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Nutrition and Parturition Date Effects on Elk: Potential Implications for Research and Management

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Introduction

Understanding and managing those mechanisms that affect population dynamics comprise, perhaps, the most fundamental aspect of wildlife management (Caughley 1977). Biologists generally categorize these

mechanisms as either top-down (predator-driven) or bottom-up (habitat- or animal-density driven). Bottom-up influences involve imbalances between increasing animal density and key habitat resources. For large ungulates, abundance and nutritive value of forage are commonly thought to be the primary mediators of bottom-up regulation (Caughley 1979, McCullough 1984). Certainly, nutritional deficiencies can have extensive and often acute effects on reproduction, growth, development and survival (Verme and Ullrey 1984, Cook 2002).

Much research has focused on nutritional effects, particularly for livestock (National Research Council 1984) but also for deer (*Odocoileus* spp.) (Verme and Ullrey 1984, Parker et al. 1999), caribou (*Rangifer tarandus*) (Thomas 1982, Cameron et al. 1993, Cameron 1994) and moose (*Alces alces*) (Schwartz and Renecker 1998). A research emphasis on nutrition has been largely lacking for elk (Cook 2002), except to some extent in Colorado (e. g., Hobbs et al. 1982) and in relation to game-farming in Canada (Haigh and Hudson 1993). Moreover, nutrition has largely been discounted in national forest models used to reconcile elk habitat quality with other land management concerns (Edge et al. 1990). This reflects an apparent perception that nutrition is not a particularly important factor affecting most elk herds. It may also reflect uncertainty regarding how to evaluate nutritional resources across large landscapes in a manner relevant to ungulate populations.

Despite increased attention to nonforage aspects of habitat, such as roads and cover, productivity and population size are declining in a number of northwestern elk herds (Irwin et al. 1994, Gratson and Zager 1999, Ferry et al. 2001). This has spurred a reconsideration of the broader range of factors that may be contributing to herd demographics. Beyond nutritional limitations, low numbers of mature bulls (e. g., less than 5 bulls to 100 cows [Schommer 1991]) was considered a potentially important cause of declines. Noyes et al. (1996, 2002) demonstrated that such low numbers of mature bulls can delay breeding up to 2 or 3 weeks, thereby delaying and desynchronizing parturition. Ultimately, such effects might reduce calf survival due to a variety of proximate causes, primarily through winter mortality and perhaps through predation.

Despite a perception that nutrition on summer range is rarely limiting in the western United States (e. g., Marcum 1975, Wallmo et al. 1977, Lyon 1980, Nelson and Leege 1982, Leege 1984, Christensen et al. 1993, Unsworth et al. 1998), we opted, in our research, to investigate the potential for summer-autumn

nutrition to contribute to bottom-up regulation. Nutritional requirements are appreciably elevated to support key summer-autumn life processes, such as lactation, juvenile growth and development, and recovery of mass lost during winter (Verme and Ullrey 1984, Oftedal 1985, Cook 2002). Forage quality and quantity may be greatest during the growing season, but it may nevertheless be insufficient to consistently satisfy high nutritional requirements during summer and autumn (e. g., Julander et al. 1961, Pederson and Harper 1978, Verme and Ullrey 1984, Merrill and Boyce 1991, Crête and Huot 1993, Parker et al. 1999, Alldredge et al. 2002).

This study was conducted from summer 1995 through spring 1998 using a captive herd of 57 cow elk to achieve three primary goals. First, we wanted to estimate the extent to which summer-autumn nutrition and parturition date could each influence reproduction and survival, and we wanted to explore the extent to which these two factors might exert interactive influence. Second, we wanted to quantify the nutritional requirements of lactating cows with calves. Third, we wanted to quantify the relationship between magnitude of nutritional restriction and magnitude of reduction in reproduction and survival.

We tested hypotheses regarding influences of summer-autumn nutrition and birth date, specifically those that pertain to direct effects of summer-autumn nutrition and birth date on reproduction and those that pertain to carry-over effects, across seasons, of nutrition and birth date on subsequent reproduction and survival. Herein, we briefly review findings of the study and discuss their implications.

Study Area and Elk Herd

The study site was 20 miles (30 km) west of La Grande in the Blue Mountains of northeast Oregon in forest zones at 4,200 to 4,400 feet (1,300–1,350 m). Facilities consisted of two pen complexes. The primary complex housed the cows year-round and consisted of six 1.85-acre (0.75-ha) pens. Small barns with stalls were built in each pen and were used for individualized feeding, weighing and handling. A smaller complex was used to hold the calves after they were weaned. It consisted of three 1-acre (0.4-ha) pens that were devoid of vegetation.

We used two cohorts of bottle-raised female elk captured from wild stock in northeast Oregon, the first born in 1991 ($n = 22$) and the second born in

1993 (n=35) (Cook et al. 1996). All bulls used for breeding were from wild stock at the Starkey Experimental Forest and Range and were at least three years old.

Methods

The study consisted of three primary experiments to evaluate relations between nutrition, birth date and reproduction-survival.

1. Cows and their calves were fed three levels of digestible energy (DE) ad libitum (Figure 1) from late June through early November in 1996 and 1997. These levels of nutrition were selected to represent dietary DE levels identified on elk summer ranges in northeast Oregon.
2. Early and late birthing treatments were induced in spring 1996 by placing a bull with half the cows in September and with the other half in October 1995. Early and late parturition was included in the summer experiments of 1997, based on postbirth stratification rather than by inducing breeding dates as during the rut of 1995.
3. Influences of summer-autumn nutrition levels and birth date on winter survival of calves were evaluated by feeding during winter a submaintenance ration, to mimic that likely to be realized under harsh winter conditions, and by monitoring number of days survived from early December through mid-March during winters 1996 to 1997 and 1997 to 1998.

Additionally, we conducted several supplementary experiments.

1. During summer 1997, cows that failed to breed the previous autumn were separated into two nutrition groups, one receiving the high nutrition, the other the low nutrition level, identical to those fed to lactating cows in the primary summer-autumn nutrition experiment of the same year. This provided insights of the potentially different effects of summer nutrition on lactating versus nonlactating cows.
2. From early December through early March 1997 to 1998, all pregnant cows were stratified into three winter nutrition levels, with the intention of comparing winter nutritional condition and late-autumn nutritional condition (i. e., ingesta-free body fat) influences on fetal survival. Results of the experiment also allowed an assessment of winter and late-autumn nutritional condition on cow survival.

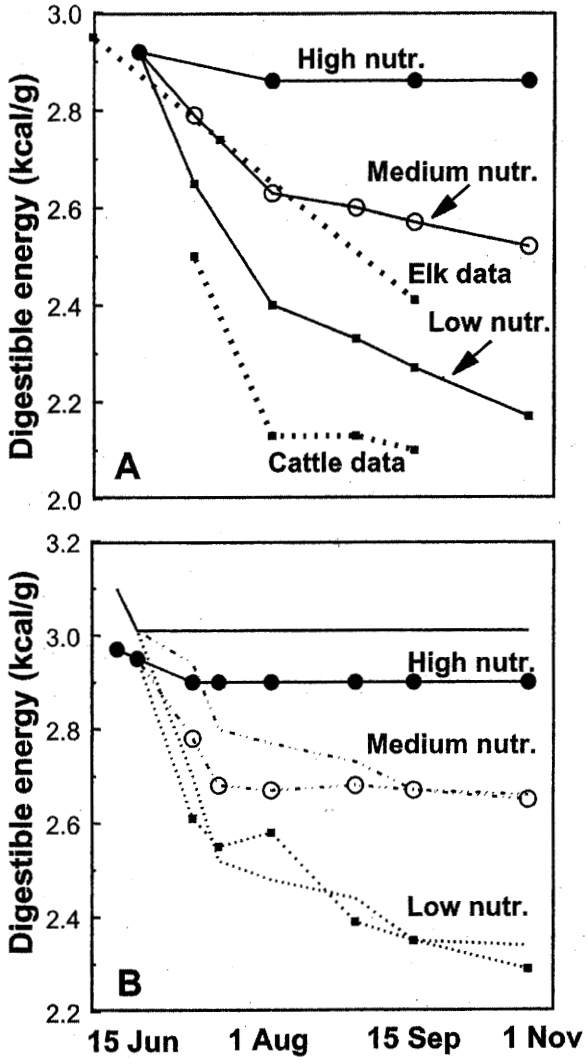


Figure 1. In graph A, target digestible energy (DE) content of food offered to cow elk and their calves from late June through early November, 1996 and 1997. Dashed lines labeled "Elk" and "Cattle" show dietary DE levels of elk (J. G. Cook, unpublished data 1995) and cattle (Holechek et al. 1981) determined during dry years at moderate to low elevations in forest zones in the Blue Mountains of northeast Oregon. The average of these two 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).

Response variables included mass change of cows, calves and yearlings, nutritional condition of cows, indexed by percent fat of the ingesta-free body (determined using the LIVINDEX score [Cook et al. 2001a]), pregnancy rates and timing of breeding of cows and yearlings, number of days of winter survived by calves during the calf winter survival experiments, and survival of cows and their fetus during the cow winter nutrition experiment. The winter experiments were designed to determine survival without allowing animals to die. Threshold criteria were established based on percent mass loss, body temperature, behavior

and appearance from which to proclaim the animals "dead." They were then removed from the experiments and provided care and abundant food (a total of 5 elk of 110 died in these trials). During the two winters preceding both summer nutrition experiments, pregnant cows were fed a moderately submaintenance diet to induce about 10 percent body mass (BM) loss, to mimic mass loss similar to that during mild to normal winters. In March of both years, elk were placed on ad libitum diets of high quality food to eliminate nutritional restriction on fetal development during the third trimester.

In all cases, significant results refer to P values less than or equal to 0.05.

Results

Summer-autumn Nutrition, Parturition Date Experiments

The induced breeding periods of autumn 1995 provided 40 pregnant cows with two parturition pulses for the summer experiments: May 26 (range = May 12 to June 10) and June 19 (range = June 11 to June 29). Breeding in autumn 1996 provided 30 pregnant cows for the summer experiments. Postbirth stratification of birth date provided early-late parturition treatments of June 1 (range = May 20 to June 9) and June 20 (range = June 10 to July 8).

In summer-autumn 1996, parturition date and nutrition significantly affected cow BM changes, but to a markedly different degree. At the end of the experiment, cows on the high nutrition treatments averaged 5 and 10 percent heavier, approximately 25 pounds (12 kg) and 50 pounds (23 kg) heavier, than cows in the medium and low nutrition treatments, respectively. The parturition date increment amounted to 2 to 3 percentage points, a mass difference of about 10 pounds (5 kg). Mass dynamics followed a similar trend during the second summer experiment of 1997. Body fat also was significantly related to summer-autumn nutrition levels in both summer experiments, but was unrelated to parturition date (Figure 2). The marked effects of the high versus low nutrition levels evident for lactating cows was not evident for nonlactating cows fed the same two dietary levels (Figure 2), indicating a substantial interaction between lactation status and summer-autumn nutrition on body fat accretion in cow elk.

The low nutrition treatment effectively precluded pregnancy by most cows (about 80 percent of these cows failed to become pregnant), and the medium nutrition treatment significantly delayed timing of breeding. Parturition date failed to influence either pregnancy or timing of breeding in either year

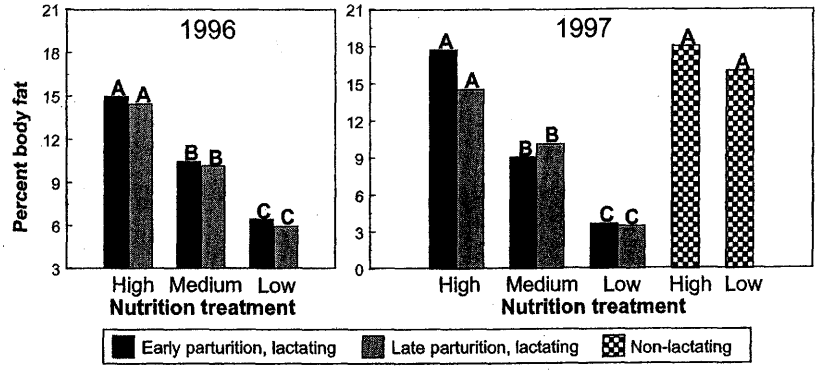


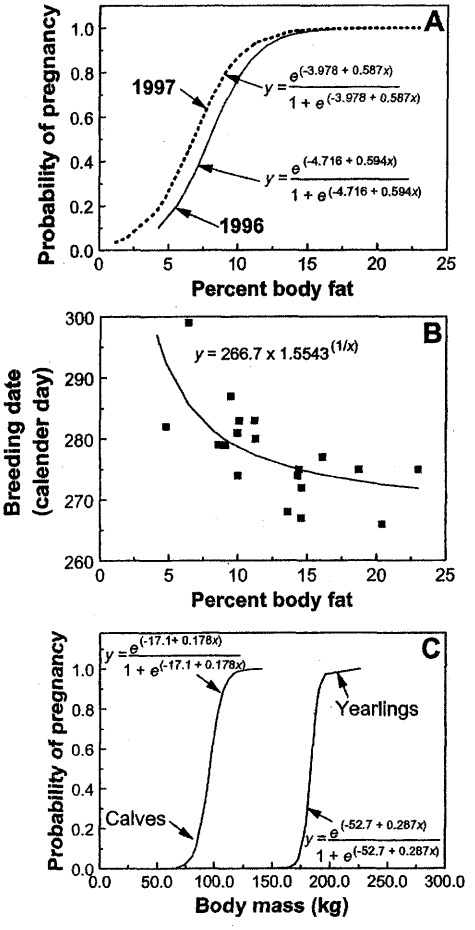
Figure 2. October ingesta-free body fat levels of cow elk across three levels of summer-autumn nutrition and two levels of parturition date. Within years, vertical bars with different letters differ significantly

(Figure 3A, B). Pregnancy failure resulted from a failure to enter estrus (Cook et al. 2001b). Body fat during the rut was significantly related to breeding probability and timing of breeding, and it provided a basis for prediction equations for both of these responses (Figure 3C).

Body size of calves by late June, when nutrition treatments were implemented, was significantly inversely correlated to their birth date and positively correlated to their birth mass. Both variables together accounted for about 90 percent of the variation in late-June BM. Results demonstrate the head-start advantage of early birth, and also indicated that daily growth rate of calves larger at birth was greater than that of smaller calves at birth. Growth starting at the time nutrition treatments were implemented in late June was profoundly influenced by nutrition (Figure 4) in both years. Body mass of calves at the end of autumn was a function of summer-autumn nutrition and, inconsistently, their birth date. Late-born calves in the low and medium nutrition groups overcame their late-start disadvantage, catching up with their early-born counterparts in their respective nutrition groups in 1996 (Figure 4A). In 1997, late-born calves in the high nutrition group also caught up with early-born counterparts (Figure 4C).

Pregnancy of yearling cows ($n = 21$) was significantly correlated to both their size as calves the previous autumn (1996) and to their size in autumn 1997 (Figure 3C). All five yearling cows in the previous-year high summer-autumn nutrition group, three of seven in the previous-year medium group and only one of seven in the previous-year low nutrition group bred (i. e., the summer-autumn nutrition treatment these yearlings received when they were calves).

Figure 3. In graph A, logistic relations between ingesta-free body fat during the breeding season and pregnancy probability of adult lactating cows in 1996 and 1997. In graph B, nonlinear relations between body fat during the breeding season and timing of breeding of lactating cows during 1997. In graph C, logistic relations between probability of breeding for yearlings in 1997, based on body mass during the rut in 1997 and body mass when these yearlings were calves the previous autumn (1996).



Calf Winter Survival Experiments

Forty calves in winter of 1996 to 1997, with BM ranging from 135 to 310 pounds (61–140 kg) (mean = 212 pounds [96.3 kg]) and 30 calves, with BM ranging from 125 to 290 pounds (57–131 kg) (mean = 222 pounds [101 kg]) in winter of 1997 to 1998 were available for these experiments. We varied feeding regimes of calves between the two winters. In the first winter, the magnitude of deficiency was increased gradually to about half of maintenance by mid-February. In the second, the magnitude of deficiency was increased relatively abruptly to half of maintenance by early January and held constant through the rest of winter.

In both winters, BM of calves was significantly correlated to the number of days of winter they were able to survive (Figure 5A, C). Smaller calves lost

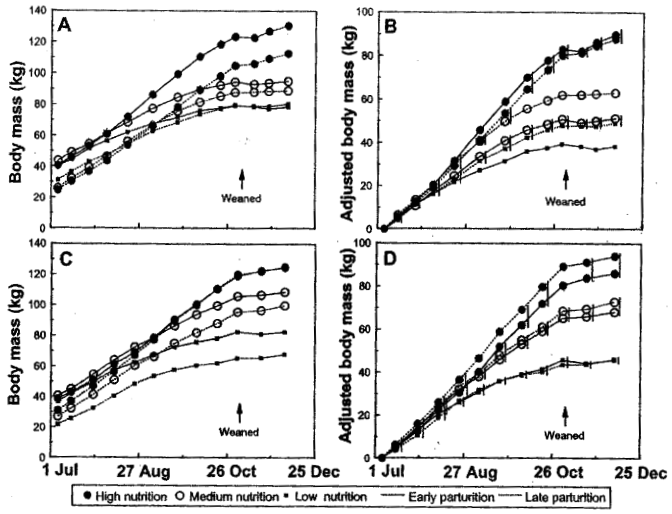


Figure 4. Body mass of elk calves during summer and autumn 1996 (A, B) and 1997 (C, D) across three levels of summer-autumn nutrition and two periods of birth date. Actual body mass is presented in graphs A and C. In B and D, body mass was adjusted to remove effects of birth date and birth mass, by subtracting mass at the start of the time period (early July) from all subsequent mass estimates. Data values not connected by vertical lines differ significantly within weekly periods.

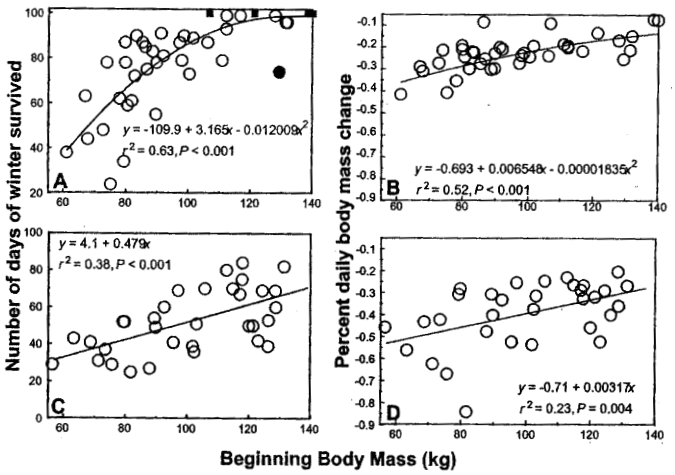


Figure 5. Number of days of winter survived (A, 1996–1997; C, 1997–1998) and rate of body mass loss (B, 1996–1997; D, 1997–1998) of elk calves as a function of their body mass at the start of winter. The four solid squares are data for calves that survived the entire winter experiment, and the solid circle indicates a data point treated as anomalous and excluded from the regression equation (but not the associated statistical parameters).

BM at a relatively faster rate than did larger calves (Figure 5B, D), indicating the mechanism accounting for reduced tolerance of smaller calves to winter undernutrition. Differences in feeding regime between the two winters probably accounted for the different functional responses of calves in the two winters (i.

e., nonlinear in 1996, linear in 1997, Figure 5A versus 5C). Additional analyses indicated that their nutrition level of the previous summer-autumn, but not their birth date, was significantly related to number of days that calves survived in winter (Cook et al. 2004).

Winter Survival of Cows and Fetuses

This experiment was conducted in 1998 with 40 pregnant cows divided equally among 4 treatment groups—high summer-autumn nutrition with high (45 percent of maintenance), moderate (55 percent of maintenance) and low (65 percent of maintenance) winter nutritional deprivation, and medium summer-autumn nutrition with low winter nutritional deprivation.

Summer-autumn nutrition and winter nutritional deprivation significantly influenced end-of-winter BM and fat levels (Figure 6A, B). Body fat of cows on the high winter nutritional deprivation treatment plummeted such that they ended winter with body fat equivalent to that of cows in the medium-summer-nutrition, low-winter-deprivation treatment group, indicating important interactive influences of summer and winter nutrition. One cow died and five particularly emaciated cows were removed from the study to prevent death. Four of these cows were in the high-summer-nutrition, high-winter-deprivation group; the other two were in the medium-summer-nutrition, low-winter-deprivation group. No cows lost their fetus prior to their removal from their study, but two aborted two weeks to two months after their removal and refeeding had been initiated. Both of these were in the medium-summer-nutrition, low-winter-deprivation group. Although limited, these data suggest elk cows may typically die before they abort. The mortality data provided an opportunity to develop a logistic model comparing effects of body fat in late autumn and the winter nutrition levels we implemented on survival probability (Figure 6C). This model probably is specific to our experimental setting and should not be considered robust across a wide variety of winter range conditions.

Discussion

Our results show that relatively small differences in DE content of food consumed by elk in summer and autumn can have very strong effects on fat accretion, timing of conception, probability of pregnancy of lactating cows, calf growth, yearling growth (see Cook et al. 2004) and yearling pregnancy rates.

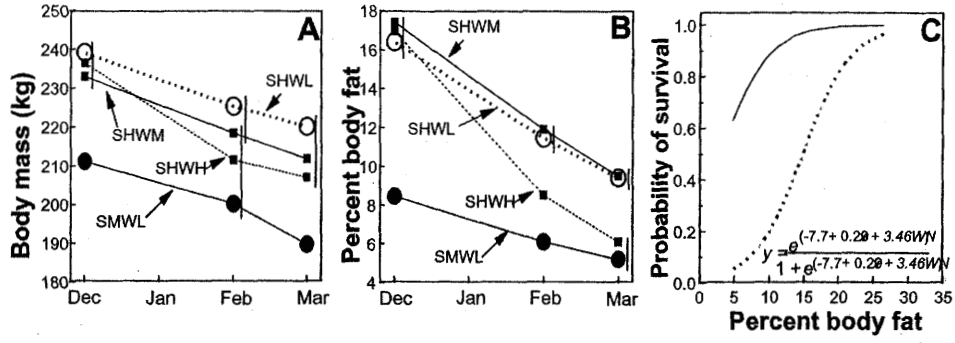


Figure 6. Body mass (A) and ingesta-free body fat (B) of pregnant cow elk during winter (1997–1998) across four summer-autumn and winter nutritional deprivation treatments: SHWL = high summer-autumn nutrition, low winter nutritional deprivation; SHWM = high summer-autumn nutrition, moderate winter nutritional deprivation; SHWH = high summer-autumn nutrition, high winter nutritional deprivation; and SMWL = medium summer-autumn nutrition, low winter nutritional deprivation. Within monthly time steps, data points not connected by vertical lines differ significantly. Data were used to calculate logistic relations (C) between probability of winter survival and late-autumn body fat ($P = 0.073$) at two levels of winter nutrition (WN) deprivation ($P < 0.05$) (low-to-moderate deprivation = solid line; high = dotted line). In the logistic equation, *WN* is an ordinal variable with values of 1 for high winter nutritional deprivation and 2 for low-to-moderate winter nutritional deprivation.

Effects of summer-autumn nutrition on fat accretion of cows and growth of calves significantly influenced their survival probability under harsh winter conditions.

Earlier birth usually resulted in larger size 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 evaluated. Despite a clear head-start growth advantage for calves due to early birth, our data suggest that delays in parturition, expected due to a very low ratio of mature bulls to cows (two to three weeks [Noyes et al. 1996, 2002]), are of insufficient magnitude to appreciably affect reproduction and survival in elk (see also Bender et al. 2002). To some extent, this finding may reflect accelerated growth of some (but not all) late-born calves that eliminated the head-start advantage of early birth. These faster-growing calves tended to be heavier at birth or were male, both of which contributed to faster growth and both of which occurred more frequently late in the parturition period. Additionally, Cook et al. (2004) reported some evidence indicating that delays in breeding did not necessarily result in similar delays in parturition, and Berger (1992) reported that late-breeding bison (*Bison bison*) in good condition shortened gestation by up to 15 days, synchronizing births with

other females. Thus, much can occur to compensate for delayed breeding on the resulting calf crop by the time calves are 6 months old, just prior to their first winter, thereby obscuring the implications of moderately-delayed breeding. But, we note a potentially important caveat. Because our captive animals were not subjected to predation, this study could not evaluate the effect of parturition synchrony on predation-related mortality (see Keech et al. 2000); thus, it may be possible that delayed and desynchronized parturition effects are realized through a predation-mediated mechanism even where calf growth and survival is not constrained by nutrition directly.

That nutrition affects reproduction and survival was hardly surprising, but the extent to which relatively small differences in DE content of food (a maximum of 20 percent between the high and low nutrition levels, Figure 1) induced large differences in animal performance was surprising. This finding confirmed the multiplier-effect noted by White (1983); it occurred due to the combination of reduced DE concentration in food and the effect of reduced food quality on daily dry matter intake, evidently a result of reduced digesta passage rates. Ruminants cannot be expected to compensate appreciably for poor forage quality simply by eating more; they instead eat less as quality declines (see also Minson and Wilson 1994, Grey and Servello 1995). Thus, wild ungulates can be limited by nutritional quality of their forage, even in the face of what might appear to be abundant food quantity (Riggs et al. 1996).

In addition to marked effects on calf growth, probably the greatest effect of summer-autumn nutrition on animal performance during this season was reduction in pregnancy rates. Our data indicated a marked threshold effect of about 9 percent body fat, below which the probability of breeding declines precipitously. However, our study also demonstrated what has been supposed (e. g., Mautz 1978) and remains a suspicion of some (Parker et al. 1999: 38)—that effects of nutritional deficiencies occurring in summer-autumn often appear after summer-autumn, particularly during the subsequent winter and spring if winter conditions are sufficiently harsh. Although observations of winter mortality at first glance may implicate winter conditions as the limiting factor (e. g., the bottleneck of winter range [Wallmo et al. 1977]), the potentially predisposing contributions of summer-autumn nutrition to winter mortality should not be categorically discounted without reliable collaborative data.

Additionally, high pregnancy rates of cows should not necessarily be considered proof that summer-autumn nutrition is adequate and, thus, is of little

concern for management. Summer-autumn nutrition that is just adequate to support high pregnancy rates is not necessarily adequate to avoid predisposition of cows to winter starvation, and it is inadequate (1) to support high growth rates of calves and yearlings, (2) to preclude predisposition of calves to winter starvation, and (3) to support high levels of breeding by yearling cows. Moreover, prime-aged animals in herds existing on marginal levels of summer nutrition just adequate to support high pregnancy rates in most years may be small-bodied (see Crête and Huot 1993), and such herds might be prone to substantial year-to-year variation in vital rates due to annual variation in weather. Under these marginal nutritional conditions, how habitats are managed may have particularly important influences on population dynamics.

A goal of this study was to identify nutritional requirements for various levels of performance. Our findings indicate DE levels of at least 82 kilocalories per ounce (2.9 kcal/g) of food over summer into early autumn are required by adult lactating cows for levels of performance approaching the genetic maximum for adult elk. Such a level resulted in daily DE intake of 162 to 172 kilocalories per pound of $BM^{0.75}$ (400–425 kcal/kg of $BM^{0.75}$). This level simultaneously satisfies requirements for lactation and recovery from previous-winter mass loss; although, it (82 kilocalories per ounce, 2.9 kcal/g) might be slightly deficient for supporting maximum growth of juveniles (Verme and Ozoga 1980) and yearlings (Cook et al. 2004). Elk in our medium nutrition treatment approximately maintained body fat levels at a constant level through early autumn (see Cook et al. 2004) and, thus, provided an estimate of maintenance for lactating cows during this period. Digestible energy content of their food ranged between 75 to 78 kilocalories per ounce (2.65–2.75 kcal/g) of food, resulting in daily DE intake of 131 to 152 kilocalories per pound of $BM^{0.75}$ (325–375 kcal/kg $BM^{0.75}$). This estimate agrees closely with that presented by Haigh and Hudson (1993), when converted to a $BM^{0.75}$ basis, and the $BM^{0.75}$ estimate calculated using a factorial approach by Cook (2002). However, it is markedly greater than previously estimated for elk by Nelson and Leege (1982, see Cook 2002). Their estimate (75–78 kilocalories per ounce, 2.65–2.75 kcal/g) may satisfy maintenance (i. e., constant body fat levels) of adult lactating cows, but it definitely will retard growth of calves and yearling cows (Cook et al. 1996, 2004) and probably will preclude recovery by adult cows of all mass lost the previous winter if the winter is harsh (Cook 2002). Occasional reproductive pauses (Cameron 1994) by individuals might occur in elk herds existing on such a maintenance plane of nutrition.

It is clear that nutritional requirement should be considered as a gradient, along which different levels of performance can be expected. Thus, nutritional requirements are most relevant in the context of animal performance targets, which of course is largely a function of what the public and wildlife managers expect or desire. One value of our research is to provide standards of performance (Table 1) with which to gauge the likelihood of nutritional limitation and to relate animal performance to nutritional resources in management settings. We mention several precautions for these guidelines. First, they are intended to apply to lactating cows because we assume that game managers are concerned primarily with productivity of their cows, not merely the maintenance of nonreproductive cows. Second, high mortality of juveniles, particularly in summer and early autumn, can mask inadequate nutrition because adults are spared to some extent the nutritional demands of raising an offspring (Verme and Ullrey 1984). It may be that overall fat levels of cows in herds experiencing high juvenile mortality in summer are greater than those in herds with low mortality, despite identical nutritional environments for both. Finally, our finding that seemingly small differences in DE content of forage have large effects on the performance of elk suggests the need for some caution for forage quality surveys. The ability of herbivores to select diets significantly greater in quality than generally available (Schwartz and Hobbs 1985) restricts the interpretive value of general forage quality surveys. Also, field and laboratory techniques that cause even a small bias of estimated DE in forage (just 10 percent) also might lead to important misinterpretations of nutritional adequacy.

Research and Management Implications

Our study 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 depends 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. This low level was based on the actual dietary quality of cattle (Holechek et al. 1981) and elk (J. G. Cook, unpublished data 1995) determined in low-to-moderate elevation in forest zones during dry years in the Blue Mountains of northeastern Oregon. Also, based on the review of Cook (2002), DE content of wild herbivore diets typically

Table 1. Estimated levels of performance expected for elk in temperate ecosystems as a function of dietary digestible energy (DE) from midsummer through midautumn. Animal performance estimates are based on late-October and November measurements. For adults, levels apply to prime-aged, roughly 3 to 12 years old, lactating cows.

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

[a] Caveats and suggestions for proper use of these guidelines are described in detail by Cook et al. (2004).

[b] "Excellent" is defined as summer-autumn nutritional levels in which there are virtually no nutritional limitations. "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.

ranges from 71 to 92 (2.5–3.25) in early summer, 64 to 85 (2.25–3.0) in midsummer, 62 to 71 (2.2–2.5) in late summer, 57 to 74 (2.0–2.6) in midautumn, and 36 to 57 kilocalories per ounce (1.25–2.0 kcal/g) in late autumn, based on western U. S. and Canadian studies ($n = 20$). 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 midsummer and (3) our low nutrition level fell within these ranges by late summer. If so, it may be reasonable to speculate that marginally adequate to inadequate summer-autumn nutritional conditions prevail in many areas of the West. Where this is in fact the case, some of the consequences that can be expected include low or declining herd productivity, reduced hunting opportunity, increased severity of die-offs in relatively harsh winters and perhaps increased animal damage on agricultural land.

Elk herd declines in the Northwest are becoming a markedly contentious issue in the region, spawning (1) a plethora of newspaper articles decrying reduced hunting opportunity, calling for widespread predator control and accusing mismanagement by state wildlife departments, (2) new, expensive research to identify causes, and even (3) state-level legislative directives. These

declines, along with the more widespread and recognized declines in mule deer populations (Carpenter 1998), are creating serious new challenges for large-ungulate biologists in the 21st century. Causes of declines are being debated (see Johnson et al. 2004), and contributions of nutrition (among other factors) have been postulated, acting through density-dependent mechanisms (McCullough 1984, Fowler 1987, Irwin et al. 1994) or via advancing forest succession in some areas (Gill et al. 1996; Bomar 2000; Peek et al. 2001, 2002) following years of fire suppression and, more recently, curtailment of timber harvest on federal land.

Despite a rich history of elk research over the last three decades, there has been little focus on influences of nutrition on elk herd abundance, productivity and demographics, nor has there been much focus on how management's influence on forage quality and quantity might affect these population attributes. Similarly, nutrition's role has been discounted in most of the habitat models and habitat evaluation procedures used by federal and state land and wildlife management agencies to manage vast areas on behalf of elk (Edge et al. 1990). Findings of our study and others indicate that nutritional attributes of habitat are at least as important for habitat modeling and planning as those habitat attributes typically included in these models and procedures (e. g., thermal cover, hiding cover, distance to roads). This is true whether elk herds are declining or not. Parker et al. (1999) noted that nutrient requirements, foraging and digestive efficiencies, and forage characteristics provide functional cause-and-effect relations that influence nutritional condition, body mass dynamics and, ultimately, reproduction and survival. And, most interrelations among them are quantitatively predictable. Thus, nutritional ecology, "offers the prospect of a quantitative, predictive and general theory of key relations between" large ungulates and their habitat (Parker et al. 1999:6). A number of efforts exist to model nutritional influences and nutrition-based carrying capacity for elk (e. g., Hett et al. 1978, Hobbs et al. 1982, Hobbs and Swift 1985, Roloff et al. 2001). But, the explicit objectives and approaches of these efforts to consider nutrition were never incorporated into the habitat effectiveness/habitat suitability approaches routinely applied on behalf of elk by most state and federal agencies in the West. We think that nutritional ecology provides a compelling basis for large-scale habitat evaluation procedures and that the need for incorporating nutrition into habitat evaluation procedures is heightened by new challenges presented by declining ungulate herds. We also think that management planning should begin explicitly accounting for nutritional values of management activities that occur on

summer-autumn ranges, in addition to those on winter ranges. Reliable, nutrition-explicit, and large-scale habitat planning and management, however, undoubtedly will require a new research emphasis that links fine-scale nutritional attributes of habitat to population dynamics of elk herds.

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