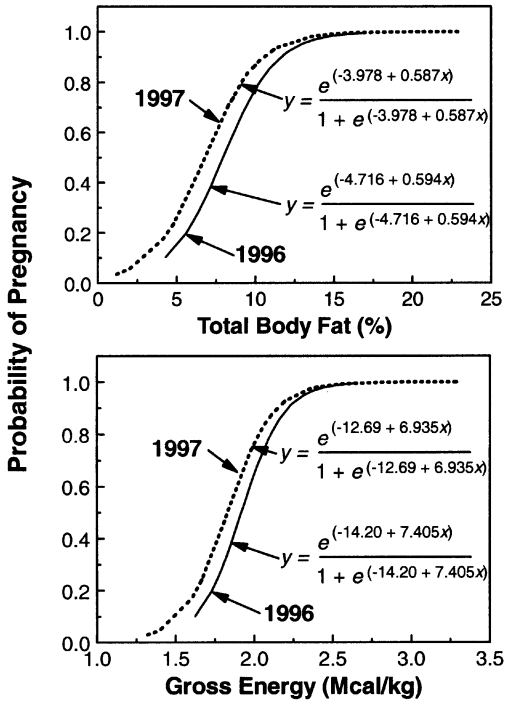

Figure 14. Logistic relations between nutritional condition during the breeding season and probability of pregnancy of lactating elk, 1996 and 1997, northeastern Oregon. Intercept ($P < 0.021$) and slope coefficients ($P < 0.008$) are significant for all logistic regression equations. Total fat and gross energy content of the ingesta-free body were calculated from body condition scores in 1996 and LIVINDEX in 1997 using equations of Cook et al. (2001*a*). For prediction, we recommend the equations for 1997 because they are based on LIVINDEX, a superior index of fat and GE compared to body condition scores.

Calf responses.—In 1996, birth mass of the entire calf crop ($n = 44$) averaged 15.0 ± 0.54 kg; birth date averaged 4 June and ranged from 12 May–29 June. Later-born calves were significantly larger at birth ($y = 3.19 + 0.075x$, where x = calendar day, $r^2 = 0.17$, $P = 0.006$). Twenty-three (52%) of the calves were females; they tended to be smaller than males at birth (14.4 ± 0.48 kg versus 15.6 ± 0.62 kg). However, when calf gender was included with birth date in the ANCOVA, BM at birth was similar between sexes ($P = 0.51$).

Forty-one calves were used for the summer-autumn experiments of 1996. Their mean birth mass was 15.5 kg, and mean mass at birth varied among treatments ≤1.4 kg (Table 5). Calf ages varied ≤7 days among nutrition groups. Calf gender, in contrast, differed markedly among the summer-autumn nutrition treatments (Table 5).

At the time the nutritional treatments were implemented in 1996, calf mass was a

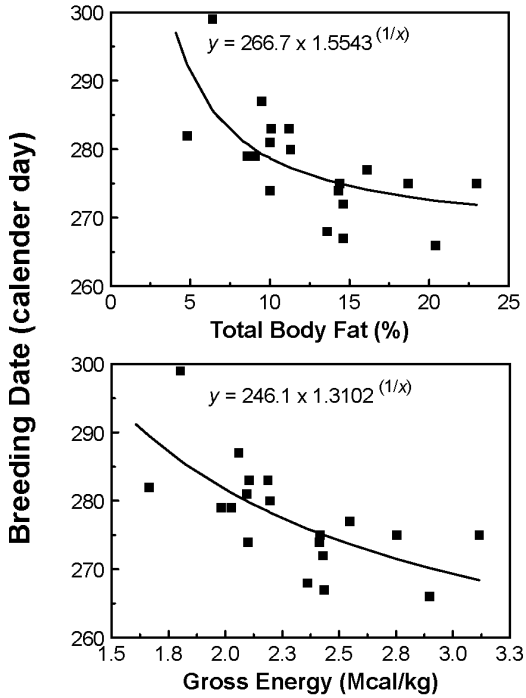

Figure 15. Relations between nutritional condition and timing of breeding by lactating elk, 1997, northeastern Oregon. Total fat and gross energy of the ingesta-free body were calculated from LIVINDEX using equations of Cook et al. (2001*a*). The nonlinear regression routine we used to calculate the curvilinear functions did not provide a coefficient of determination. A linear approximation indicates that $r^2 \geq 0.45$.

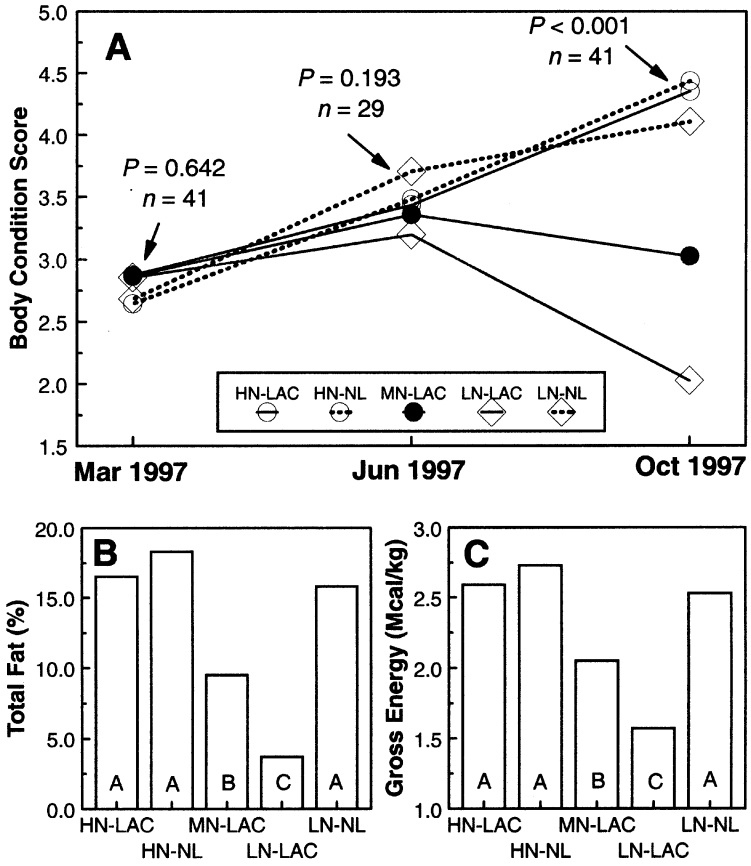

Figure 16. Body condition scores for lactating and nonlactating elk, spring through autumn 1997 (A), northeastern Oregon. The *P* and *n* values relate to 1-way ANOVAs conducted at each time period to identify differences in nutritional condition among cows in different treatment groups. Estimates of total fat (B) and gross energy content (C) of the ingesta-free body for cow elk in October 1997 were calculated from LIVINDEX (Cook et al. 2001*a*). Vertical bars with different letters differ ($P \leq 0.05$). The treatment codes are: HN-LAC = high nutrition and lactating; HN-NL = high nutrition and not lactating; MN-LAC = medium nutrition and lactating; LN-LAC = low nutrition and lactating; LN-NL = low nutrition and not lactating.

predictable function ($r^2 = 0.94$) of birth date ($P < 0.001$) (Fig. 17A) and birth mass ($P < 0.001$): $y = 117.05 - 0.68x_1 + 1.62x_2$, where y = calf mass on 3 July, x_1 = calendar day of birth, and x_2 = birth mass (kg). Adding birth mass into the equation increased the r^2 from 0.85 to 0.94, and residual analysis also indicated an appreciable affect of this variable (Fig. 17B). Body mass on 3 July was unaffected by calf gender or cow age ($P \geq 0.55$).

Response by calves to nutrition and birth date was simultaneously evaluated starting in early July 1996. An initial repeated measures ANOVA indicated an insignificant 5-way interaction between time, nutrition, birth date, cow age, and calf gender ($P = 0.93$). Of all other interaction terms that included either calf gender or cow age, only the 4-way interaction containing calf gender (e.g., time × nutrition × birth date × calf gender) was significant ($P = 0.047$). However, differences in growth between sexes were inconsistent and followed no biologically relevant pattern that we could discern (Fig. 18A). We concluded that gender probably had little potential to confound our analysis of nutrition and birth date effects on calf growth and excluded it from further analysis.

Subsequent analysis indicated a significant ($P = 0.001$) interaction among time, nutrition, and birth date on calf growth between early July and early December 1996 (Fig. 19A,B). Nutrition had a considerable influence on growth. Its effect increased

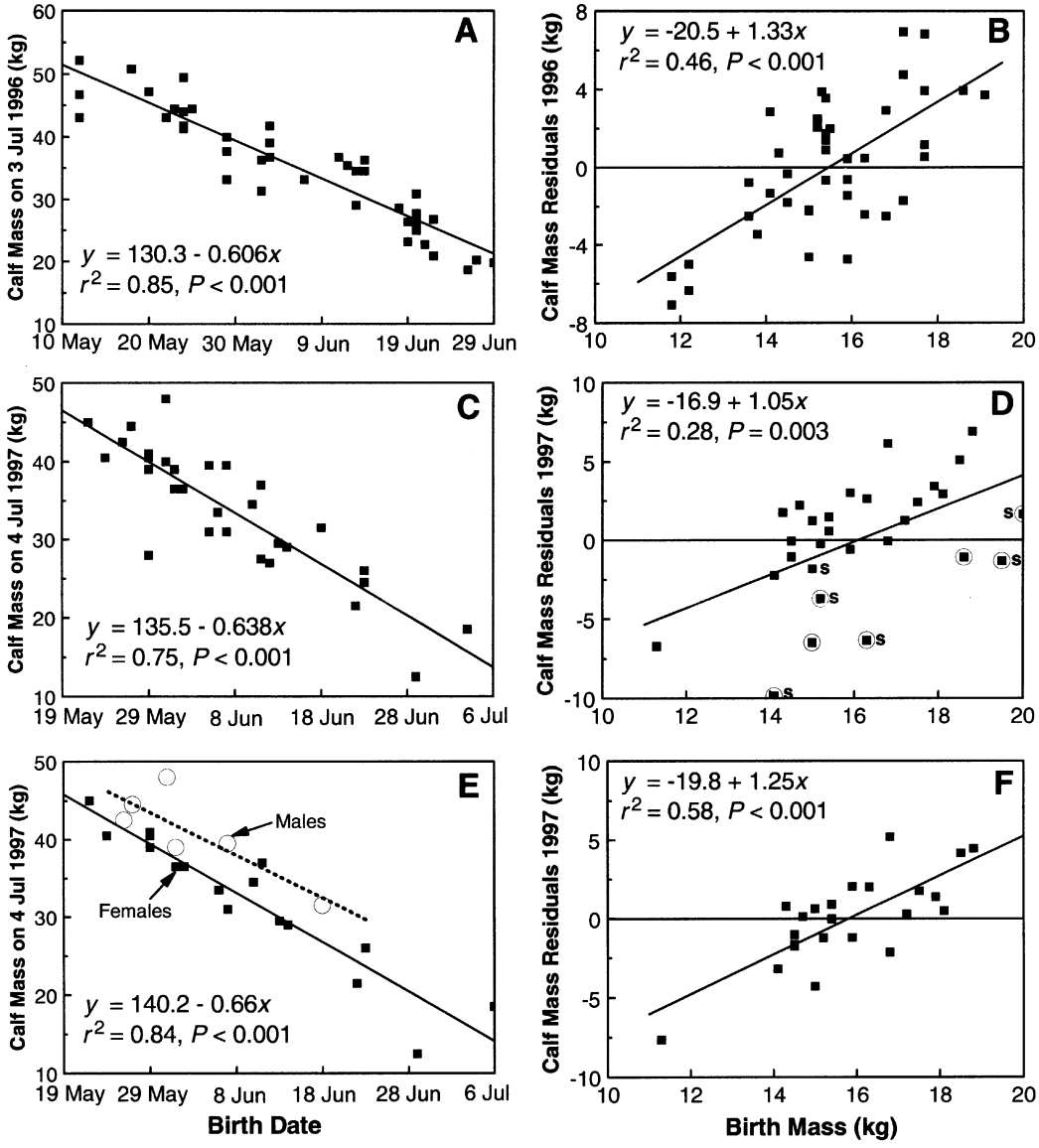

Figure 17. Relations between birth date of elk calves and their body mass at the start of the summer-autumn nutritional treatments in 1996 (A) and 1997 (C,E), northeastern Oregon (x = calendar day). Relations between birth mass and mass at the start of the summer-autumn nutritional treatments, with effects of birth date eliminated through residuals analysis (i.e., the regression for the calf mass-birth date relation was calculated, and resultant residuals were regressed with birth mass) for 1996 (B) and 1997 (D,F). In graph D, the circled data points indicate suspected outliers, nearly all of which were from calves observed to be sick (denoted with an "s") during the neonatal period. All suspected outliers were removed and data re-analyzed with results presented in graphs E and F. A significant gender effect on calf mass resulted from the re-analysis and is illustrated in graph E. The equation of graph E is for both sexes combined.

markedly from mid-summer through autumn, resulting in pronounced differences in BM by late autumn (Fig. 19A). Except for a brief period at weaning, calves in the high nutrition group grew rapidly through autumn. Low-nutrition calves ceased growth by mid-September, and medium-nutrition calves ceased growth by mid-October.

The significant interaction among time, nutrition, and birth date reflected faster growth of some late-born calves. Late-born

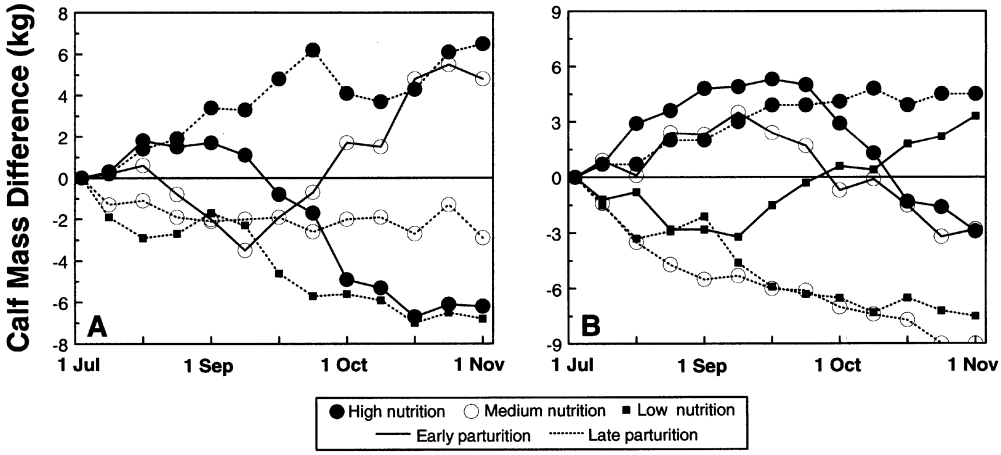

Figure 18. Differences in body mass (BM) between male and female elk calves (i.e., BM of males minus BM of females, within summer-autumn and parturition-date treatment groups each week) in 1996 (A) and 1997 (B), northeastern Oregon. Positive values indicate male calves grew more rapidly than females. These data indicate little evidence of a consistent gender effect on calf growth either year.

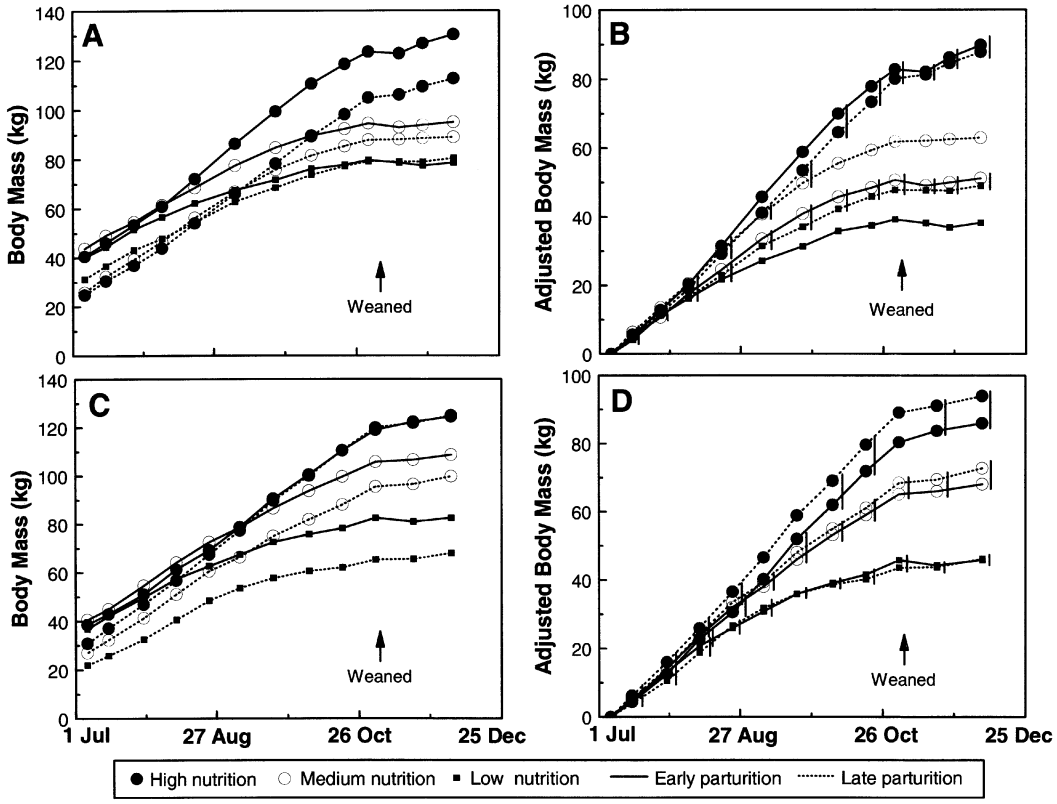

Figure 19. Growth of elk calves during summer and autumn 1996 (A,B) and 1997 (C,D) across 3 levels of nutrition and 2 periods of parturition date, northeastern Oregon. Actual body mass is presented in graphs A and C. In B and D, body mass was adjusted to remove effects of birth date and birth mass occurring during the neonatal period, by subtracting mass at the start of the time period (3 or 4 July) from all subsequent mass estimates. Data values not connected by vertical lines differ significantly ($P \leq 0.05$) within weekly periods.

calves in the low and medium nutrition groups weighed as much by late autumn as did their early-born counterparts. However, late-born calves in the high nutrition group did not catch-up (Fig. 19A,B). Thus the 10–15 kg advantage for early born calves lasted through late autumn only in the high nutrition group.

A final 5-way ANCOVA on unadjusted BM of calves at weaning in mid-November indicated significant effects of nutrition ($P < 0.001$), birth date ($P < 0.001$), birth mass ($P < 0.001$), and insignificant effects of gender ($P = 0.24$) and cow age ($P = 0.75$). The interaction of birth date and nutrition also was significant ($P = 0.014$) (because of the large number of possible interaction terms and moderate sample size, we could not include all possible interactions in the analysis, so we included the primary term of interest, i.e., the birth date × nutrition term). This interaction confirms a similar result from the repeated measures ANOVA described previously that late-born calves in the low and medium nutrition groups tended to grow faster than early-born calves. The residuals analysis for these variables further illustrates an important birth mass effect (Fig. 20). Birth mass of late-born calves in the low and medium nutrition groups was 1.1–1.4 kg greater than that of their early-born counterparts (Table 5), and may explain why late-born calves in the low and medium groups grew faster than early-born calves in the low and medium groups. Differences in gender (Table 5) evidently did not account for their faster growth (Fig. 20).

Thirty-six calves were born in 1997. Birth mass averaged 16.1 ± 0.3 kg, and mean birth date was 6 June (±1.8 days; range was 20 May–4 Jul); thus, calves tended to be heavier and born later in 1997 than in 1996. Twenty-two (61%) were females. Six of the 36 calves were either abandoned (3) or died because of diseases that caused severe diarrhea, fever, and loss of appetite. All of these calves were reasonably large at birth (≥15.4 kg), suggesting that low birth mass did not predispose to death or abandonment (e.g., Thorne et al. 1976). Mean birth mass among treatment groups used in the summer experiments ranged from 15.3–17.1 kg, and mean birth date ranged from 31 May–25 June (Table 5).

Calf size attained by the time nutrition treatments were implemented again was a significant function of birth date ($P < 0.001$) (Fig. 17C) and birth mass ($P < 0.001$): $y = 114.24 - 0.66x_1 + 1.51x_2$, where y = calf mass on 4 July, x_1 = calendar day of birth, and x_2 = birth mass (kg). Including birth mass into the equation increased r^2 from 0.75 to 0.87, again indicating an appreciable effect of birth mass on early growth. Results of ANCOVA indicated no significant influences of calf gender ($P = 0.94$), cow age ($P = 0.19$), or previous-year summer-autumn nutrition level of their mothers ($P = 0.71$). However, the residuals analysis of birth mass effects indicated about 7 anomalous data values (Fig. 17D). Six calves were observed sick (diarrhea, reduced activity that typically lasted 4–7 days), including 5 of the 7 calves whose data include the anomalous points (Fig. 17D). We eliminated these 7 points from the data set and reran the ANCOVA and multiple regression. Birth mass and birth date remained highly significant ($P < 0.001$), gender became significant (i.e., males were larger) ($P = 0.035$), and previous-year nutrition remained insignificant ($P = 0.19$). The multiple regression equation for this subset of data was: $y = 113.3 - 0.66x_1 + 1.71x_2$, where y = calf mass on 4 July, x_1 = calendar day of birth, and x_2 = birth mass (kg), $r^2 = 0.95$).

The initial repeated measures ANOVA of calf growth after early July 1997 indicated an insignificant 5-way interaction between time, nutrition, birth date, mother's previous-year nutrition, and calf gender ($P = 0.13$). Both 4-way interactions also were insignificant ($P = 0.11$ for the time × birth date × nutrition × gender interaction; $P = 0.07$ for the time × birth date × nutrition × previous-year nutrition interaction). From these results, we concluded that calf gender (Fig. 18B) and previous-year nutrition were not likely to confound our test of birth date and summer/autumn nutritional influences on calf growth.

Dropping gender and previous-year nutrition, the ANOVA indicated an insignificant ($P = 0.54$) 3-way interaction between time, nutrition, and birth date and an insignificant interaction between time and birth date ($P = 0.15$). Only the interaction between nutrition and time was significant ($P < 0.001$). Thus, from early July through early December, nutrition levels over summer and autumn had the greatest influence on calf

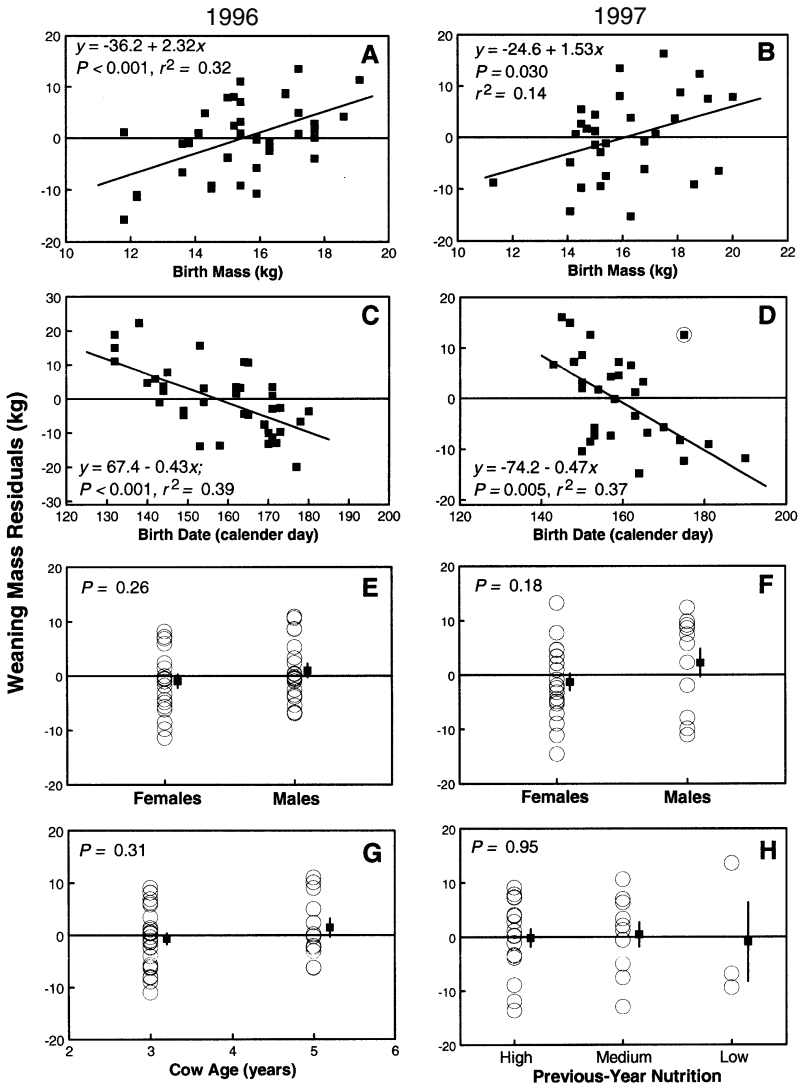

Figure 20. Residuals analyses of variables (birth mass, birth date, calf gender, cow age, and previous-year summer-autumn nutrition) potentially contributing to mid-November weaning mass of elk calves in 1996 and 97, northeastern Oregon. Relations between each variable and weaning-mass residuals are presented with the effects of all other variables removed (i.e., the analysis of covariance model was calculated with all but 1 variable included [summer-autumn nutrition was included in all ANCOVAs thereby removing the effects of nutrition from all analyses], and the residuals from that analysis were then regressed only with the excluded variable, once for each variable). The circled data point in D was excluded to calculate the regression coefficients, but was included to calculate significance levels. For graphs of categorical independent variables (E–H), solid squares and vertical lines indicate means and SEs.

growth of all variables measured (Fig. 19C,D). Calves in the low nutrition group ceased growth by late September, and growth of calves in the medium group lagged significantly behind that of calves in the high group by early October (Fig. 19D). Magnitude of nutritional influences increased from mid-summer through autumn.

The final 5-way ANCOVA on unadjusted BM at weaning in mid-November indicated significant effects of nutrition ($P < 0.001$), birth date ($P = 0.005$), and birth mass ($P = 0.030$); neither gender ($P = 0.18$) nor pervious-year nutrition of the mother ($P = 0.95$) were significant. (Inclusion of any of the interaction effects into the model rendered all terms insignificant; thus, no interactions

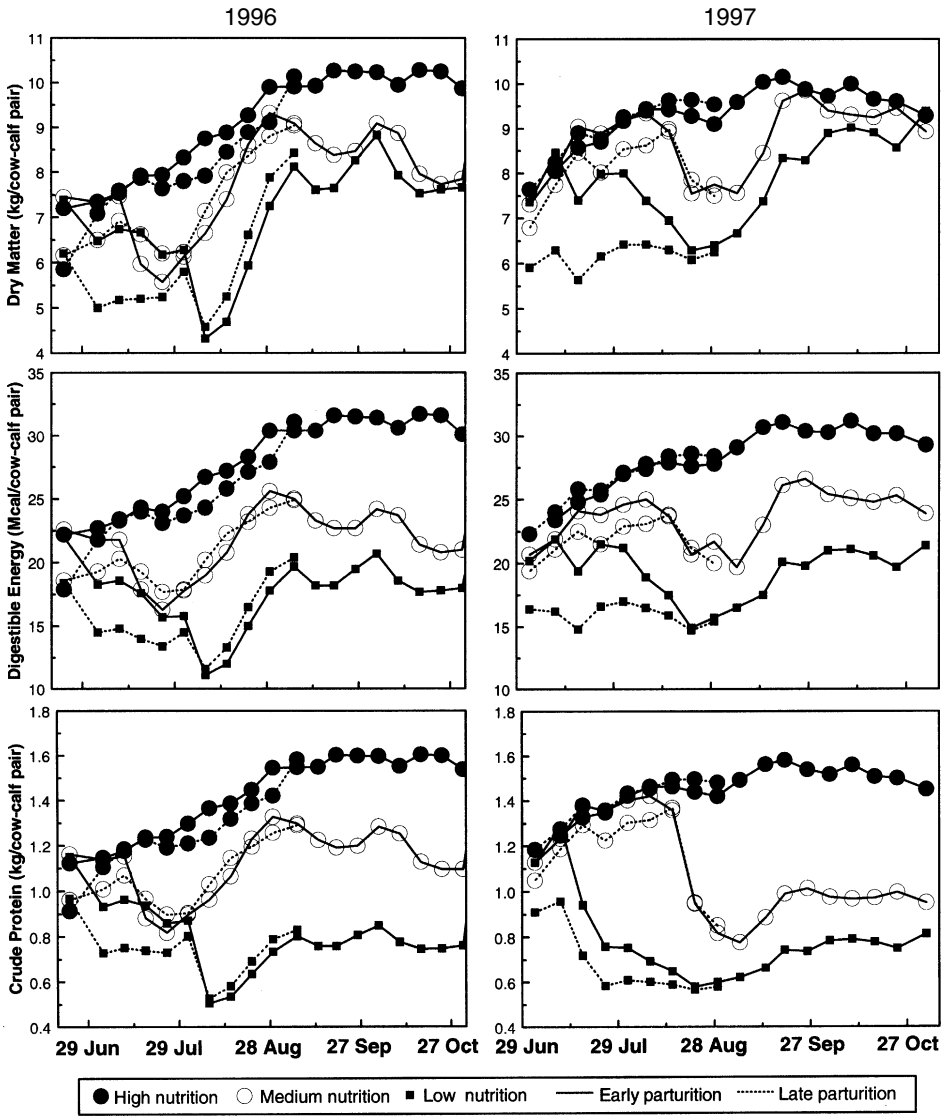

Figure 21. Weekly means of daily dry-matter, digestible energy, and crude protein intake of cow-calf pairs of elk by nutrition and birth date groups during summer and autumn in 1996 and 1997, northeastern Oregon. Because cow-calf pairs were combined within nutrition treatments across parturition-date treatments at the start of the rut in early September, intake estimates thereafter were combined across parturition-date treatments.

were included in this analysis). The advantage of early birth was again diluted by late autumn to some extent. Mass differences in mid-autumn of 1997 attributable to birth date were maintained by calves in the low and medium nutrition groups, but not in the high nutrition group (Fig. 19C), suggesting that late-born calves in the high nutrition group compensated late birth. This contrasts with apparent compensation patterns observed in the low and medium groups in 1996 (compare Figs. 19A,C). Faster growth of late-born calves in the high nutrition group again may be attributed to greater birth mass of late-born than their early-born counterparts (Table 5, Fig. 20).

Food intake by cows and calves.—Intake by cow-calf pairs showed marked differences between summer and autumn, among nutrition treatment groups, and, in early to mid-summer, between birth date groups (Fig. 21). In both years, cows giving birth late

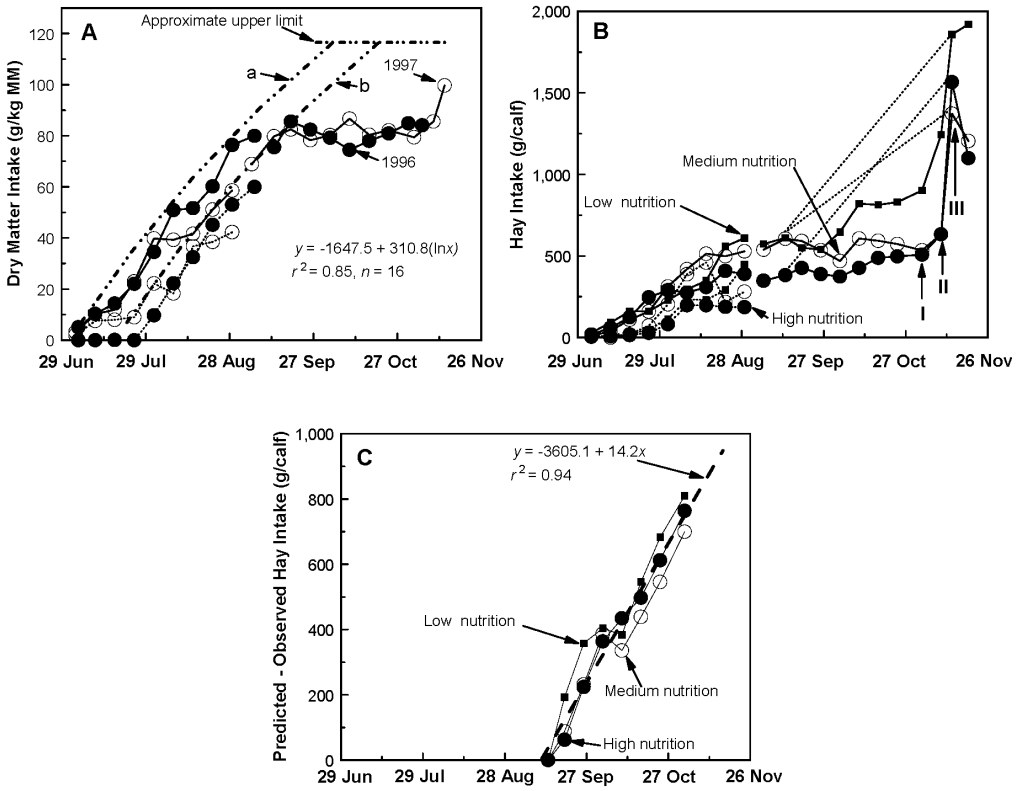

Figure 22. In graph A, observed daily dry-matter intake of solid food of elk calves, northeastern Oregon, fed high quality rations (high nutrition group) during summer and autumn in 1996 and 1997. Intake levels from our study were plotted with age- and metabolic-mass-specific (MM = body mass$^{0.75}$) solid food intake levels in other studies (summarized by Cook et al. 1996). Solid lines indicate data for our early-born calves; dotted lines indicate data for our late-born calves. The equation was derived from these summarized studies, and plotted as lines a and b (both lines are identical except both were date-shifted to correspond to our early and late parturition periods). This graph suggests that the plateau of solid food intake we observed in mid-September actually resulted from calves consuming hay intended for their mothers. In graph B, measured hay intake by calves in the 3 nutrition groups through the end of the autumn nutrition treatment period of 1997 (ending at I), the next 5 days when total hay offered to cows was reduced (II), and the next 4 days during which calves had no access to hay offered to the cows (III). Differences in intake between I and III provide an estimate of the amount of hay calves were taking from cows at the end of the experiment. Assuming that calves consumed very little hay intended for their mothers before mid-September, the dotted lines in graph B represent an approximate level of hay intake of the calves, and the difference between the dotted lines and observed intake (solid lines) provides an estimate of amount of the cow's hay consumed by the calves, plotted in graph C. The resulting equation (x = calendar day) was used to apportion hay intake initially attributed to cows to hay intake by calves.

consumed less food in July than cows giving birth early, particularly those in the low nutrition treatment. After mid-July, birth date differences gave way to differences induced by changing diet quality, despite ad libitum feeding. By late July, pairs in the low nutrition group consumed only 50–60% of that consumed by pairs in the high group in 1996 and 1997. However, cows in the medium and low nutrition groups subsequently began to increase intake by late August and early September. Nevertheless, intake of cow-calf pairs in the medium and low nutrition groups generally did not achieve intake levels by elk in the high group. Differences in intake of DE and crude protein were more pronounced among groups than differences in dry-matter intake, because of lower content of energy and protein in the food of elk in the medium and low groups (Fig. 21).

Measured intake by calves doubled when hay intended for cows was inaccessible to calves during the 4-day trial in November 1997 (Fig. 22B), indicating that calves had been consuming an appreciable portion of hay intended for their mothers by the end of the experiments. Plotting total dry-matter intake of solid food of our calves with that reported in

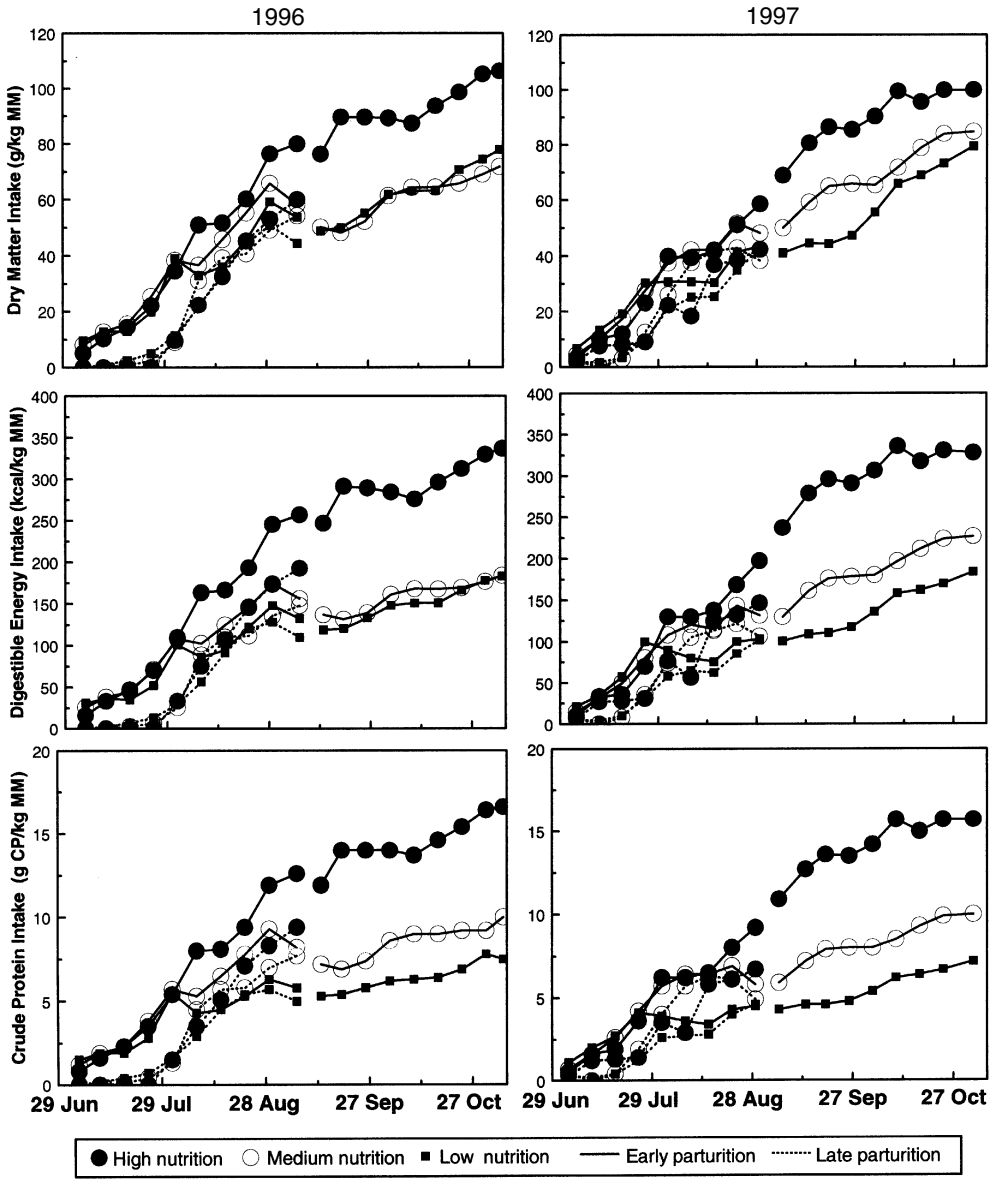

Figure 23. Estimates of dry-matter, digestible energy, and crude protein intake of solid food per kg of metabolic mass (MM = $BM^{0.75}$) for elk calves by nutrition and birth-date treatment groups in summer and autumn, northeastern Oregon. These estimates were adjusted to account for hay intended for cows that was actually consumed by calves as described in Fig. 22. Because cow-calf pairs were combined within nutrition treatments across parturition-date treatments at the start of the rut in early September, intake estimates thereafter were combined across parturition-date treatments.

other studies suggested that our calves began consuming cows' hay in early September (Fig. 22A). Based on this estimate of beginning bias and the estimate of hay calves were stealing based on the 4-day trial, we predicted how much total hay calves actually consumed between mid-September and early November (Fig. 22B). The difference between predicted and observed hay intake was consistent among nutrition treatment groups and was well-correlated to calendar day (Fig. 22C); we used this difference to adjust our estimates of cow and calf hay intake.

With this adjustment, intake of solid food by calves varied with nutrition and, to a lesser extent, with birth date (Fig. 23). Early-

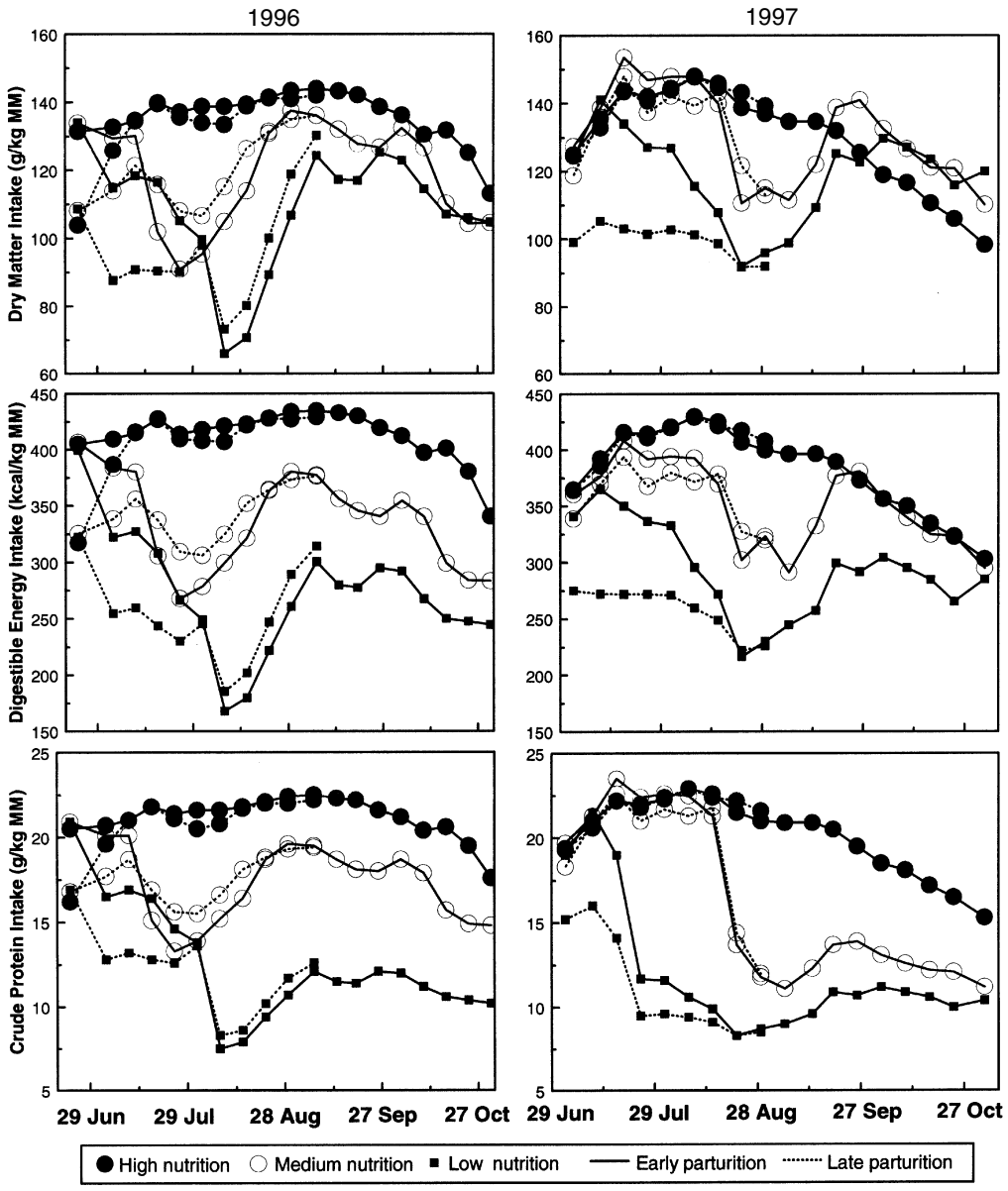

Figure 24. Estimates of dry matter, digestible energy, and crude protein intake for elk cows per kg of metabolic mass (MM = $BM^{0.75}$) by nutrition and parturition-date treatment groups in summer and autumn, northeastern Oregon. These estimates were adjusted to account for hay intended for cows that was actually consumed by calves as described in Fig. 22. Because cow-calf pairs were combined within nutrition treatments across parturition-date treatments at the start of the rut in early September, intake estimates thereafter were combined across parturition-date treatments.

born calves consumed appreciable amounts of solid food by late June, but late-born calves did not begin consuming solid food until mid-July. Differences caused by nutrition emerged by late July and increased thereafter. Digestible energy and crude protein intake by calves in the high nutrition group averaged about twice that by calves in the other nutrition groups by early October.

Parturition date and nutrition evidently affected dry-matter intake of lactating cows (Fig. 24). A declining trend in intake also was evident starting in early September in all nutrition groups. Dry-matter intake in the

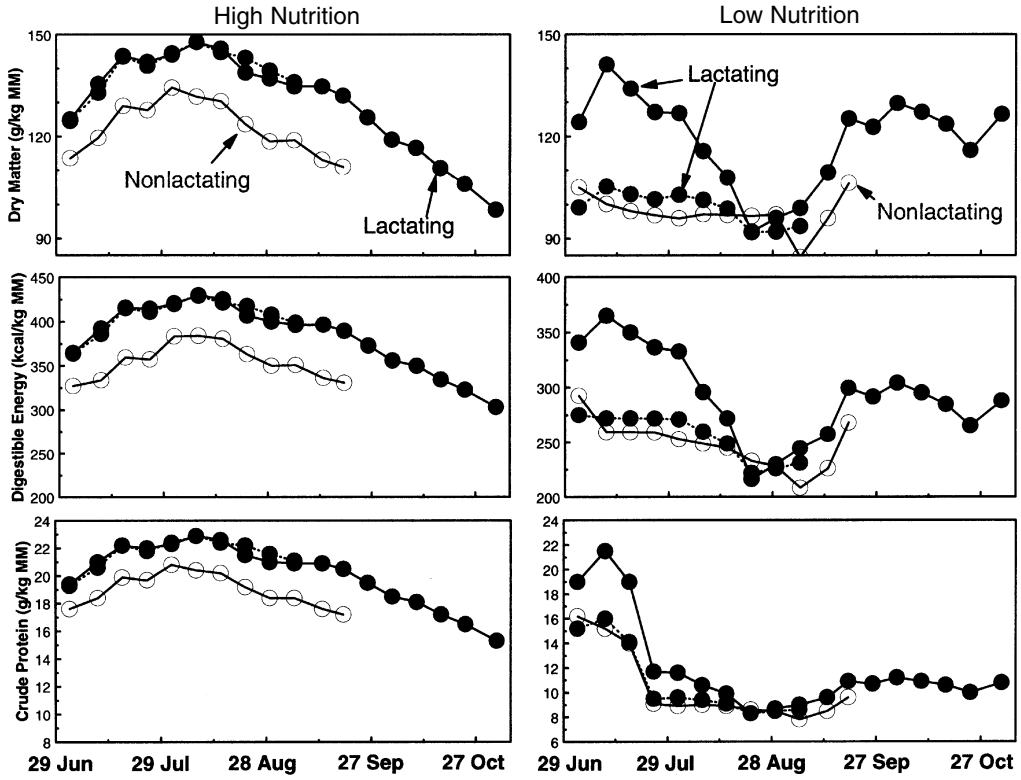

Figure 25. Estimates of dry-matter, digestible energy, and crude protein intake per kg of metabolic mass (MM = $BM^{0.75}$) for lactating and nonlactating elk cows during summer and autumn 1997, northeastern Oregon. We collected data on nonlactating cows until mid-September because they were placed at that time in a breeding pen without facilities to measure intake. Solid and dotted lines indicate data for cows in the early- and late-parturition treatment groups.

medium and low nutrition groups was similar both years, except that the mid-summer decline in intake was more acute in the first year than in the second. Also, dry-matter intake of the high nutrition group began a seasonal decline earlier in 1997 than in 1996, perhaps reflecting lesser intake needs for supporting their own growth.

Nonlactating cows in summer 1997 in the high nutrition group consumed less food than did lactating cows also fed the high nutrition ration (Fig. 25). More complex was the difference between lactating and nonlactating cows fed the low nutrition ration. Nonlactating cows consumed approximately the same amount of food as cows giving birth late, but both groups consumed less food than cows that gave birth early. However, by mid-August, food intake of all 3 groups converged, and no evidence of differences in intake existed by late August (Fig. 25).

Yearling growth, intake, and breeding.—Nine of the 19 yearling cows in this experiment were assigned to the high nutrition group and 10 were assigned to the medium nutrition group in late April 1997 (the medium nutrition treatment was implemented 1 Aug). Mean BM of both groups was virtually identical in late April (85.5 versus 84.9 kg with ranges of 67–130 kg and 61–110 kg in the high and medium groups, respectively). Yearlings grew rapidly over summer, doubling BM between early May and early September (Fig. 26A). The high nutrition group gained 90.6 ± 1.73 kg; the medium group gained 83.6 ± 2.60 kg (P = 0.039). Growth was virtually identical between the 2 nutrition groups over the summer until the nutrition level of the medium group was reduced in early August (Fig. 26A), corresponding to a substantial decline in DE intake (Fig. 26B). Intake of dry-matter and DE was high prior to August, equivalent to

the highest levels of intake of lactating cows, when expressed on a $BM^{0.75}$ basis.

Ten of the 19 yearlings became pregnant during the rut of 1997, 5 in each of the 2 nutrition groups, suggesting that the 1-month (August) moderate reduction in DE content of food was insufficient to appreciably affect yearling pregnancy. All 5 yearling cows in the previous-year high nutrition group, 3 of 7 in the previous-year medium group bred, and only 1 of 7 in the previous-year low nutrition group bred. Yearlings with greater BM as calves the previous autumn were more likely to breed ($P < 0.001$) (Table 6). These data suggest that pregnancy probability as yearlings was established to a large degree during summer-autumn of their first year of life.

Logistic regression confirmed the importance of BM as a predictor of pregnancy for yearlings (Fig. 26C, Table 7). Yearlings <170 kg in early September had <50% chance of pregnancy, whereas cows >180 kg had >90% chance of pregnancy. Probability of pregnancy as yearlings also was related to BM the previous autumn of their first year of life (Fig. 26C). Differences in DE content of the 2 summer nutritional regimes may have been too small and implemented too late to affect yearling pregnancy probability ($P > 0.50$ for summer yearling nutrition when included in the logistic regression).

Carry-over Effects of Summer-Autumn Nutrition and Parturition Date

Winter survival of cows and fetuses.—This experiment was conducted with 40 pregnant cows in 1998: 9 cows in the SHWH treatment group, 10 in the SMWH group, 10 in the SNWM group, and 11 in the SNWL group. Although it was not the intent of the feeding regimes to reduce cows to dangerously low levels of condition, 1 cow died and 5 were removed from the study to prevent death. The mortality occurred on 27 February. She and 3 other cows removed from the study on the same day were in the SNWL group. The last 2 cows, from the SMWH group, were removed on 28 February and 6 March. Both required intensive monitoring and extra care for 1–2 months to prevent death. The former of these 2 cows aborted 21 March, 2 weeks after ad libitum feeding started, whereas the latter aborted in mid-May, over 2 months after ad libitum feeding started. The fetus of the cow that died appeared normal and viable upon post-mortem examination.

Cows fed high nutrition in winter (SHWH, SMWH) lost 7–11% of their BM, 3–5 percentage points more than did pregnant cows in the 2 previous winters, despite receiving what was intended to be the same diets each winter. Subsequent nutrient analysis of the pellets fed this winter (1998) suggested the manufacturer inadvertently switched pellet formulations, such that we fed a pellet of substantially lower quality in winter 1998 than in previous winters (Table 1). Although this complicates comparisons among winters, the within-winter comparisons of 1998 are unaffected because only quantity was varied among the treatment groups of elk.

Winter nutrition significantly affected changes in condition during winter ($P < 0.001$). Cows receiving the lowest winter diet lost the most mass, whereas mass loss by cows in the SMWH and SNWM groups was moderate (Fig. 27A). All cows except those in the SMWH group began winter in good condition (16–18% body fat, 1.5–2.7 Mcal/kg of gross energy), whereas cows in the SMWH group began winter in substantially poorer condition (Fig. 27B,C). Condition of cows in the SNWL group plummeted, and by the end of winter, their condition was significantly less than that of the SHWH and SNWM groups and equivalent to that of the SMWH group (Fig. 27B,C). Mid-February characteristics of the cow that died and the others removed from the study differed significantly from cows that completed the experiment: 190 ± 8.1 versus 216 ± 2.7 kg of BM, 4.4 ± 0.73 versus 10.5 ± 0.51% fat, 1.63 ± 0.06 versus 2.13 ± 0.35 Mcal of gross energy, 4.24 ± 0.163 versus 5.04 ± 0.08 cm of loin thickness ($P \leq 0.001$ for all comparisons based on individual *t*-tests).

Loin muscle thickness, an alternate index useful at low levels of condition (Cook 2000), provided a slightly different perspective of changes in condition during winter than LIVINDEX (Fig. 27D). Loin thickness of cows in the SMWH declined precipitously between February and March, indicating acute muscle catabolism of the 2 cows removed from the study, despite refeeding 2

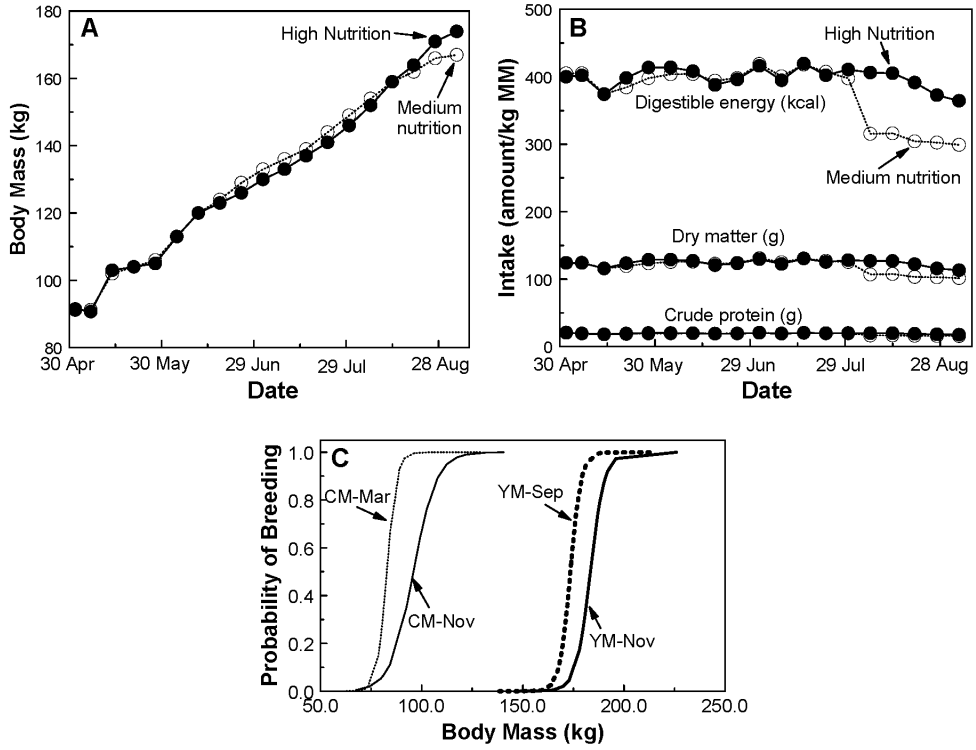

Figure 26. Body mass of yearling cow elk during summer 1997, northeastern Oregon (A) and estimates of daily intake of DE, dry matter, and crude protein per kg of metabolic mass (MM = $BM^{0.75}$) of these yearling cows (B). Cows in both nutrition groups received identical food through July. Starting 1 August, digestible energy (DE) was shifted from 3.2 to 2.9 kcal/g for elk in the medium nutrition group. Hay was fed ad libitum to both over the entire summer period. Graph C illustrates the probability that these yearling cows became pregnant as yearlings (autumn 1997) as a function of their body mass as (1) calves in late November 1996 (CM-Nov), (2) calves in late March 1997 (CM-Mar), (3) yearlings in early September 1997 (YM-Sep), and (4) yearlings in early November 1997 (YM-Nov) (see Table 7 for logistic regression equations).

Table 6. Body mass (kg) of pregnant (n = 10) and nonpregnant (n = 9) yearling cow elk before and after the rut of autumn 1997, northeastern Oregon.

			Nonpregnant		Pregnant		
Age class	Month	Year	Mean	Range	Mean	Range	P[a]
Calf	Nov	1996	81.5	67–99	113.2	84–140	0.001
Calf	Mar	1997	73.7	61–83	98.0	78–129	0.001
Yearling	Sep	1997	160.7	137–174	184.8	169–215	0.001
Yearling	Nov	1997	172.0	146–191	193.2	181–226	0.001

[a] Probability level of t-test comparisons for each age class (n = 19 cows).

Table 7. Logistic regression equations for predicting probability of pregnancy of yearling elk in autumn 1997 ($Pr(p_{97})$), northeastern Oregon, based on their body mass (BM)(kg) at different growth stages.

Age class	Month	Year	Equation	P[a]
Calf	Nov	1996	$Pr(p_{97}) = \exp(-17.099 + 0.178BM) / (1 + \exp(-17.099 + 0.178BM))$	0.031
Calf	Mar	1997	$Pr(p_{97}) = \exp(-34.339 + 0.415BM) / (1 + \exp(-34.339 + 0.415BM))$	0.091
Yearling	Sep	1997	$Pr(p_{97}) = \exp(-65.813 + 0.379BM) / (1 + \exp(-65.813 + 0.379BM))$	0.079
Yearling	Nov	1997	$Pr(p_{97}) = \exp(-52.688 + 0.287BM) / (1 + \exp(-52.688 + 0.287BM))$	0.037

[a] Level of significance of slope coefficient of logistic regression (n = 19 cows).

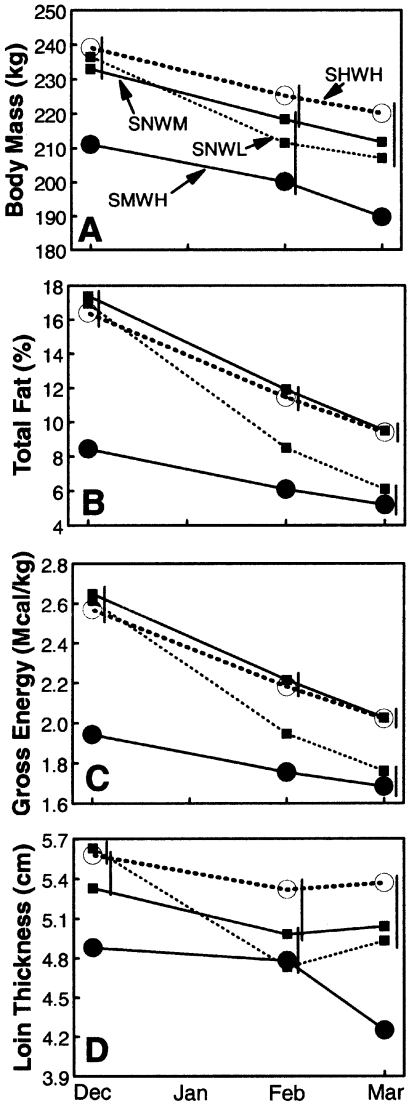

Figure 27. Body mass and nutritional condition of cow elk during winter of 1997–98, northeastern Oregon. Data are presented for 4 treatment groups: SNWM = high nutrition and nonlactating in summer, medium nutrition in winter; SNWL = high nutrition and nonlactating in summer, low nutrition in winter; SHWH = high nutrition and lactating in summer, high nutrition in winter; SMWH = medium nutrition and lactating in summer, high nutrition in winter. Total fat and gross energy content of the ingesta-free body were calculated from LIVINDEX (Cook et al. 2001*a*,*b*). Loin muscle thickness provides a measure of muscle catabolism most useful at low levels of condition (Cook 2000). Within time periods, data values connected with vertical lines do not differ ($P \geq 0.05$).

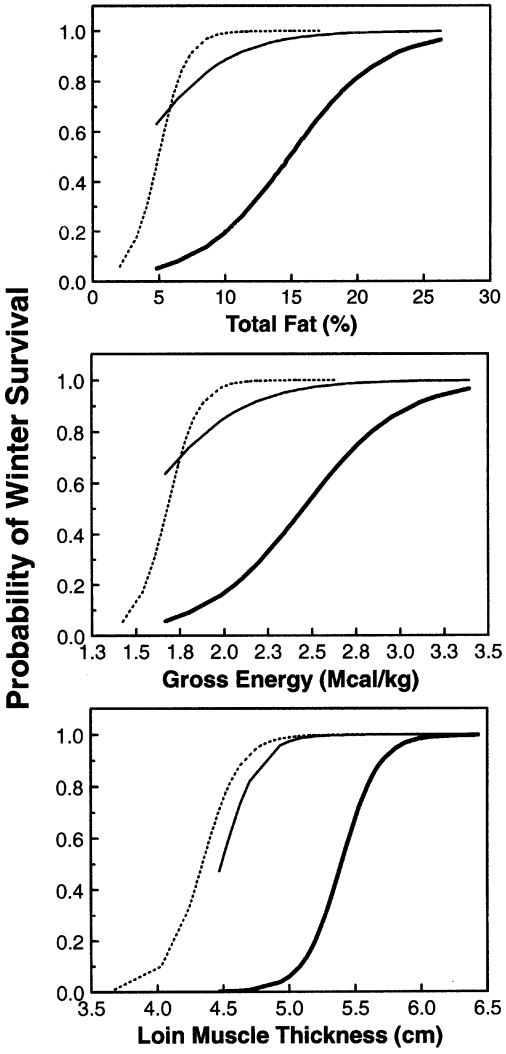

Figure 28. Logistic relations between probability of winter survival (1998) of pregnant elk cows, northeastern Oregon, and nutritional condition (see Table 8 for logistic equations) in 3 situations: (1) severe winter nutritional restriction equivalent to that fed to the winter-low-nutrition group (thick, solid lines); (2) moderate winter nutritional restriction equivalent to that fed to the winter-high-nutrition group (thin, solid lines); and (3) probability of surviving from mid-February through early March based on nutritional condition in mid-February and any of the winter nutrition treatments fed in this experiment (narrow, dotted lines). Total fat and gross energy content of the ingesta-free body were calculated from LIVINDEX (Cook et al. 2001*a*,*b*). Loin muscle thickness provides a measure of muscle catabolism most useful at low levels of condition (Cook 2000).

weeks before the loin measurement was taken for 1 cow and 1 week for the other.

Treating all animals removed from the study as "dead," we developed logistic regressions to predict probability of winter survival as a function of autumn condition, mid-winter condition, and winter nutrition (Fig. 28, Table 8). We first regressed survival on autumn condition and winter nutrition.

Table 8. Logistic regression equations for predicting probability of winter survival during winter 1997–98, northeastern Oregon, of adult cow elk based on (1) nutritional condition in December 1997 and winter nutrition and (2) condition in mid-February 1998. Probabilities are for survival over a 3-month winter season of nutritional deprivation for the former (S_{Win}) and for survival from mid-February through late winter (S_{Lwin}) for the latter.

Dependent variable[a]	Equation[b]
Estimated fat (%)	
	S_{Win} = exp(–7.763 + 0.290FAT + 3.455WNUT) / (1 + exp(–7.763 + 0.290FAT + 3.455WNUT))
	S_{Lwin} = exp(–4.717 + 0.955FAT) / (1 + exp(–4.717 + 0.955FAT))
Estimated gross energy (Mcal/kg)	
	S_{Win} = exp(–12.07 + 3.555GE + 3.353WNUT) / (1 + exp(–12.07 + 3.555GE + 3.353WNUT))
	S_{Lwin} = exp(–19.14 + 11.41GE) / (1 + exp(–19.14 + 11.41GE))
Loin thickness (cm)	
	S_{Win} = exp(–44.41 + 7.047LOIN + 6.403WNUT) / (1 + exp(–44.41 + 7.047LOIN + 6.403WNUT))
	S_{Lwin} = exp(–30.54 + 7.033LOIN) / (1 + exp(–30.54 + 7.033LOIN))

[a] Independent variables were: (1) total fat (FAT) of the ingesta-free body, (2) gross energy (GE) of the ingesta-free body, (3) loin muscle thickness (LOIN), and (4) winter nutrition levels (WNUT), an ordinal variable with values of 1 for low nutrition and 2 for moderate nutrition. FAT and GE were calculated from LIVINDEX from equations of Cook et al. (2001*a*).

[b] Coefficients of FAT ($P = 0.073$) and GE ($P = 0.078$) in the S_{Win} equations approached significance; all other slope coefficients in all equations were significant ($P < 0.050$).

Data for elk in the winter-high and winter-medium nutrition treatments were combined, because performance of elk in these groups was virtually identical (Fig. 27). Both winter nutrition and autumn condition were significantly related to probability of overwinter survival (Fig. 28, Table 8). Our data indicated that during harsh winters of marked nutritional restriction, equivalent to that fed elk in the winter-low nutrition group, winter survival primarily is a function of fat levels at the beginning of winter.

From mid-February through the end of winter, survival was significantly related to condition in mid-February but unrelated to the winter nutrition levels we implemented (Table 8), suggesting that fate of the elk was determined to a large extent by mid-February and was a significant function of their condition at this time. Probability plots with mid-February condition indicated steeper slopes than those of autumn condition, and suggest a threshold level occurring at about 3–5% body fat and 4.2–4.4 cm of loin thickness, below which survival probability was low. This by no means indicates that probability of mortality was irreversible by mid-February, only that probability was set as long as either of the 2 winter feeding levels remained unchanged until early March.

Calf Winter Survival.—In winter 1996–97, data from 22 female and 18 male calves were available to evaluate factors that influenced winter survival. Average mass at the beginning of the experiments in early December was 96.3 kg and ranged from 61–140 kg. Male calves averaged slightly larger than females (92.8 ± 4.44 kg versus 100.6 ± 4.94 kg).

The first winter experiment was conducted from 11 December–20 March. Over this time, all except 4 calves were removed (i.e., simulated death) from the study, most in February and March (Fig. 29A). Three calves died during this winter. One was the first removed from the study (4 Jan). She was ill with elevated temperature, had lost only 10% of her BM, and had peritonitis of unknown causes, based on veterinary necropsy. The second calf failed to recover after removal from the study (10 Feb); the third calf died during the night (8 Mar), probably from hypothermia.

At the time calves were removed from the study, they had lost an average of 18.6 ± 0.62% (range = 10–26.6%) of their starting BM. They lost an average, from 11 December–20 January, 0.09 kg per day or 0.11% of their beginning BM per day, and lost 0.24 kg per day, or 0.26% of their beginning mass per day, from the beginning to the point at which they were removed. Males lost 18.8% overall and 0.27%/day and females lost 18.3% overall and 0.26%/day, indicating virtually identical mass loss between sexes.

Mass lost by calves and timing of "mortality" strongly reflected calf mass at the beginning of winter. Number of days of winter

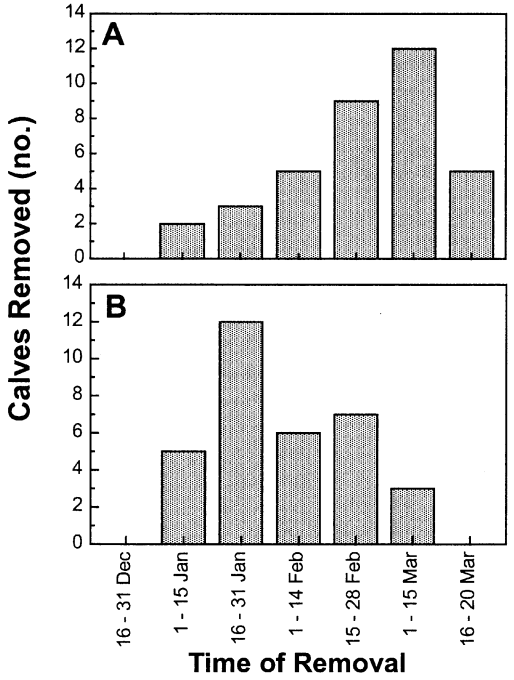

Figure 29. Timing of removal (i.e., simulated mortality) of elk calves from winter survival experiments in 1996–97 (A) and 1997–98 (B), northeastern Oregon.

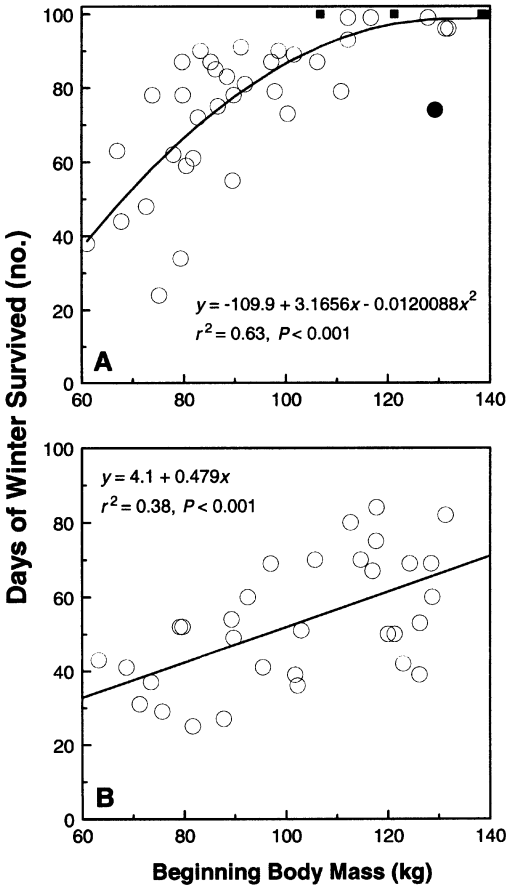

Figure 30. Relations between number of days of winter survived by elk calves and their body mass at the start of winter in 1996–97 (A) and 1997–98 (B), northeastern Oregon. Both winter experiments were conducted from mid-December to mid-March. In graph A, the 4 solid squares are data for calves that survived the entire winter experiment, and the solid circle indicates a data point treated as anomalous and excluded from calculation of the regression equation. Differences in regression relations between years reflect differences in feeding regimes between years.

survived was a significant ($P < 0.001$), nonlinear function of BM at the beginning of winter (Fig. 30A). The nonlinear relation for 1996–97 approached an asymptote; calves at least 105 kg at the beginning of winter had a high probability of surviving at least 90 days of winter. Number of days survived diminished markedly as BM declined below 105 kg. The 4 calves that survived winter averaged 126.6 ± 7.8 kg at the beginning of winter. By comparison, calves that died or were removed averaged 92.9 ± 3.13 kg. Survival was marginally affected by calf gender ($P = 0.11$).

Longer survival of larger calves apparently resulted from greater tolerance of nutritional deficiencies and winter weather. The smallest calves began losing appreciable mass early in winter, despite only moderate nutritional deficiencies, whereas the largest calves lost little mass until after mid-February (Fig. 31), when feeding levels were reduced appreciably (Table 3). The amount of mass lost daily to the time of removal was a nonlinear function of beginning BM ($P < 0.001$) (Fig. 32A). Additionally, larger calves were capable of losing more mass as a percent of their beginning BM (evident only when influences of day of the experiment were controlled using multiple regression): $y = -20.9 + 0.134x_1 - 0.1229x_2$, where y = total mass loss (%) to the time of removal, x_1 = mass at beginning of winter ($P = 0.008$), x_2 = number of days past 11 December ($P = 0.027$) ($r^2 = 0.18$, $P = 0.026$). Nonetheless, daily rate of mass loss, which ultimately determined the number of days of winter survived, was most affected by beginning mass.

Finally, the 2-way ANOVA, to identify influences of nutrition the previous summer

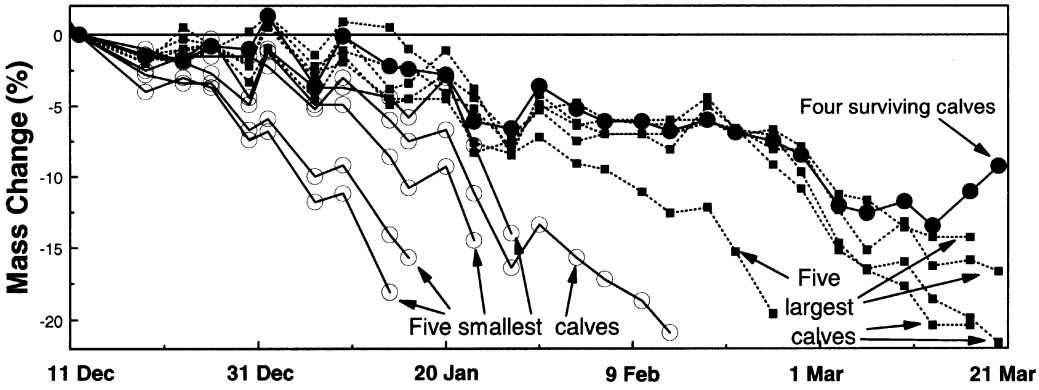

Figure 31. Body mass changes of elk calves during winter 1996–97, northeastern Oregon. Data are presented for the 4 calves that survived the entire winter (weekly averages of the 4), and the 5 smallest and 5 largest calves that "died" during winter.

and autumn, birth date, and their interaction, on winter survival of calves, indicated a strong effect of nutrition ($P < 0.001$), little or no effect of birth date ($P = 0.18$), and no interactive effect ($P = 0.60$). An initial 3-way ANOVA (summer-autumn nutrition, birth date, and calf gender) with all interactions indicated no influences of gender on winter survival ($P \geq 0.47$).

Thirty-three calves were available for the second winter experiment (1997–98). Three of these calves were abandoned soon after birth and bottle-raised (were not used in the summer-autumn experiments); all others were dam-reared and used in the summer-autumn experiment. Data from the 3 calves were included to evaluate relations between starting BM and winter survival, but were excluded from ANOVA tests of effects of birth date and summer nutrition on winter survival. The 33 calves averaged 100.7 ± 3.80 kg (range = 56.5–131.3 kg) at the beginning of the second winter experiment. The 20 females averaged 97.8 ± 5.3 kg and the 13 males averaged 105.2 ± 5.14 kg, but were not significantly different ($P = 0.33$, $t = -0.95$, df = 31). During the second winter, calves were removed earlier (Fig. 29) and lost mass about 50% faster compared to the first winter, and none of the 33 calves "survived." These differences probably were caused by greater nutritional restriction induced early in the second winter (Table 3). Even so, percent of mass lost at the time calves were removed from the study was virtually identical to that of the previous year (18.6 ± 0.56%; range = 13–24%).

"Mortality" and rate of mass loss again were significantly related to mass at the start of winter ($P \leq 0.004$). Beginning BM accounted for less variation (38%) in number of days of winter survival than in the first winter, and this relation was linear rather than nonlinear (Fig. 30B). Calves lost 0.39 ± 0.025% daily (no gender differences were evident, e.g., 0.39% versus 0.39% for males and females). Rate of mass loss was significantly

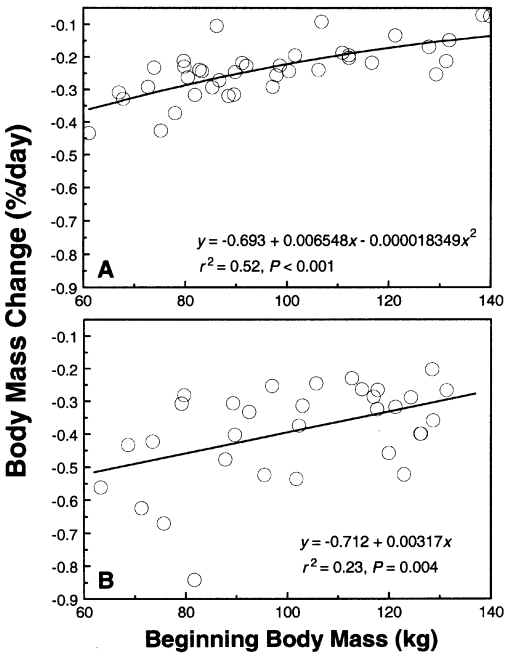

Figure 32. Daily rate of mass loss of elk calves from the start of the calf winter survival experiments in mid-December until time of removal (simulated "death") during 1996–97 (A) and 1997–98 (B), northeastern Oregon.

correlated to BM at the start of the experiment, but to a lesser extent than during the first winter experiment (Fig. 32). In contrast, larger calves were not capable of losing more mass, expressed as a percent of starting BM, than smaller calves. Thus, larger calves survived longer because their rate of mass loss relative to their total BM was lower.

The final 2-way ANOVA indicated a strong effect of nutrition ($P = 0.001$), no effect of birth date ($P = 0.63$), and no interaction effect ($P = 0.74$). An initial 3-way ANOVA (summer-autumn nutrition, birth date, and calf gender) with all interactions indicated no influences of gender on winter survival ($P > 0.11$).

Calf birth characteristics and gestation length.—Failure of most elk in the low nutrition group to become pregnant in both summer-autumn experiments indicates a marked carry-over effect of summer-fall nutrition on reproduction the subsequent year. However, it also reduced our sample to evaluate carry-over effects of summer-autumn nutrition and parturition date on subsequent year's calf birth characteristics. We therefore combined our 2 years of data, added "year" as a predictor variable, and included calf gender to account for this potentially confounding factor. Based on a total sample of 44 cows, calf gender ($P = 0.001$), year of the study ($P = 0.001$), and the cow's previous-year parturition date ($P = 0.033$) accounted for significant variation in birth mass (Fig. 33A). Neither previous-year summer-autumn nutrition ($P = 0.77$) nor the interaction of previous-year nutrition and previous-year parturition date ($P = 0.30$) (nor any other interaction of interest) were significant. Replacing previous-year summer-autumn nutrition and previous-year parturition date with body fat in autumn, the ANCOVA also suggested that gender and year primarily accounted for variation in birth mass ($P = 0.079$ and 0.012); autumn body fat was no more related to birth mass ($P = 0.77$) than previous-year nutrition. Finally, replacing previous-year autumn body fat with body fat in March in the ANCOVA failed to indicate that condition during the first 2 trimesters of gestation significantly influenced birth mass ($P = 0.56$). Winter nutrition of these cows was approximately constant each year, so winter nutrition was excluded from these analyses.

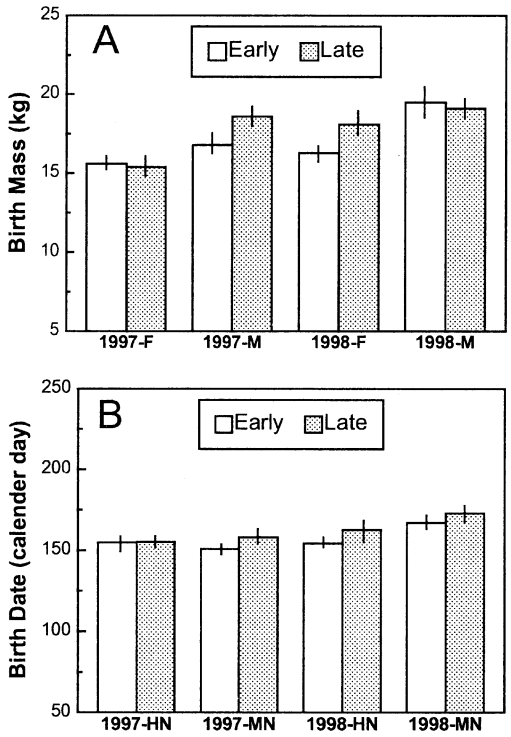

Figure 33. In graph A, influences of year, fetal gender (M = males, F = females), and the mother's parturition date the previous spring (early, late) on birth mass of elk calves born in 1997 and 1998, northeastern Oregon. In graph B, influences of year and previous-year nutrition treatment of the mother (HN = high nutrition, MN = medium nutrition) and previous-year parturition date of the mother on birth date of calves in 1997 and 1998. Vertical lines denote SEs. All graphed effects exhibited significant influences ($P \leq 0.05$) on birth mass and birth date.

The winter experiment examining survival of cows and fetuses provided a limited basis to evaluate winter nutrition's influence on birth mass. Birth mass of calves born to cows in the winter medium and winter low nutrition treatments (SNWM and SNWL groups) ranged from 13–16.8 kg across both treatment groups of cows, and average birth mass was similar (14.7 versus 15.5 kg). Birth mass was unaffected ($P = 0.84$) by change in body fat levels from autumn through early March, even though condition of 3 cows in the SNWL group reached critically low levels in late February. Neither fetal gender nor the interaction of gender and change-in-fat influenced birth mass ($P \geq 0.63$).

Current-year parturition date, in contrast, varied in response to previous-year summer-autumn nutrition ($P = 0.010$), which was

expected because of the effect of previous-year nutrition on breeding date (Figs. 12 and 13). The effect of previous-year nutrition (i.e., higher nutrition, earlier birth) was evident mainly during the second year (Fig. 33B) ($P = 0.027$ of the year × nutrition interaction). Replacing previous-year nutrition with autumn body fat confirmed the carryover effect of autumn condition ($P = 0.004$). The interaction of autumn body fat with year was not significant ($P = 0.98$). However, the simple linear regression relating autumn body fat to subsequent parturition date accounted for a small portion of the variation in parturition date ($y = 169.7 - 0.93x$; $r^2 = 0.14$; $P = 0.003$; $n = 63$, where x = autumn body fat).

Previous-year parturition date also was related to current year parturition date ($P = 0.004$). Cows giving birth earlier the previous year also tended to give birth earlier the current year. Effect of previous-year parturition date was similar across years and nutrition treatments ($P > 0.269$ for both 2-way interactions: previous-year parturition date × year and previous-year parturition date × previous-year nutrition) (Fig. 33B).

Breeding observations in 1997 permitted direct evaluation of factors influencing gestation length ($n = 16$ cows). Gestation length was 250.9 ± 2.28 days (range = 240–271). Current-year parturition date was only weakly related to previous-year breeding date ($P = 0.074$; $r^2 = 0.21$; $y = 0.606x - 4.8$, where y = calendar day of birth and x = calendar day of breeding). Neither previous-year nutrition nor previous-year autumn body fat, body fat in March, or calf gender ($P > 0.23$) were significantly related to gestation length. Only timing of birth the previous year was significantly related to gestation length (i.e., earlier births the previous-year corresponded to shorter gestation length in the current year) ($P = 0.021$), corresponding to findings of previous-year parturition date influences above (Fig. 33B). This suggests that those cows that give birth early do so because they tend to have shorter gestation lengths, assuming all else (e.g., nutrition) being equal.

However, of the 21 cows that were nonlactating in autumn 1997 and fed the medium and low diets during winter 1998 (the SNWM and SNWL treatment groups), parturition dates ranged over a 45-day period in spring 1998. Given the excellent condition of all these nonlactating cows during the breeding season (Fig. 16), differences in parturition date probably resulted from differences in winter nutritional regimes (Fig. 34). Change in nutritional condition from autumn to early spring accounted for 50–60% of the variation in parturition date ($P < 0.001$). Thus, for those cows beginning winter with 15–25% body fat, depletion of 90% of their reserves extended parturition date 34 days on average, if dietary conditions ceased to be limiting beginning by mid-March (Fig. 34).

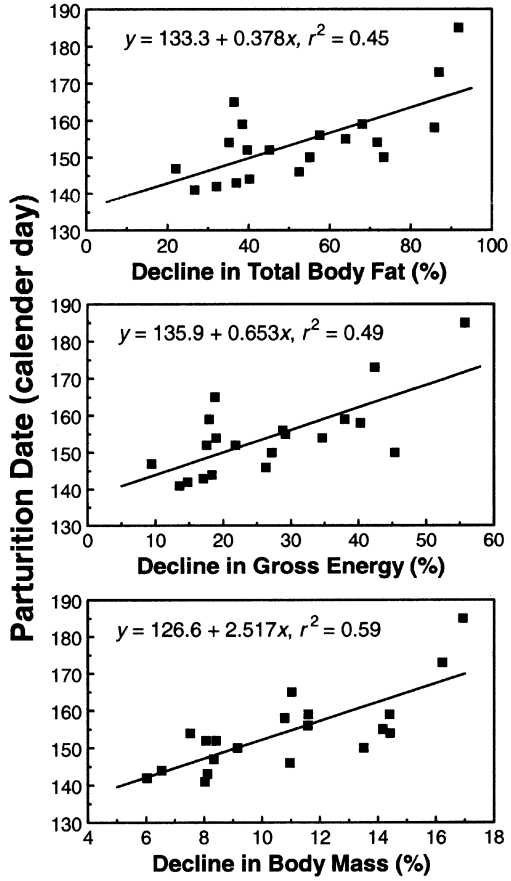

Figure 34. Influences of over-winter declines in nutritional condition and body mass of elk cows during winter 1996–97 on their parturition date in spring 1997, northeastern Oregon. Cows in this experiment were pregnant and in excellent condition in autumn and nonlactating and well-fed the previous summer (see Fig. 27). These results suggest elk cows can markedly extend gestation to compensate for relatively severe winter nutritional deficiencies.

DISCUSSION

Our data indicate that relatively small differences in DE content of food consumed by elk in summer and autumn have strong effects on fat accretion, timing of conception, probability of pregnancy of lactating cows, growth of calves, yearling growth, and yearling pregnancy rates. Effects of summer-autumn nutrition on fat accretion of cows and growth of calves significantly influenced their survival probability during winter under the harsh winter nutritional conditions that we mimicked. Earlier birth resulted in larger BM of calves in late autumn, but we were unable to document significant, consistent effects of parturition date on any other reproductive or survival attribute we estimated. Neither summer-autumn nutrition nor the cow's parturition date had biologically meaningful effects on birth mass of calves the following year.

Direct Effects

Calf responses.—Earlier work on elk suggested that breeding is delayed ≤3 weeks (Noyes et al. 1996) when yearling bulls dominate the breeding. Delayed parturition, whatever its cause, can reduce calf survival over summer (Guinness et al. 1978*b*, Clutton-Brock et al. 1982, Keech et al. 2000), over winter (Guinness et al. 1978*b*, Singer et al. 1997), and can reduce fitness of those that do survive (Festa-Bianchet et al. 2000).

A biologically relevant effect of birth date on winter survival depends on a key assumption–that late-born calves have little capability to catch up by late autumn with their early-born counterparts, thereby reducing or eliminating the "head-start" benefit of early birth. Additionally, the potential for an interaction between summer-autumn nutrition and birth date on late-autumn BM reflects the supposition that optimal birth date arises from the synchrony between the peak in forage quality and the peak in nutritional demands of the lactating mother. Hence, calves may have reduced ability to catch-up if they are born well after forage quality begins to decline and may lag behind calves that are born earlier, if nutritional restriction has a greater negative effect on very young calves than on older calves.

Our data failed to support this interaction hypothesis between birth date and summer-autumn nutrition. In 1996, we found a significant interaction between birth date and nutrition on calf growth. But this interaction resulted from faster growth of late-born calves (Fig. 19B). In 1997, the interaction between birth date and nutrition was not significant, nor did it approach significance. Our analysis also suggested that potential confounding by gender, cow age, and, in 1997, previous-year nutrition levels of the mother, probably do not account for these results and inconsistencies between years. Therefore, our data provide little evidence that (1) late-born calves are more disadvantaged, as summer nutrition becomes increasingly deficient, than are early-born calves and (2) elk calves are physiologically capable of accelerated growth to compensate for late birth.

The primary benefit of early birth in respect to calf BM by late autumn was simply due to a longer period of time for growth. But this head-start advantage was diluted to some extent before winter because some late-born calves grew faster. Understanding causes of this dilution is key for understanding whether early birth of about 3 weeks is truly an advantage.

Faster growth of these late-born calves was evident in the low and medium nutrition groups in 1996 and the high nutrition group in 1997 (Fig. 19A,C). Their faster growth probably resulted from complex interactions among birth date, gender, and birth mass. Even though Hudson et al. (1991) reported that male elk calves grow more rapidly than females, our data suggest that greater birth mass probably was more responsible than was gender for faster growth of late-born calves. Across both years, in each of the 3 nutrition groups where late-born calves caught up, (1) larger calves at birth grew faster (Fig. 35) and (2) late-born calves on average were larger at birth (Table 5). Conversely, (1) male calves grew faster and (2) there was a greater proportion of males in the late-born groups, but only in 2 of the 3 nutrition groups where late born calves caught up (Fig. 35, Table 5). Finally, in the low nutrition group of 1996, the tendency for faster growth by calves that were heavier at birth was more evident in males than females, and males predominated in the

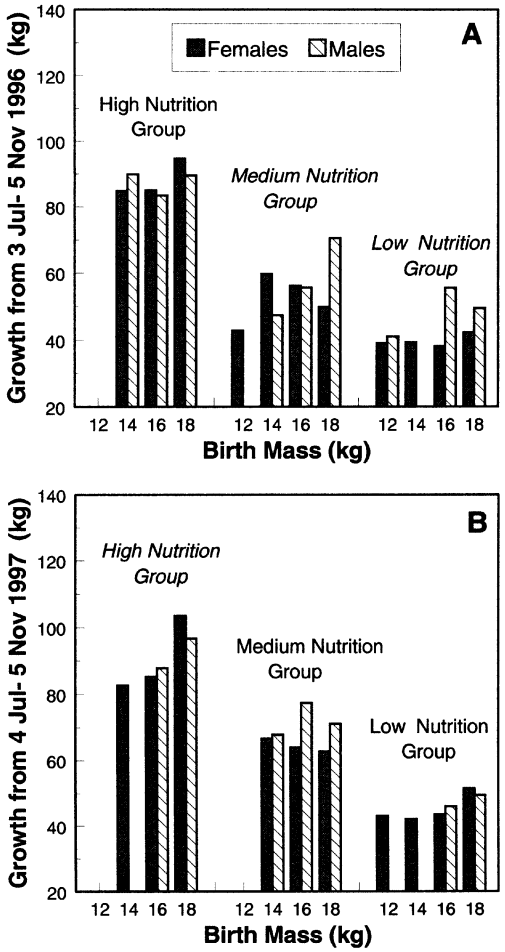

Figure 35. Relations between birth mass, gender, and growth from early July until weaning in early November, 1996 (A) and 1997 (B), by nutrition treatment groups of elk calves, northeastern Oregon. Late-born calves exhibited faster growth and caught up with their early-born counterparts in the italicized nutrition groups.

late-born group (Fig. 34, Table 5).

This qualitative evaluation (Fig. 34) is not conclusive. Nevertheless, it suggests that the early-birth advantage, and its dilution over summer and autumn, depends on the distribution of birth mass and perhaps gender across the parturition period. If larger calves at birth, particularly if they are male, occur more frequently late during the parturition period, then the advantage of early birth will wane before winter. On the other hand, if larger birth mass and male births are more frequent early in parturition, then calves born late may fall further behind their early-born counterparts over summer and autumn. Of our 3 calf crops (n = 118 calves), we found no evidence that heavier birth mass or males were more common early in parturition. In contrast, in 2 of the 3 years, birth mass, within gender, increased significantly as parturition progressed. Further, males comprised 36% of 73 early births (born on or before 10 June) and 52% of 45 late births (born after 10 June). Smith et al. (1997) reported that male elk calves were born later than females and were larger at birth, although they found no evidence that birth mass, within gender, increased as parturition progressed. We conclude that as long as birth mass and gender are relatively constant across the parturition period, the head-start advantage of early birth will be maintained through autumn. But if calves are heavier or males are relatively more abundant later in the parturition period, the head-start advantage of early birth will diminish by late autumn.

Nutrition during summer and autumn had marked influences on calf growth that overshadowed effects of all other variables we measured, and demonstrated once again (Holter and Hayes 1977; Verme and Ozoga 1980*a*,*b*; Cook et al. 1996) the sensitivity of growth to nutrition. Digestible energy content of food affected growth by influencing daily intake levels of solid food by calves and probably by influencing milk yield. The effect of nutritional deprivation on milk yield can be rapid, substantial, and independent of nutrition prior to the onset of lactation (Barnicoat et al. 1949, Peart 1968, Loudon et al. 1984, Oftedal 1985). Loudon et al. (1984), for example, reported that milk production in red deer was 1.6 times greater in females maintained on pastures with 1,800 kg/ha at 69% digestibility than in females using forages of "low density" with 60% digestibility.

Of the other influences on calf performance we investigated, birth mass was most important. Larger newborns grew more rapidly through early summer than did smaller newborns. A calf of 18 kg at birth would grow 3–5 kg more over the first month of life and weigh 7–8 kg more after 1 month than a calf weighing 13 kg at birth, a 20% difference in BM at 1 month. This probably occurs because absolute growth (kg/day) is greater in large calves, despite similar

incremental growth (%/day) (Bailey and Mears 1990). Advantages of heavier birth mass remained through weaning in both years (Fig. 20). Enhanced growth due to larger birth mass was reported at least to 6 months of age for fallow deer (*Cervus dama*) (Pelabon 1997), at least to 10 months of age for moose (*Alces alces*) calves (Keech et al. 1999), and to 2.5 years of age for white-tailed deer (Schultz and Johnson 1995).

Influences of calf gender, cow age, and in 1997, previous-year nutrition level on growth were mixed. Gender significantly influenced growth from birth to early July in the second, but not the first year. Influences of gender on growth indicated no biological relevant pattern we could discern over summer and autumn and was unrelated to BM at weaning in mid-autumn in either year. We were unable to find significant effects of cow age or previous-year nutrition of the mother on calf growth over summer and autumn.

Cow responses.—As with calves, we expected that parturition date and nutrition would interact to affect fat accretion, conception date, and pregnancy rates of cows (i.e., cows giving birth earlier would be less affected by summer-autumn nutritional deficiencies than late-birthing cows, because nursing demands and thus nutritional demands placed on cows diminish starting when calves are about 4 weeks old [Robbins et al. 1981]). However, we found no significant interactions of parturition date and nutrition on BM, nutritional condition, or breeding dynamics over summer and autumn in either year. Yet each factor had significant, separate effects.

Seemingly small differences in DE content of food during summer and autumn had pervasive effects on every response variable measured for cows over the summer-autumn period. Significant differences in BM appeared by mid-July, only 3 weeks after nutrition treatments were initiated and before strong divergence in DE levels occurred (Figs. 6B and 8B). Even at the point of greatest divergence of forage quality, DE for the medium and low nutrition groups was reduced only 10% and 20% below that of cows in the high nutrition group. Yet, fat levels varied about 75% and 300% between cows on high nutrition versus those on medium and low nutrition.

These results demonstrate a "multiplier" effect (White 1983) regarding forage quality effects on animal performance. In our study, the effect resulted from differences in DE content of food and the reductions in daily food intake as DE content of food declined. Positive relations between forage quality and daily dry-matter intake have long been recognized (Spalinger et al. 1986, Ketelaars and Tolkamp 1991, Minson and Wilson 1994, Grey and Servello 1995). Our results further demonstrate that ruminants cannot substantially compensate for appreciably low forage quality simply by eating more.

The moderate level of nutrition significantly delayed conception date, and the low level effectively precluded pregnancy of most cows. Neither failure to implant nor early embryonic mortality were responsible for these low pregnancy rates; these cows simply failed to enter estrus (Cook et al. 2001*c*).

Significant relations of nutrition, condition, and BM with pregnancy rates and timing of conception have been presented for red deer and caribou (e.g., Guinness et al. 1978*a*, Hamilton and Blaxter 1980, Thomas 1982, Cameron et al. 1993). In elk, significant correlation has been reported between BM and pregnancy rates (Hudson et al. 1991), kidney fat and pregnancy rates (Trainer 1971, Kohlmann 1999), and between kidney fat and timing of conception (Trainer 1971). Nutritional condition is probably more related to pregnancy probability than BM. In our study, estimates of nutritional condition indicated thresholds that may be used for monitoring nutritional status of wild herds. Pregnancy rates declined precipitously as body fat declined below ≤9%, and fat ≤5% precluded pregnancy. Timing of breeding was early and unaffected when fat exceeded 13%, but was increasingly delayed as fat declined below 13%. Of the few cows with 5–7% body fat that bred, timing of breeding was delayed ≤1 month.

Our logistic curves of pregnancy probability as a function of body fat (Fig. 14) differ from that of Kohlmann (1999) (Fig. 36) (we converted his estimates of kidney fat to a body fat basis using equations of Cook et al. 2001*a*). Kohlmann's logistic regression equation, developed using a large sample ($n > 1{,}000$) of elk in Oregon, predicts pregnancy rates ≥40%, no matter how low the

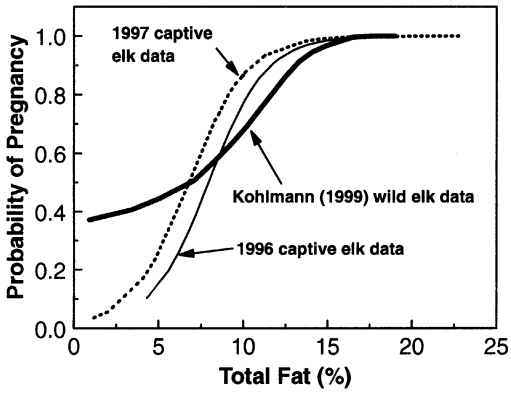

Figure 36. Comparison of pregnancy probability of captive cow elk, as a function of total body fat levels, in our study, northeastern Oregon, and hunter-killed wild elk collected 2 to 4 months post-rut throughout Oregon as presented by Kohlmann (1999). Differences between studies perhaps reflect differences in timing of collection of fat data (i.e., Oct in our study, Nov–Jan in Kohlmann's study).

level of body fat, despite empirical evidence to the contrary (e.g., Gerhardt et al. 1997, Heard et al. 1997, Testa and Adams 1998). Kohlmann's prediction of moderate pregnancy rates at very low levels of condition probably is an artifact of when samples were collected; samples were obtained from hunter-harvested elk from November through January, 2–4 months after the normal breeding season. Elk in his study probably had more fat during the breeding season in September and early October than when they were harvested.

Parturition date's influence on BM and condition of cows in late autumn was significant in only 1 of 2 years and was substantially weaker than that of summer-autumn nutrition. On average, early parturition increased body fat of cows by 1–3 percentage points in autumn, an effect evident only in 1996. We can only speculate about the differences between years, but, in 1996, two-thirds of the cows were in the younger cohort (3 years old) and probably still growing. The additional demands of their growth may have increased their sensitivity to parturition date. We were unable to find a significant influence of parturition date on timing or probability of pregnancy in either year.

Cow age, calf gender, and previous-year nutrition had some influences on cow performance over summer. In 1996, the 3-year-old cows tended to gain more mass or lose less mass than their 5-year-old counterparts. This tendency mirrored mass changes of the previous winter and spring (1995–96) (J. Cook, unpublished data) and probably was caused by an ongoing propensity to grow. We saw no evidence of this tendency during the subsequent winter and spring (1996–97) (J. Cook, unpublished data) or the summer-autumn period of 1997. Thus, this tendency to grow waned after 3.5 years of age. Male calves significantly reduced mass gain, or increased mass loss, of their mothers only in 1996 and only during early July of this year (Fig. 7A). We found no significant gender effect on body mass changes of their mothers in summer-autumn of 1997.

The carry-over effect of summer-autumn nutrition in 1996 on cow BM dynamics in 1997 was surprising. We hypothesized a priori that this carry-over effect would be manifested as a reduction in cow or calf performance caused by nutritional restriction the previous year. However, our findings suggested that cows compensated for previous-year nutritional limitations despite raising a calf (Fig. 9), but this compensation waned by late July. The ability to compensate while lactating for prior nutritional deprivation may reduce the frequency of reproductive pauses. However, Cameron (1994) noted that caribou raising a calf across successive years lost about 13% of their endogenous body reserves each year, eventually inducing failure to conceive. Relations between summer compensation and reproductive pauses undoubtedly depend on levels of forage quality and quantity during summer and the magnitude of nutritional deficiencies occurring in winter.

Finally, our experiment in 1997 to compare influences of nutrition on condition of nonlactating versus lactating cows provided insights about interactions between lactation status and summer nutrition. The low nutrition level that was responsible for poor condition, poor calf growth, and low pregnancy rates of lactating cows nevertheless allowed nonlactating cows to accrue fat and muscle tissues at nearly the same rate as lactating cows fed high nutrition (Fig. 16). Thus, autumn fat levels of nonlactating cows in free-ranging settings are probably less affected by variations in forage quality and quantity than are lactating cows.

Further, lactating cows in mid-autumn typically have lower BM and lower fat levels than nonlactating cows, a lactation increment that can depress pregnancy rates (e.g., Lowe 1969, Trainer 1971, Mitchell and Lincoln 1973, Guinness et al. 1978*a*, Hudson et al. 1991). Although it is tempting to conclude that such a differential is an inevitable cost of lactation, our data indicated that lactating cows can satisfy the costs of raising a calf and simultaneously accrue as much fat by mid-autumn as nonlactating cows, as long as forage quality is adequate. This evidently occurs simply because lactating cows consume more food (Fig. 25). But our data indicated that fat accretion by lactating cows diminishes to a greater extent, as DE content of food declines, than does that of nonlactating cows. Clutton-Brock et al. (1983) showed that pregnancy rates of lactating red deer cows declined significantly (presumably because of declining nutritional condition), but remained high for nonlactating cows, as population density increased. Thus, knowledge of summer forage quality may be important to explain alternate-year breeding or low pregnancy rates given its influence on cow recovery of body fat during lactation.

Yearling responses.—Summer growth of yearling cows was sensitive to DE content of their food. Reducing the DE content of diets from 3.2 to 2.9 kcal/g of the medium nutrition group in early August initiated a slight decline in dry-matter intake (from 125 to 110 g of DM/kg $BM^{0.75}$), and a substantial decline in total DE intake (from 405 to 310 kcal/kg $BM^{0.75}$) and growth rate (0.78 kg/day versus 0.46 kg/day over 28 days in Aug) (Fig. 26A). Growth of yearling cows reported by Cook et al. (1998) was 0.40 kg/day at 300 kcal/kg $BM^{0.75}$ in 1994 and 0.36 kg/day at 280 kcal/kg $BM^{0.75}$ in 1992 (DE content was about 2.9 kcal/g of food; feeding rate was held below ad libitum). These data provide a preliminary equation linking DE intake and growth rate of yearlings (Fig. 37) that is remarkably similar to that for elk calves (Cook et al. 1996).

Onset of puberty of females varies appreciably and usually is considered to be a function of BM (Hamilton and Blaxter 1980, Verme and Ullrey 1984, Sæther and Heim 1993). Hudson et al. (1991) indicated that cow elk must achieve 65–70% of their adult BM before they will breed. The percentage of yearling elk cows pregnant has been reported to be as low as 0–7 (Murie 1951, Cheatum and Gaab 1952, Trainer 1971, Noyes et al. 1996), and as high as 50 (Hudson et al. 1991). Statewide estimates for Oregon were <20% (Kohlmann 1999). Greer (1968) reported that no yearling cows ≤152 kg were pregnant; 10% weighing 152–163 kg were pregnant; and 25% weighing 163–169 kg were pregnant. These data support our observation of BM-specific yearling pregnancy rates (Fig. 26C).

Our data indicate that if summer nutrition is adequate to avoid limitations on calf and yearling growth, then yearling pregnancy rates should typically approach 100%, even in years following severe winters. Yet, the low pregnancy rates typical of yearlings in free-ranging herds suggest that forage on summer-autumn ranges routinely fail to support growth rates necessary for most yearling cow elk to breed. However, there are examples of high yearling pregnancy rates. Buechner and Swanson (1955) reported that 19 of 30 2-year-old cows were lactating in autumn of 1954 in Northeast Oregon, indicating a minimum yearling pregnancy rate of 58%. Hancock (1957: cited by Taber et al. 1982) reported 66% of yearling's ovulating following a mild winter in a Utah herd. Our data indicated that probability of pregnancy as yearlings is to a large extent set by autumn when these animals are calves (Fig. 26C). There may be little opportunity for yearlings

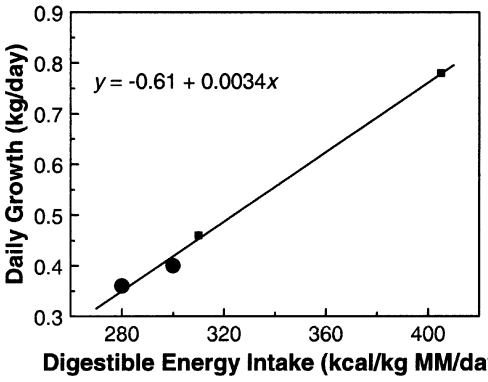

Figure 37. Relation between growth rate of yearling cow elk and digestible energy consumption, northeastern Oregon. Data points represented by squares are from this study (Fig. 26B, in Aug); data points represented by circles are for captive yearling cows during summer presented by Cook et al. (1998). MM = metabolic mass ($BM^{0.75}$).

to sufficiently compensate during their second summer and autumn of life for inadequate nutrition during their first summer and autumn.

Food intake patterns.—Despite our inability to statistically compare differences in food intake among summer-autumn nutrition and parturition-date groups, it was clear the DE treatments influenced dry-matter intake rates and, in turn, DE and protein intake. But the magnitude of the effect was time-specific. Cows adjusted to some extent to the lower DE levels and increased dry-matter intake by late summer. Increasing adaptation of rumen microbes may have contributed, although this should not require more than 2 weeks (Yokoyama and Johnson 1988). Also, elk on the lower quality diets may have increased gut fill by increasing rumino-reticular capacity, such that they were able to process a greater volume of food each day (Hofmann 1988, Owen-Smith 1994). Elk in the low nutrition group developed a more "round" appearance when viewed from the rear by early autumn, compared to a more "elliptical" appearance of elk in the high nutrition group, suggesting gut capacity and content increased in the low nutrition group. Baker and Hobbs (1987) observed this adaptation in mule deer, whereas elk failed to do so in their study. They used nonlactating, nonpregnant animals fed winter forages, and thus their animals did not have the nutritional demands of ours. Differences in nutritional need resulting from differences in production stage or fat levels greatly alter appetite and intake (Ketelaars and Tolkamp 1991, Romsos 1998), so it is not clear that results of Baker and Hobbs (1987) apply to our experimental setting.

Declines we observed in intake of dry matter, DE, and protein as dietary quality declined were greater the first year compared to the second (Fig. 24). The pellet:hay ratio in May and June, before the summer-autumn nutrition trials began, was changed from 55:45 in 1996 to 40:60 in 1997 to better adapt our cows to hay-dominated diets before the nutrition treatments were implemented. This may have accounted for the reduced mid-summer decline in intake observed in 1997. Nevertheless, the negative influences of the low and medium nutrition treatments on cows and their calves were as great or greater in 1997 than they were in 1996.

Additionally, dry-matter intake by cows on the high nutrition treatment began to wane earlier in summer in 1997 than in 1996. Cows in 1996 consumed ≥140 g dry matter/kg $BM^{0.75}$ from mid-July through late September, whereas cows in 1997 maintained this only through mid-August. This difference may reflect greater nutritional requirements of the younger cows to maintain their growth in 1996. The late-summer decline in intake during 1997 is congruent with the set-point concept as applied to large ungulates (Renecker and Samuel 1991). That is, as body fat approaches some upper physiological threshold, appetite and daily intake diminish (Bines and Morant 1983, Price and White 1985). A negative feedback between plasma leptin, originating from adipose tissue, and hypothalmic regulation of appetite (Romsos 1998) may have been responsible.

Our ability to determine the effects of parturition date on intake was limited. Nevertheless, some trends were clear. During early summer, parturition date seemed to interact with nutrition to affect daily food intake, particularly in 1996. Cows giving birth late consumed less food in early July than did early-birthing cows, particularly cows in the low nutrition group. This suggests that dry-matter intake by cows soon after giving birth (<3 weeks) may be suppressed to some extent, particularly if forage quality is relatively poor. The effect seemed transient and of little relevance to cow performance in our data, but if our nutrition treatments had been implemented earlier in the year (e.g., late May versus late June), we may have observed greater negative influences of late parturition on cows in this study.

The dry-matter intake levels we observed (140–150 g/kg $BM^{0.75}$, Fig. 24) by lactating cows are some of the highest reported for elk (Cook 2002). A slightly higher estimate of 150–155 g/kg $BM^{0.75}$ was reported for subadult nonlactating cows during early summer (Jiang and Hudson 1994). Robbins et al. (1981) reported intake of approximately 125 g/kg $BM^{0.75}$ for noncompensating elk cows (i.e., cows not compensating from

winter mass loss) fed high quality alfalfa hay. Intake of the high nutrition group of cows in our study was nearly double that of nonlactating, noncompensating cows fed similar diets in other studies (70–80 g/kg $BM^{0.75}$) (Cook 2002). This large difference merely reflects the considerable nutritional cost of lactation (Oftedal 1985), particularly when combined with the nutritional costs of recovery from winter mass loss (Cook 2002).

Summer-autumn nutritional influences on solid-food intake by calves also were considerable in both years. By mid-September, calves in the high nutrition group consumed 50–100% more than did calves in the medium and low treatment groups. Birth date also influenced intake through most of summer. Our calves began consuming solid food about 40 days after birth, as did those reported by Robbins et al. (1981). Late-born calves started consuming solid food 2–3 weeks later than did early-born calves, a difference about equal to the difference in birth date between the 2 groups.

Digestible energy requirements.—Our data identify general DE requirements for lactating cow elk and their calves during summer and autumn. Here, we emphasize cows because such estimates for calves were identified in a study focusing entirely on calves (Cook et al. 1996). All estimates we present are expressed on a daily, dry-matter basis.

Identifying requirements depends on prior identification of target performance levels and nutritional condition (e.g., see National Research Council 1984). Based on body fat levels, cows in the medium nutrition group were nearly able to maintain their condition across the summer-autumn period (Fig. 16A), and thus their DE level should provide a reasonable estimate of maintenance requirement. After mid-summer, DE was 2.65–2.75 kcal/g (about 60% in vitro digestible DM), and they consumed from 325–375 kcal of DE/kg $BM^{0.75}$/day or about 21,000 total kcal/elk/day (assuming BM of 235 kg), matching estimates calculated for maintenance using a factorial approach by Cook (2002) and those of Haigh and Hudson (1993). But if cows enter the summer period in substantially lower condition than ours did following winter, this level of DE (2.65–2.75 kcal/g) apparently is inadequate for recovery of fat and muscle catabolized during winter (Cook 2002) and will not provide adequate energy for rapid growth of calves during summer and autumn.

Our data for cows in the high nutrition group indicate DE of 2.9–3.0 kcal/g (about 65% in vitro digestibility) satisfies DE requirements to replace winter mass loss of 10%, support lactation, enter winter at ≥15% fat, and provide for rapid calf growth. Cows on this diet consumed 400–425 kcal of DE/kg $BM^{0.75}$/day, or about 25,000 total kcal/elk/day, slightly greater than that calculated by Cook (2002) for elk losing 10% BM over winter (i.e., 385 kcal of DE/kg $BM^{0.75}$/day and 23,000 kcal in mid-July). Declining intake by cows in the high nutrition group after early August in 1997 (Fig. 24) also suggests that slightly lower DE content (e.g., 2.85–2.90 kcal/g, ~63% in vitro digestibility) will support those fat levels we observed in the high nutrition group (although it might take slightly longer to achieve these levels). Digestible energy content ranging above 2.9 kcal/g through mid- to late summer and 2.65–2.7 kcal/g through mid-autumn also may permit equivalent fat accretion, because DE requirement for lactation wanes at this time (Robbins et al. 1981). But such a decline probably would reduce calf growth, and may preclude full recovery of winter mass loss if it is appreciably >10% (Cook 2002).

Only our highest DE level in this study (2.9–3.0 kcal/g) sustained growth approaching the highest levels reported for elk calves (e.g., Hudson and Adamczewski 1990, Cook et al. 1996). It agrees closely with that for the solid food component of diets consumed by elk calves calculated by Cook (2002). Calves in our study consumed 325–350 kcal of DE/kg $BM^{0.75}$ from solid food by the end of the experiments (early November). Cook et al. (1996) reported that rapidly growing calves required 350–370 kcal/kg $BM^{0.75}$ (from milk and solid food combined). The difference probably is accounted for by milk's contribution to DE intake (which we did not measure). Food DE levels required by calves to maintain rapid growth through early November begin to exceed that required by their lactating mothers after early September (assuming winter mass loss of cows is about 10%).

Calf growth ceased in the low and medium groups in mid-September and early October. Food DE levels of 2.3–2.6 kcal/g resulted in DE intake of 125–175 kcal/kg $BM^{0.75}$/day at this time. Cook et al. (1996) reported that calves stop growing at about 150 kcal of DE/kg $BM^{0.75}$.

Digestible energy needs of rapidly growing yearlings are as high as those for calves. Yearlings receiving diets averaging 3.2 kcal of DE/g of food consumed nearly as much dry matter per day (125–130 g/kg $BM^{0.75}$) as did lactating cows. Their DE intake averaged about 400 kcal/kg $BM^{0.75}$/day, slightly higher than that of calves (perhaps not if DE intake from milk were taken into account). This high level of DE intake supported daily growth of 0.75 kg/day and was similar to growth of calves in the high nutrition group (0.70 kg/day), from late May through late August. Hence, growth potential of yearlings and calves, and DE requirements to support this growth, was similar.

In the context of pregnancy probability, however, summer DE requirements of yearlings also probably depend on BM acquired before this summer period. If yearlings face mild to moderate winter conditions as calves, then summer DE requirements might be lower. However, if growth rate was moderate when these animals were calves, then mild winters probably would not reduce the need for forage of very high quality during summer when these animals are yearlings (and so on). Our data clearly show that if these animals face harsh winter conditions, then forage quality during summer and autumn of both the first and second year of life must be high (>2.9 kcal of DE/g) to provide for high rates of yearling pregnancy.

Carry-over Effects

Winter calf survival.—The carry-over effect of greatest initial interest to us was that of summer-autumn nutrition and birth date on the ability of calves to survive their first winter. The hypothesis that delayed breeding and birthing influences juvenile survival during winter assumes that larger body size at the start of winter appreciably enhances survival probability in winter. However, smaller animals might compensate by accumulating considerable fat reserves in autumn (partition less dietary energy for growth and more to accrue fat) and by reducing activity in winter (Verme and Ozoga 1980*a*).

In both winters, calf BM exerted the dominant effect on calf survival. Differences in the relation between starting BM and survival between the 2 years probably reflects differences in our winter feeding regimes. The nonlinear, or perhaps asymptotic relation, between survival and starting BM in the first winter (Fig. 30A) suggests a threshold, above which increasing BM provides little additional advantage. But this threshold is probably an artifact of the experiment's design. Substantially reducing feeding level after mid-winter increased rate of mass loss of the large calves still alive in late-winter (e.g., after 15 Feb, Fig. 31). This feeding regime probably accounts for the nonlinear relation of Fig. 32A as well. Without this reduction, most of the calves that were removed in the last several weeks probably would have "survived" the entire experiment, and probably would have continued to survive if the experiment had been conducted for several more weeks. The latter in particular would eliminate the nonlinear, or asymptotic nature of the first winter's data. In other words, the length of winter and timing and magnitude of negative energy balance over winter will determine the specific relation between BM and number of days that the animals survive. Nevertheless, our data demonstrate a considerable advantage of large body size for surviving harsh winters.

Varying the severity of winter nutritional restriction between winters, from gradually declining to abruptly declining (Table 3), provided some insight regarding how robust the body size-survival relation might be across different winter nutritional regimes. Through mid-January of the 1996 winter experiment, the lowest DE level fed was only about 30% below that normally considered maintenance (e.g., 180 kcal/kg $BM^{0.75}$, Cook 2002). Through the end of January, the largest calves in the study lost only about 5% of their BM and thus appeared resilient to this nutrition level. Yet BM of the smallest calves plummeted, and 5 were removed from the experiment by late January. Not until we reduced DE levels to half of maintenance (mid-Feb) did the larger calves begin to lose appreciable mass (≥10% by late Feb). If the first winter experiment had been

terminated in late February, and thus mimicked better winter forage conditions, 16 of 22 calves weighing <95 kg would have "died," whereas only 4 of 18 that were >95 kg would have "died."

With abruptly declining feeding regime in winter of 1997, calves were removed earlier, and starting BM accounted for less variance (38% versus 63%) in the number of days of winter survived, than in 1996. Nevertheless, our results from both winters indicated greater vulnerability of small calves than large calves to winter conditions over a wide range of simulated winter conditions. Although the nutritional conditions we imposed on these calves were extreme, overwinter mortality rates of ≥75% have been reported for elk calves (Houston 1982).

Why small calves are more vulnerable is not immediately clear, particularly in an experimental setting in which predation, competition for food, and other factors are eliminated or held constant. All calves received equal amount of food in relation to $BM^{0.75}$. Converting to a whole body basis ($BM^{1.0}$), smaller calves actually received more food per kg of mass than did large calves. Smaller calves may have less fat relative to total BM and may have relied more on protein, rather than fat, as a source of endogenous energy. Thus, they would have to catabolize body tissues at a faster rate to provide metabolic energy requirements than would larger calves, because catabolism of protein reaps less useable energy for metabolism than does fat. However, Verme and Ozoga (1980*a*) showed that smaller white-tailed deer fawns accrued substantial fat before winter, despite levels of under nutrition that effectively stunted growth.

Additionally, surface area relative to volume, and thus heat loss, increases with decreasing body size. Small calves on submaintenance diets, therefore, must catabolize more muscle and fat to maintain body temperature than do large calves, and this effect can be substantial (Parker and Robbins 1985). If this is an important cause of differences between small and large calves, then the susceptibility of small calves to winter conditions may be greater in areas appreciably colder or wetter than we encountered (see Cook et al. 1998 for a review of winter temperature and precipitation on western elk winter ranges). Greater difficulty traveling in snow, because of shorter stature, less ability to access and compete for food, and greater susceptibility to predation all might increase winter mortality of small calves in the wild relative to that observed in our study.

Although we found that calf BM at the start of winter significantly influenced winter survival, and birth date was significantly related to BM at the start of winter, we failed to find a significant relation between birth date and winter survival. Only summer-autumn nutrition was significantly related to winter survival. This result does not prove that birth date is unimportant. Rather, it demonstrates that the magnitude of differences in early winter BM resulting from a birth-date difference of about 3 weeks was insufficient to influence calf winter survival under the conditions we simulated. Our data should facilitate modeling calf survival under conditions of more delayed birthing and different nutritional regimes.

Winter cow survival.—This experiment provided an initial evaluation of the relative influence of body condition in autumn versus winter nutrition on winter survival of pregnant cows and their fetuses. The "high" winter nutrition treatment averaged 65% of maintenance and induced about 10% loss in BM (about 15% when adjusted for products of conception), which we assumed to be representative of mass loss of cows in "moderate to normal" winters. The low winter nutrition level ranged from 30–50% of maintenance from late December through early March and was intended to represent severe nutritional conditions during relatively harsh winters. By mid-February, the low nutrition level caused the death of 1 cow, and 3 others had to be removed prematurely (4 of 11 elk). On average, these cows depleted body fat at a rate of 0.83% of beginning fat daily, whereas cows in the high winter nutrition group lost fat at 0.5%/day. Cows in the high group ended winter with about 10% body fat, still in relatively good condition.

Overwinter performance also differed between cows fed medium and those fed high nutrition diets during summer and autumn. Reduced rate of fat loss of the thinner elk (the medium group) suggested some

ability to conserve endogenous body reserves compared with the fatter cows. Nevertheless, body fat by late winter was significantly lower, and 2 of the 10 cows fed medium nutrition diets during summer were removed to prevent death. Further, these cows subsequently aborted despite intensive care and refeeding.

The abrupt decline in loin muscle thickness (Fig. 27D) of these cows also attests to the greater overwinter vulnerability of elk that enter winter in relatively poor nutritional condition. This decline was most evident in the 2 cows removed from the study, despite refeeding 1–2 weeks before the loin was measured. Rapid loin depletion is indicative of advanced catabolism of muscle tissue, and may result in death, perhaps via "mass organ failure" syndrome described by Saltz and White (1991) for mule deer.

Graphs of survival probability (Fig. 28) illustrate the interplay between winter nutrition and late-autumn condition. Under the harshest of our winter nutritional regimes, only cows with at least 15–17% body fat in late autumn had a 50% chance of surviving the winter. Cows entering winter with 7–8% body fat had virtually no chance of survival on this winter nutrition level and had only an 80% chance of survival on our highest winter nutrition level. Thus, vulnerability to nutritional deprivation in winter increases markedly as late-autumn fat levels decline. These results empirically demonstrate for elk what Hobbs (1989) modeled for mule deer.

Birth characteristics and gestation length.—A primary assumption of the hypothesis that skewed sex ratios (i.e., young bulls predominate in the herd) reduces calf survival is that differences in conception date do, in fact, cause similar differences in parturition date. But considerable variation has been reported for gestation length in elk (Taber et al. 1982, Haigh 2001), and the strength of the relation between breeding and parturition date, on which this hypothesis rests, may be weak. Differences in breeding date imposed in 1995 resulted in approximately equal differences in parturition dates of our cows the following spring. But over the next 2 years, the relation was diluted across winter. First, influences of nutrition and body condition on subsequent parturition date were significant only the second of the 2 years, despite being highly related to breeding date both years. Second, autumn condition accounted for 50% of the variation in breeding dates (Fig. 15), but only 14% of the variation in parturition date. Finally, breeding date in 1997 accounted for only 21% of the variation in parturition date the following spring for the 16 cows for which breeding date was known. Berger (1992) reported that late-breeding bison (*Bison bison*) in good condition shorten gestation by up to 15 days, evidently to synchronize births with other females. Our study did not rigorously test the assumption of a strong relation between conception date and parturition date, but our data nonetheless suggest caution regarding this key assumption.

Surprising was our finding that parturition date of the previous year had significant effects on current year's parturition date, gestation length, and birth mass (Fig. 33). This result seems spurious because parturition date did not affect subsequent breeding date and autumn cow condition. The significant relation between parturition date and subsequent gestation length (i.e., cows that gave birth earlier had shorter gestation lengths the following gestation period) possibly suggests a genetic component that would explain the significant relation between previous-year parturition date and current-year parturition date. We documented no carryover effects of summer-autumn nutrition or autumn condition on gestation length or birth mass the following spring.

Parturition date after the cow survival experiment of winter 1998 was correlated to extent of winter nutritional deprivation during this experiment (Fig. 35). Despite severely stressing cows in the low winter nutrition treatment, nutrition did not affect birth mass. These data therefore indicate elk have considerable ability to compensate for winter nutritional deprivation and produce calves with viable birth mass (mean of 15 kg, range of 13–17 kg in our case) by extending gestation length. Moderate extensions ($\leq$15 days) in gestation to compensate for winter starvation were reported for white-tailed deer (Verme 1965, Johannesen 1984). Schwartz and Hundertmark (1993) reported that cow moose fed at 70% of ad libitum and losing 281 g/day in

BM over winter gave birth on average 27 days later than moose fed ad libitum through winter. This compares to about 34 days later on average for our cows that depleted the most fat (90%) overwinter (Fig. 35).

We expected to find evidence that summer-autumn nutrition and winter nutrition would influence birth mass the following spring. For example, Blaxter and Hamilton (1980) reported that, for every 10 kg increase in the mother's mass during the rut, red deer calves weighed 0.5 kg more at birth. However, Hudson et al. (1991) reported that birth mass of elk calves was unrelated to mass of their mothers the previous autumn. Schwartz and Hundertmark (1993) found, as we did, that birth mass of moose calves was unaffected by extent of winter undernutrition.

Nutrition and fat levels after the rut probably have greater influence on birth mass than fat levels during rut. Keech et al. (2000) reported that birth mass of moose calves was positively correlated to body fat levels of their mothers in late winter. Smith et al. (1997) reported temperature in December and January was positively correlated to birth mass of elk at the elk refuge in Jackson, Wyoming, USA. In cattle, Holland and Odde (1992) indicated that influences of nutritional restriction on birth mass remain unclear, but that fetal growth can be affected by severe energy deficiencies.

Additionally, there seems to be general agreement that nutrition during spring has a substantially greater influence on birth mass than does nutrition in winter (Clutton-Brock et al. 1982, Oldemeyer et al. 1993). Clutton-Brock et al. (1982), with red deer, and Smith et al. (1997), with elk, found that birth mass was positively correlated to ambient temperature in spring. Both indicated this was probably caused by effects of warmer temperature on growth of plants. Our decision to provide more than ample nutrition starting earlier (early to mid-March) than most wild herds typically may encounter (Cook 2002) may have masked any potential carryover effects of nutrition or nutritional condition the previous autumn.

MANAGEMENT IMPLICATIONS

Despite our findings of marked effects of summer-autumn nutrition on reproduction and survival, we did not directly test the hypothesis that forage conditions in summer and autumn do, in fact, exert strong limiting influences on free-ranging elk. The extent to which our findings are indeed relevant to management largely depend on how well our nutrition treatments represent the range of forage quality consumed by free-ranging elk. This caveat is particularly important for the low nutrition treatment because its effect was so debilitating. Cook (2002) summarized dietary DE estimates of free-ranging ungulates across much of the western U.S. and Canada (n = 20 studies). Deleting 3 extreme, possibly anomalous data sets, the studies reported ranges of 2.5–3.25 in early summer, 2.25–3.0 in mid-summer, 2.2–2.5 in late summer, 2.0–2.6 in mid-autumn, and 1.25–2.0 kcal/g in late autumn. If these studies provide reasonable estimates of actual diets for wild elk, then (1) the DE levels in our high nutrition group generally exceeded that of free-ranging elk by late summer, (2) our medium nutrition level generally mimicked the higher range of these estimates after mid-summer, and (3) our low nutrition level fell within these ranges by late summer. Thus, if we can assume that these studies collectively represent the range of summer-autumn nutrition of wild elk, we can conclude that all 3 of our summer-autumn nutritional treatments are relevant to wild elk during summer and autumn, at least in the areas reviewed by Cook (2002). It follows that forage quality on some elk summer ranges is inadequate to support rapid growth of calves and subadults or high levels of fat accretion in adults. These in turn may elevate mortality, delay onset of puberty, and induce occasional reproductive pauses.

Nutrition's influence, and particularly the relative importance of nutrition in summer versus that in winter, undoubtedly varies among ecological settings. Years ago, Verme (1969) proposed a classification system that reflected the differential role of nutrition on population demographics among regions for deer in the upper Midwestern U.S. Across the western U.S., plant community composition and plant phenology vary greatly as a function of climate, soils, and topography. Nutrition's influence undoubtedly varies as a result. Trainer (1971) noted

significant differences in fat levels and herd productivity between coastal-Cascade environments and those of inland Oregon. Bomar (2000) reported that broad-scale patterns of recruitment in elk herds in Idaho were significantly related to patterns of climate and vegetative dynamics. Both concluded that nutrition probably was a fundamental mechanism linking biophysical attributes and elk population dynamics. Within a given ecological setting, nutrition's influence probably varies as a function of (1) large-scale changes in habitat that appreciably alter forage abundance and quality, such as from timber harvest (Hett et al. 1978, Gill et al. 1996, Cook 2002) or fire, and (2) herbivore density, because the balance between nutrient demand and nutrient availability is altered as density changes (Fowler 1987).

The key role of habitat for wildlife has long been recognized. But in the case of elk, nutrition's influence on population dynamics has been infrequently studied. Instead, habitat's influences have been examined mainly via radiotelemetry studies of habitat selection. As typically conducted, these studies are fundamentally incapable of accounting for influences of nutrition, or those of other potentially limiting habitat factors, on reproduction, survival, and carrying capacity. Without attendant data on limiting factors, some of the inferences derived from telemetry studies are being questioned (Hobbs and Hanley 1990, Morrison 2001). Probably as a consequence of habitat selection studies, most models developed for large-scale evaluation of habitat suitability for elk largely ignored nutrition or concentrated on variables that simply index forage supply without regard to forage quality (Edge et al. 1990, Cook et al. 1998).

One value of our research is to provide standards of performance with which to gauge the likelihood of nutritional limitation in natural settings (Table 9). Much of our criteria pertain to performance of pregnant or lactating cows. Our data (Fig. 16) indicated that estimates of body condition and breeding performance of nonlactating cows provide less inference of summer-autumn nutritional limitations. These data also illustrate an issue discussed by Verme and Ullrey (1984): as nutritional limitations increase and juvenile survival declines,

Table 9. Estimated levels of performance expected for elk in temperate ecosystems as a function of dietary digestible energy (DE) from mid-summer through mid-autumn[a]. Animal performance estimates are based on late-October and November measurements. For adults, we assume prime-age, roughly 3–12 years old. Adult cow fat levels pertain only to those that lactated over most of summer and autumn; our data indicate nonlactating cows will be fatter than lactating cows, particularly at the lower levels of DE.

Sum–aut nutritional status[b]	Dietary DE (kcal/g of food)[c]	Calf mass (kg)	Yearling cow mass (kg)[d]	Lactating adult cow fat (%)	Yearling pregnancy (%)	Adult pregnancy (%)	Adult cow breeding date
Excellent	>2.90	125 to 145	195 to 230	16 to 25[e]	≥90	≥90	≤30 Sep
Good	2.75 to 2.90	105 to 125	180 to 195	12 to 16	30 to 90	≥90	≤5 Oct
Marginal	2.40 to 2.75	90 to 105	160 to 180	8 to 12	0 to 30	≥70	≤10 Oct
Poor	<2.40	<90	<160	<8	<5	<70	>10 Oct

[a] Relations between nutrition and performance indicated here assume that direct extrapolation from captive to wild settings is reasonable and that the relations are robust across at least moderate variations in winter severity. Thus, these relations are preliminary and should be updated as per findings of additional research. These criteria were developed based on performance of individual elk; some mistakes may result if herd averages are applied to these criteria. For example, if mean fat of lactating cows in a herd in autumn is 14%, this table would predict pregnancy of this herd to be ≥90% and breeding to occur <5 Oct. However, if fat for this herd ranges from 7–20%, then predicted pregnancy rate may be <90% and some cows may bred >5 Oct. Thus, predicting pregnancy and breeding date should be based on fat levels of individuals, rather than on herd averages. Equations of Fig. 14 and 15 and Table 7 provide a means to do so.

[b] "Excellent" summer-autumn nutritional status refers to settings in which there are virtually no nutritional limitations in summer and autumn; therefore, these performance levels approximate the maximum for elk. "Good" is defined as summer-autumn nutrition levels that exert minor limitations on performance, but the magnitude of this effect probably is too small to be of practical relevance. "Marginal" pertains to nutrition levels that may influence reproduction or survival (e.g., enhanced probability of death in winter, delayed breeding, delayed puberty). "Poor" pertains to nutrition levels that markedly affect reproduction and reduce survival probability.

[c] These estimates of DE reflect requirements of captive existence. Energy expenditure of wild elk may be greater, and thus these DE levels should be considered minimum requirements for each level of performance.

[d] Based on our post-rut (Nov) body mass measurements.

[e] The higher levels (>22%) were observed in nonlactating cows.

pregnancy rates tend to remain high because an increasingly large proportion of females escape the nutritional demands of lactation. This may be particularly important where predation on juveniles in summer after birth is relatively high. Thus, high pregnancy rates do not necessarily indicate sufficient nutrition for the complete reproduction cycle (Verme and Ullrey 1984). Conversely, pregnancy rates of prime-aged cows with calves at heel below about 85% probably indicate important summer-autumn nutritional limitations. Similarly, we predict that overall fat levels might be greater in herds experiencing high levels of juvenile mortality in summer than in herds without high juvenile mortality, even if nutrition in both situations is identical. Such an effect might confound comparison of fat levels (Table 9) among herds that experience markedly different levels of juvenile mortality in summer or early autumn.

Our data also provide monitoring standards regarding evaluation of forage and dietary quality (Table 9). Our study adds to the growing body of literature (e.g., see Holter and Hayes 1977, Verme and Ozoga 1980*b*, Lyford and Hubert 1988, Cook et al. 1996, Parker et al. 1999) that indicates energy, at least as much as protein, should be emphasized in studies of forage and dietary quality. But our finding that seemingly small differences in DE content of forage have large effects on the performance of elk suggests some cautions. First, the ability of herbivores to select diets significantly greater in quality than generally available limits the value of general forage quality surveys, except perhaps for relative comparisons across space or time. Dietary quality evaluations that employ direct observations of food selection (Schwartz and Hobbs 1985) provide more reliable data. Second, field and laboratory techniques that cause even a small bias of estimated DE in forage (just 10%) might lead to important misinterpretations of nutritional adequacy. Finally, wild elk may have greater energy demands attributable to free-ranging existence compared to our cows. If so, then our estimates of DE requirements might be conservative.

In our study, influences of parturition date, where they occurred, were relatively minor. Our average difference in parturition date was 24 days in 1996 and 19 days in 1997, and we conclude that influences on breeding date that result in differences in parturition date of 3 weeks or less (Noyes et al. 1996) probably will not have much effect on nutritional condition and pregnancy rates of cows and growth and winter survival of calves. Therefore, productivity of populations probably will be little affected even if the preponderance of breeding is by yearling bulls. In a study of 3 Rocky Mountain elk populations in Washington where calf:cow ratios were declining and mature bull:cow ratios were low (<1.5 branched-antlered bulls:100 cows), Bender et al. (2003) reported that the increasing bull and branched-antlered bull ratios, resulting from changes in bull harvest strategies, failed to influence calf recruitment.

We mention 2 caveats, however. First, a span in parturition date greater than 3 weeks probably would increase parturition date's effect on reproduction and survival. Late breeding caused by either poor nutrition or few mature bulls, harsh winter weather that extends gestation, and late vegetative growth in spring present accumulating stresses that may greatly delay parturition, perhaps sufficiently to reduce reproduction and survival of calves. Second, our study precluded influences of other mortality factors, especially predation, that might interact with parturition date to influence survival. Clutton-Brock et al. (1982) reported that unusually early or late parturition reduces survival over the first several months of life. In predator-rich environments, the classical perception is that juveniles born during the peak period of parturition are less susceptible to predation, because of a "swamping" effect. The more synchronous the parturition period, the greater the degree of swamping. From a nutrition and growth perspective, the earlier the birth the better (to a point, of course), and so the 2 perspectives are not necessarily congruent. Keech et al. (2000) argued for moose in Alaska that the latter is of greater relevance even in predator-rich environments. Findings of other studies that focused on the effect of birth date on juvenile survival are mixed, further clouding the issue. Fairbanks (1993) reported birth date did not influence survival of pronghorn (*Antilocapra americana*) fawns. Guinness et

al. (1978*b*) reported marked increases of mortality during summer and winter for red deer calves born very late (as late as August), but otherwise noted little effect of birth date on calf mortality. Singer et al. (1997) reported that birth date of elk calves in Yellowstone was unrelated to mortality from predation in summer ($P = 0.146$), was marginally related to mortality from all causes in summer ($P = 0.066$) and in winter ($P = 0.065$), and that birth mass had greater influences on survival than did birth date. We suspect that the magnitude of differences in birth date and differences in causes of mortality may account for different results among studies.

Our study implicates, but provides no direct proof of nutrition's contribution to declines of elk herds. Nor did it provide insights regarding the changing role of nutrition, i.e., if nutrition was adequate to support the growth of herds over most of the past century, why has it become inadequate in recent years? Density-dependence, an oft-cited mechanism of bottom-up population regulation (Fowler 1987), provides one explanation. Recent population declines following many years of growth support this concept, and evidence indicates increasing influences by elk populations on vegetative composition and successional trajectories (Kay 1995, Riggs et al. 2000) on summer-autumn ranges. Herbivore-induced changes in the value of the forage base over time could cause density-dependent feedbacks to be manifest over time at sequentially lower herbivore densities (Irwin et al. 1994, Riggs et al. 2000). Advancing plant succession that increases overstory canopy cover and decreases understory vegetation may have important effects on carrying capacity (Hett et al. 1978, Peek et al. 2001) and herd productivity (Gill et al. 1996), and has been implicated as a cause of declining ungulate herds in the Pacific Northwest (Bomar 2000, Peek et al. 2002). Interactions between herbivore density and episodic disturbance regimes (e.g., fire, logging) probably modify the influence of chronic herbivory on vegetative trajectories and stable states, and thus on herbivore carrying capacity over time (Riggs et al. 2000).

At the same time, cougars (*Puma concolor*) (e.g., Keister and Van Dyke 2002) and bears (*Ursus americana*), large predators capable of killing elk, apparently are increasing in the Northwest. Thus, the issue of how to manage elk productivity is developing into a classic top-down versus bottom-up controversy, as it has already regarding declines in western deer herds (Carpenter 1998). Such either-or explanations are likely to be unrealistically simplistic in most situations, particularly over the long term. Our data implicate a chronic nature of nutritional influence that in turn suggests an additive or interactive relation between nutrition and predation. Whereas reductions in predation rates may elevate herd productivity, particularly in the short-term, long-term vegetative trajectories and attendant density-dependent thresholds are more likely to function as ultimate limiting factors.

Considerably more knowledge is needed regarding influences of habitat, nutrition, and predation/hunting effects on ungulate populations. Nutrition is the habitat feature most likely to have a predominant influence on reproduction, survival, and thus population demographics (Cook et al. 1998). If nutrition's influences are to be understood, conventional studies of habitat selection must be augmented with innovative and rigorous designs that explicitly examine contributions of limiting resources. Referring to wildlife-habitat studies, Morrison (2001) observed that "We seem to be stuck in a revolving framework of endless site- and time-specific studies," and as a result, "our understanding of the causes of distribution, abundance, and performance are not advancing." Similarly, simple predation studies may document the occurrence of predation, but in many cases provide insufficient information to conclude predation's effect as a regulating or limiting factor. At least such studies should examine the effects of multiple regulating and interacting factors. Our study demonstrates that nutrition during summer and autumn is a key factor that should no longer be dismissed as inconsequential.

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Received 2 July 2002
Accepted 21 January 2003