



We dedicate this publication to Rocky Spencer (1952–2007), a colleague and friend. Rocky began his career with the Washington Department of Fish and Wildlife in 1978 and became the District Wildlife Biologist in King–Pierce County in the 1980s. His work encompassed many species of wildlife including cougars, bears, deer, elk, mountain goats, loons, and bighorn sheep. Rocky was extremely skilled at darting and net-gunning wildlife from a helicopter, and this skill led to the capture of many animals included in our study. Rocky’s exceptional field skills, his love for wildlife, his sense of humor, and most importantly, his friendship, are missed. Photo credit: Bruce K. Johnson.



Regional and Seasonal Patterns of Nutritional Condition and Reproduction in Elk

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ABSTRACT Demographic data show many populations of Rocky Mountain (*Cervus elaphus nelsoni*) and Roosevelt (*Cervus elaphus roosevelti*) elk have been declining over the last few decades. Recent work suggests that forage quality and associated animal nutritional condition, particularly in late summer and early autumn, influence reproduction and survival in elk. Therefore, we estimated seasonal nutritional condition of 861 female elk in 2,114 capture events from 21 herds in Washington, Oregon, Wyoming, Colorado, and South Dakota from 1998 to 2007. We estimated ingesta-free body fat and body mass, and determined age, pregnancy status, and lactation status. We obtained estimates for most herds in both late winter–early spring (late Feb–early Apr) and in autumn (Nov–early Dec) to identify changes in nutritional condition of individuals across seasons.

Body fat levels of lactating females in autumn were consistently lower than their non-lactating counterparts, and herd averages of lactating elk ranged from 5.5% to 12.4%. These levels were 30–75% of those documented for captive lactating elk fed high-quality diets during summer and autumn. Body fat levels were generally lowest in the coastal and inland northwest regions and highest along the west-slope of the northern Cascades. Adult females in most herds lost an average of 30.7 kg (range: 5–62 kg), or about 13% (range: 2.6–25%) of their autumn mass during winter, indicating nutritional deficiencies. However, we found no significant relationships between spring body fat or change in body fat over winter with winter weather, region, or herd, despite markedly different winter weather among herds and regions. Instead, body fat levels in spring were primarily a function of fat levels the previous autumn. Thinner females in autumn lost less body fat and body mass over winter than did fatter females, a compensatory response, but still ended the season with less body fat than the fatter elk.

Body fat levels of lactating females in autumn varied among herds but were unrelated to their body fat levels the previous spring. Within herds, thinner females exhibited a compensatory response during summer and accrued more fat than their fatter counterparts over summer, resulting in similar body fat levels among lactating elk in autumn despite considerable differences in their fat levels the previous spring. Level of body fat achieved by lactating females in autumn varied 2-fold among herds, undoubtedly because of differences in summer nutrition. Thus, summer nutrition set limits to rates of body fat accrual of lactating females that in turn limited body condition across the annual cycle.

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Pregnancy rates of 2- to 14-year-old females ranged from 68% to 100% in coastal populations of Washington, 69% to 98% in Cascade populations of Washington and Oregon, 84% to 94% in inland northwestern populations of Washington and Oregon, and 78% to 93% in Rocky Mountain populations. We found evidence of late breeding, even in herds with comparatively high pregnancy rates. Mean body mass of calves ($n = 242$) in 3 populations was 75 kg, 81 kg, and 97 kg, representing 55–70% of potential mass for 6- to 8-month-old calves on high-quality diets. Mean mass of 11 yearling females caught in autumn was 162 kg, approximately 70% of potential for autumn, and pregnancy rate was 27%. Mean mass of 28 yearlings caught in spring was 163 kg and pregnancy rate was 34%.

Our data suggest widespread occurrence of inadequate summer nutrition. Summer ranges of just 3 herds supported relatively high levels of autumn body fat (11–13% body fat) and pregnancy rates (>90%) even among females that successfully raised a calf year after year. Most other summer ranges supported relatively low autumn levels of body fat (5–9% body fat), and reproductive pauses were common (<80% pregnancy rates). Overall, our data failed to support 2 common assumptions: 1) summer and early autumn foraging conditions are typically satisfactory to prevent nutritional limitations to adult fat accretion, pregnancy rates, and calf and yearling growth; and 2) winter nutrition and winter weather are the principal limiting effects on elk productivity. Instead, a strong interaction existed among level of summer nutrition, lactation status, and probability of breeding that was little affected by winter conditions—adequacy of summer nutrition dictated reproductive performance of female elk and growth as well as growth and development of their offspring in the Northwest and Rocky Mountains. Our work signals the need for greater emphasis on summer habitats in land management planning on behalf of elk. © 2013 The Wildlife Society.

KEY WORDS body condition scoring, body fat, *Cervus elaphus*, elk, nutritional condition, nutritional limitations, pregnancy, productivity, reproduction, rump fat, summer, ultrasonography, winter.

Patrones Regionales y Estacionales en el Estado Nutricional y la Reproducción del Alce

RESUMEN Los datos demográficos disponibles muestran que las poblaciones de alce de las Montañas Rocosas (*Cervus elaphus nelsoni*) y de alce de Roosevelt (*Cervus elaphus roosevelti*) han ido disminuyendo en las últimas décadas. Estudios recientes sugieren que la calidad del forraje y el estado nutricional del alce, especialmente a finales del verano y principios del otoño, influyen en su reproducción y supervivencia. En consecuencia, se decidió estimar el estado nutricional de 861 hembras de alce, en 2114 eventos de captura, de 21 rebaños en Washington, Oregón, Wyoming, Colorado y Dakota del Sur desde 1998 al 2007. Se estimó la grasa corporal (sin incluir el bolo alimentario) y la masa corporal y también se determinó la edad, el estado de embarazo y el estado de lactancia de estos animales. Estas estimaciones fueron obtenidas, para la mayoría de los rebaños, a finales del invierno y principios de la primavera (finales de febrero y principios de abril) así como en otoño (noviembre y principios de diciembre) con el fin de identificar los cambios en el estado nutricional de los individuos a través de las estaciones.

En otoño, los niveles de grasa corporal de las hembras que daban de lactar fueron consistentemente más bajos que aquellos de las hembras que no daban de lactar y el promedio de hembras en estado de lactancia varió entre 5.5% y 12.4%. Estos niveles equivalen al 30–75% de aquellos documentados en la literatura para hembras en cautividad, en estado de lactancia y alimentadas con dietas de alta calidad durante el verano y el otoño. Los niveles de grasa corporal fueron generalmente más bajos en regiones costeras y al interior del Noroeste americano, mientras que los niveles más altos fueron observados a lo largo de la ladera occidental de las Cascadas del Norte. Durante el invierno, las hembras adultas en la mayoría de los rebaños perdieron un promedio de 30.7 kg (rango: 5–62 kg), o alrededor del 13% (rango: 2.6–25%) de la masa corporal registrada en otoño, lo que es indicativo de deficiencias nutricionales. Sin embargo, no se encontraron correlaciones significativas entre la grasa corporal registrada en primavera, o el cambio en la grasa corporal durante el invierno, y el clima invernal, la región o el rebaño, a pesar de los diferentes climas invernales entre los rebaños y las regiones. Por otro lado, se observó que los niveles de grasa corporal en la primavera fueron principalmente una función de los niveles de grasa del otoño precedente. Las hembras más delgadas perdieron menos grasa corporal y masa corporal durante el invierno que las hembras más gordas—lo que podría interpretarse como una respuesta compensatoria—pero aún así terminaron la temporada con menos grasa corporal que las hembras más gordas.

Los niveles de grasa corporal de las hembras que daban de lactar en otoño variaron entre los rebaños, pero no guardaron ninguna relación con los niveles de grasa corporal de la primavera anterior. Dentro de los rebaños, las hembras más delgadas mostraron una respuesta compensatoria durante el verano y acumularon más grasa que las hembras más gordas a lo largo del verano, dando lugar a similares niveles de grasa corporal entre las hembras que daban de lactar en otoño a pesar de las considerables diferencias en sus niveles de grasa de la primavera anterior. El

niveau de gras corporel acquis par les femelles qui allaient en automne variait le double entre les troupeaux, sans doute en raison des différences dans l'alimentation pendant l'été. Ainsi, le niveau de nutrition atteint pendant l'été semble avoir établi des restrictions sur les taux d'accumulation de gras corporel des femelles qui allaient, ce qui à son tour a limité leur condition physique à travers le cycle annuel.

Les taux de grossesse des femelles de 2 à 14 ans d'âge variaient entre 68 % et 100 % dans les populations côtières de Washington, entre 69 % et 98 % dans les populations de Cascade de Washington et d'Oregon, entre 84 % et 94 % dans les populations de l'intérieur du nord-ouest de Washington et d'Oregon, et entre 78 % et 93 % dans les populations des Montagnes Rocheuses. On a trouvé des preuves de reproduction tardive même dans les troupeaux avec des taux de grossesse relativement élevés. La moyenne de masse corporelle des veaux ($n = 242$) dans trois populations était de 75, 81 et 97 kg, ce qui équivaut à 55 % et 70 % de la masse potentielle des veaux de 6 à 8 mois d'âge nourris avec une alimentation de haute qualité. La moyenne de masse corporelle de 11 vaches capturées en automne était de 162 kg, ce qui équivaut à environ 70 % de sa masse potentielle en automne; son taux de grossesse était de 27 %. La moyenne de masse corporelle de 28 vaches capturées au printemps était de 163 kg et son taux de grossesse était de 34 %.

Nos données suggèrent une large prévalence de malnutrition pendant l'été. Les zones d'alimentation d'été de seulement trois troupeaux soutenaient des niveaux relativement élevés de gras corporel d'automne (11–13 %) et des taux de grossesse (>90 %) même chez les femelles qui ont réussi à élever un veau d'une année à l'autre. La majorité des autres zones d'alimentation d'été soutenaient des niveaux de gras corporel relativement faibles (5–9 %) et dans ces zones les pauses reproductives étaient courantes (taux de grossesse <80 %). En général, nos données ne soutiennent pas deux hypothèses communes : 1) les conditions de recherche de nourriture pendant l'été et au début de l'automne sont généralement satisfaisantes pour éviter les limitations nutritionnelles associées à l'accumulation de gras chez un adulte, les taux de grossesse et la croissance des veaux et des vaches; 2) la nutrition hivernale et le climat hivernal sont les principales limites de la productivité d'un adulte. Au contraire, il existe une forte interaction entre le niveau de nutrition en été, l'état de lactation et la probabilité de reproduction qui a été peu affectée par les conditions hivernales—une bonne nutrition en été a déterminé le succès reproductif des femelles d'été ainsi que la croissance et le développement de leurs élevages dans le nord-ouest américain et les Montagnes Rocheuses. Notre travail souligne la nécessité de donner plus d'importance aux habitats d'été lorsque l'on considère la planification de la gestion territoriale en faveur de l'adulte.

Tendances Régionales et Saisonnières Observées sur L'état Nutritionnel et la Reproduction du Wapiti

RÉSUMÉ Des données démographiques montrent que de nombreuses populations de wapitis des Rocheuses (*Cervus elaphus nelsoni*) et de wapitis de Roosevelt (*Cervus elaphus roosevelti*) ont connu un déclin au cours des dernières décennies. Des récents travaux semblent indiquer que la qualité du fourrage et son effet sur l'état nutritionnel de l'animal, notamment à la fin de l'été et au début de l'automne, influencent la reproduction et la survie du wapiti. Nous avons estimé l'état nutritionnel saisonnier de 861 femelles dans 21 troupeaux au cours de 2 114 campagnes de capture réalisées dans les états de Washington, de l'Oregon, du Wyoming, du Colorado et du Dakota du Sud entre 1998 et 2007. Nous avons estimé le taux de lipides sans ingesta et la masse corporelle et avons établi l'âge, le taux de gestation et le taux de lactation. Pour la plupart des troupeaux, nous avons fait nos estimations à la fin de l'hiver/au début du printemps (fin fév.–début avr.) et à l'automne (nov.–début déc.) afin de déterminer si l'état nutritionnel des individus variait au cours des saisons.

Le taux de lipides des femelles lactantes à l'automne était toujours plus faible que celui des femelles non lactantes, et le pourcentage moyen de femelles en lactation dans les troupeaux variaient entre 5,5 % et 12,4 %. Ce taux correspondait à 30–75 % des réserves lipidiques documentées pour des femelles lactantes en captivité et qu'on nourrissait avec du fourrage de haute qualité à l'été et en automne. Les troupeaux des régions côtières et des régions intérieures du nord-ouest présentaient généralement les taux de lipides les plus bas, tandis que ceux situés sur le flanc ouest de la partie nord de la chaîne des Cascades présentaient les taux les plus élevés. Dans la plupart des troupeaux, les femelles adultes perdaient une moyenne de 30,7 kg (intervalle: 5–62 kg) ou environ 13 % (intervalle: 2,6–25 %) de leur masse automnale au cours de l'hiver, ce qui indique une carence nutritionnelle. Par contre, nous n'avons pas trouvé de relations significatives entre les réserves lipidiques printanières ou des variations dans les réserves lipidiques au cours de l'hiver et les conditions météo en hiver, la région ou le troupeau, en dépit des conditions météo hivernales vraiment différentes observées entre les troupeaux ou les régions. Au contraire, le taux de lipides printanier était plutôt une fonction du taux de lipide de l'automne précédent. Les femelles plus maigres à l'automne ont perdu moins de graisses et de masse corporelle durant l'hiver que les femelles plus grasses, une réaction compensatoire certes, mais qui n'a pas empêché les femelles plus maigres d'avoir moins de réserves lipidiques à la fin de la saison que les femelles plus grasses.

Le taux de lipides des femelles lactantes à l'automne variait parmi les troupeaux, mais n'était pas relié à leur taux de lipides du printemps précédent. À l'intérieur d'un même troupeau, une réaction compensatoire se déclenchait en été chez les femelles plus maigres, et elles accumulaient plus de graisses en été que les femelles plus grosses, si bien que toutes les femelles lactantes à l'automne avaient le même taux de lipides en dépit de différences considérables au printemps. Le taux de lipides des femelles lactantes à l'automne variait du simple au double entre les troupeaux, en raison sans aucun doute de différences dans leur régime alimentaire d'été. C'est donc la nourriture consommée en été qui a limité le taux d'accumulation des lipides chez les femelles en lactation et qui a donc limité leur état d'engraissement au cours du cycle annuel.

Le taux de gestation des femelles âgées entre 2 et 14 ans variait de 68% à 100% dans les populations côtières de l'état de Washington, de 69% à 98% dans celles de la chaîne des Cascades de l'état de Washington et de l'état de l'Oregon, de 84% à 94% dans celles des régions intérieures du nord-ouest de l'état de Washington et de l'état de l'Oregon et de 78% à 93% dans celles des Rocheuses. Nous avons noté des cas d'accouplement tardif, même chez les populations ayant un taux de gestation relativement élevé. La masse corporelle moyenne des petits ($n = 242$) dans 3 populations était de 75 kg, 81 kg, et 97 kg, ce qui représentait 55% à 70% de la masse potentielle des petits âgés de 6 à 8 mois avec un régime alimentaire de haute qualité. La masse moyenne de 11 femelles âgées d'un an et capturées à l'automne était de 162 kg, environ 70% de la masse potentielle d'une femelle à l'automne, et le taux de gestation était de 27%. La masse moyenne de 28 femelles âgées d'un an et capturées au printemps était de 163 kg et le taux de gestation était de 34%.

Nos données semblent indiquer que les wapitis ont un régime alimentaire inadéquat en été et qu'il s'agit d'une situation généralisée. Les aires de répartition estivales de seulement 3 troupeaux sont parvenus à soutenir un taux de lipides et un taux de gestation relativement élevés en automne (taux de lipides de 11–13% et taux de gestation >90%), même parmi les femelles qui avaient réussi, année après année, à élever un petit. La plupart des autres aires de répartition soutenaient un taux de lipides peu élevé en automne (5% à 9%), et il était courant de voir des pauses reproductives (taux de gestation <80%). Dans l'ensemble, nos données n'ont pas réussi à démontrer deux hypothèses répandues: 1) les conditions de fourrage en été et au début de l'automne sont généralement satisfaisantes pour prévenir les carences nutritionnelles chez les adultes en matière d'accrétion des lipides, de taux de gestation et de croissance des petits et des jeunes wapitis d'un an; et 2) l'alimentation et les conditions météo hivernales sont les principaux facteurs limitatifs dans la reproduction du wapiti. Au contraire, nos données ont montré qu'il existait une très forte corrélation entre le régime alimentaire d'été, le taux de lactation et la probabilité d'accouplement, corrélation qui était peu influencée par les conditions hivernales. C'était plutôt le caractère adéquat du régime alimentaire d'été qui régissait la performance reproductive des wapitis femelles et la croissance et le développement de leur progéniture dans les montagnes des régions du nord-ouest et des Rocheuses. Nos travaux démontrent la nécessité de mettre davantage l'accent sur les habitats d'été dans les plans d'aménagement forestier en ce qui concerne les wapitis.

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INTRODUCTION

Understanding and managing mechanisms that affect population dynamics compose perhaps the most fundamental aspects of wildlife management (Caughley 1977). However, identifying specific factors that influence population dynamics in large-ungulate populations is challenging, largely because of the complexity of interacting factors and feedback mechanisms that vary greatly spatially and temporally. Biologists generally categorize these mechanisms as either top-down (mortality-driven via predation and hunting) or bottom-up (habitat- and/or animal density-driven). Quantity and quality of forage are commonly thought to be the primary mediators of bottom-up regulation for large herbivores (Caughley 1979, McCullough 1984, Parker et al. 1999) because nutritional deficiencies can affect reproduction, growth and development, and survival (Verme and Ullrey 1984, Cook 2002, Parker et al. 2009).

Bottom-up regulation operates through density dependence due to the increasing imbalance between ungulate populations and forage supplies as ungulate populations increase (Caughley 1976, 1979; Fowler 1987). The concept largely originated from early studies of spectacular density-dependent interactions between herbivore populations and their food supply (Leopold 1943, Klein 1968, Caughley 1970), and is bolstered by long-term studies of moose density-forage dynamics (*Alces alces*) on Isle Royale (Vucetich and Peterson 2004) and observations of huge, 50- to 100-year oscillations of barren ground caribou and reindeer (*Rangifer tarandus*) populations (Meldgaard 1986; Skogland 1986, 1990; Couturier et al. 1990; Crête and Huot 1993; Manseau et al. 1996). These patterns imply that depressing effects of poor or inadequate nutrition on populations are influential primarily when populations approach carrying capacity (Skogland 1986, Fowler 1987). However, nutritional limitations can also occur when nutritional resources are marginal regardless of herbivore density, an effect that may be caused by environmental influences on forage quality and quantity in summer or winter, such as drought, poor soils, plant succession, or deep snow (Merrill 1987, Crête and Courtois 1997, Peek et al. 2002).

Understanding the extent of bottom-up regulation of elk (*Cervus elaphus*) has become increasingly important. Beginning in the 1960s, new federal legislation, including the National Environmental Policy Act of 1969, National Forest Management Act of 1976, and others mandated new emphasis on non-commodity resources such as wildlife in the execution of public land management. One early result of the new legislation was that agencies designated featured species on which they could focus planning to meet legal requirements (Thomas 1982), and elk were granted featured-species status on federal lands (Christensen et al. 1993).

The new legislation ushered in an era of research and habitat management on federal lands on behalf of elk in the West (Thomas 1982). At the time, logging was escalating on public lands, and logging impacts were a principal concern of wildlife managers by the mid-1970s (Hieb 1976, Thomas et al. 1979, Thomas et al. 1988b) and thereafter (Christensen et al. 1991). Aided by advances in radio-telemetry, habitat-use studies articulated influences of roads and logging on elk distributions

and provided the basis for new habitat suitability or effectiveness models (e.g., Black et al. 1976; Thomas et al. 1979, 1988a; Lyon 1980, 1983; Leege 1984; Lyon et al. 1985; Wisdom et al. 1986). These models were widely used to aid formal planning by federal agencies across an enormous geographic area (Thomas et al. 1988b, Edge et al. 1990, Christensen et al. 1993), and many remain in use to this day.

For the most part, those guidelines, and particularly their application, deemphasized nutritional resources as a factor that limited habitat suitability or effectiveness (Edge et al. 1990, Cook et al. 1998), and those that attempted to do so (e.g., Thomas et al. 1988a) largely ignored forage quality per se (Edge et al. 1990). Deemphasis of nutritional attributes of habitat is understandable in light of the bio-politics of the time, because elk populations were increasing in many areas (Christensen et al. 1999), and because early telemetry studies were fundamentally unable to identify nutritional influences on habitat use and/or population dynamics (Hobbs and Hanley 1990, Garshelis 2000, Morrison 2001). Consequently, nutrition's effects were deemed to be relatively unimportant (Nelson and Leege 1982, Leege 1984, Christensen et al. 1993, Coughenour and Singer 1996, Unsworth et al. 1998), although alternative views existed (Collins and Urness 1983, Hobbs and Swift 1985, Wisdom et al. 1986, Harper 1987, Merrill and Boyce 1991).

Much has changed over the last 2 decades. Declining elk calf recruitment is now evident in the long-term data streams of many populations, and some populations in the northwestern states have declined (Ferry et al. 2001, Noyes et al. 2002, Vucetich et al. 2005, Washington Department of Fish and Wildlife 2006, White et al. 2010), even as logging was being greatly curtailed on federal forest lands. Thus, past concerns regarding the removal of cover and construction of new roads probably is less warranted today. Instead, understanding what habitat features explicitly influence population dynamics is of substantially greater interest.

Inadequate nutrition, largely because of long-term forest succession, is sometimes highlighted as a possible cause of declining recruitment and population size (Irwin et al. 1994; Gill et al. 1996; Bomar 2000; Peek et al. 2001, 2002; Johnson et al. 2005). This contention has infrequently been tested, and, more generally, much remains unknown about the influences of nutrition on dynamics of elk populations in North America. For example, a prevailing belief is that nutritional limitations are primarily limited to winter for elk (Hobbs et al. 1982, Houston 1982, Leege 1984, Christensen et al. 1993, Coughenour and Singer 1996) and other large ungulates (Klein 1968, Wallmo et al. 1977, Adamczewski et al. 1987, Skogland 1990, Weladji and Holand 2003). Although forage quality and quantity are highest during the growing season and lowest in winter, nutritional requirements for late gestation, lactation, juvenile growth and development, and recovery of mass lost during winter are also high (Verme and Ullrey 1984, Oftedal 1985, Parker et al. 1999, Cook 2002, Cook et al. 2004a). Research on elk (Trainer 1971, Merrill and Boyce 1991, Alldredge et al. 2002, Cook 2002, Hutchins 2006) and other ungulates in the northern hemisphere (Table 1) suggest that nutritional requirements are unsatisfied during summer in many ecological settings, despite greater forage quality and quantity during the growing season.

Table 1. Literature reporting limiting effects of summer nutrition on northern temperate ungulates other than elk.

Publication	Species	Productivity parameters
Julander et al. (1961)	Mule deer	Reproduction, body mass
McEwan (1968)	Caribou/reindeer	Juvenile growth
Klein (1970)	Caribou/muskoxen	Juvenile growth
Bobek (1977)	Roe deer	Population numbers
White (1983)	Arctic grazers	Reproduction, survival, growth
Reimers et al. (1983)	Caribou/reindeer	Juvenile growth, body mass, calving time
Verme and Ullrey (1984)	White-tailed deer	Reproduction, survival, growth
Sæther (1985)	Moose	Body mass
Messier et al. (1988)	Caribou/reindeer	Population numbers, reproduction
Huot (1989)	Caribou/reindeer	Body composition
Cook (1990)	Bighorn sheep	Juvenile survival
Sæther and Heim (1993)	Moose	Juvenile growth, age of maturation
Couturier et al. (1990)	Caribou/reindeer	Population numbers, reproduction
Bø and Hjeljord (1991)	Moose	Body mass
Lavigueur and Barrette (1992)	Caribou/reindeer	Juvenile growth
Crête and Huot (1993)	Caribou/reindeer	Body composition, juvenile growth, milk production, survival, reproduction
Crête et al. (1993)	Caribou/reindeer	Reproduction, growth, body composition
Langvatn et al. (1996)	Red deer	Age at first breeding
Crête and Courtois (1997)	Moose	Calf production
Gerhart et al. (1996)	Caribou/reindeer	Reproduction
Hjeljord and Histol (1999)	Moose	Body mass
Parker et al. (1999)	Black-tailed deer	Body composition
Post and Klein (1999)	Caribou/reindeer	Reproduction, juvenile survival
Solberg et al. (1999)	Moose	Calf recruitment, population growth
Mysterud et al. (2001)	Red deer	Body mass
Ericsson et al. (2002)	Moose	Juvenile growth
Peek et al. (2002)	Mule deer	Population numbers
Valkenburg et al. (2003)	Caribou/reindeer	Juvenile growth
Cameron et al. (2005)	Caribou/reindeer	Reproduction, body composition
Herfindal et al. (2006a, b)	Moose	Body mass
Tollefson (2007)	Mule deer	Body composition, juvenile growth, milk production, reproduction
Dale et al. (2008)	Caribou/reindeer	Juvenile growth
Post and Forchhammer (2008)	Caribou/reindeer	Juvenile survival
McArt et al. (2009)	Moose	Body composition
Monteith et al. (2013)	Mule deer	Body fat and protein reserves

Focused research is needed to identify the extent, causes, and implications of nutrition limitations for elk.

Understanding influences of nutrition on demographics of wild ungulate herds has been hampered by a lack of practical and effective techniques for monitoring nutrition and nutritional condition (Harder and Kirkpatrick 1994, Saltz et al. 1995, Cook 2002). Estimates of nutritional condition are critical for understanding the dynamics of bottom-up influences on populations because they integrate the separate effects of nutritional adequacy of the environment with the nutrient demands of the animals (Parker et al. 2009). To our knowledge, body fat of free-ranging female elk, independent from data included herein, has been reported in only a few instances, 2 from live-animal studies (Stewart et al. 2005, Conner et al. 2007) and the rest from hunter-killed or starved elk using kidney or marrow fat in Oregon (Trainer 1971, Stussy 1993, Kohlmann 1999, Noyes et al. 2002), the Yellowstone area (Greer 1968, Houston 1978, Mech et al. 2001), and Canada (Flook 1970, Huggard 1993).

Recent development of new approaches for measuring nutritional condition using ultrasonography of subcutaneous rump fat thickness (Stephenson et al. 1998; Cook et al. 2001a, b) and nutritional condition scoring (Gerhart et al. 1996; Cook et al. 2001a, b) can improve estimates of condition of free-ranging animals. Collecting nutritional condition data on live animals allows for flexibility in timing of data collection and unbiased sampling (i.e., unrestricted by hunting seasons or

predator kills) as well as repeated sampling on the same individual across time.

To provide a comprehensive evaluation of nutritional condition and productivity of elk herds, we used those emerging techniques to survey 21 elk herds in 5 western states from 1998 to 2007. Working with state, tribal, and federal agencies, we collected data on body fat, body mass, lactation and pregnancy status, age, and, where possible, body mass of calves. We selected body fat of female elk as our primary variable of interest because it 1) is a direct function of energy expenditure and forage quality and quantity available to elk (Cook et al. 2004a, Parker et al. 2009); 2) directly and indirectly influences a host of reproductive and survival variables (e.g., lactation yields and thus calf growth, probability of pregnancy, timing of conception, probability of overwinter survival, age at first breeding; Cook et al. 2004a, Parker et al. 2009); and 3) may reflect the general fitness (Harder and Kirkpatrick 1994) of the population. We sampled individual elk sequentially in early spring and mid-autumn to track annual cycles in body fat dynamics and reproduction.

Our data extend knowledge of nutritional influences on elk that began in the mid-1990s with controlled experiments of nutrition and reproduction using captive elk (Cook et al. 2001c, 2004a). These controlled experiments quantified how nutrition affects performance and identified thresholds of performance useful for helping to understand the role of nutrition in wild elk populations. We integrated our assessment of nutritional

condition of wild elk with previous data derived from captive experiments using a multi-seasonal, multi-regional approach to enhance understanding of nutrition's effects in wild settings.

We tested 2 overarching hypotheses: 1) nutritional limitations occur in winter and summer, but in contrast to prevailing perceptions, nutritional limitations in summer may have greater effects on demography and productivity of elk herds than those in winter in many areas of the western United States; and 2) nutritional limitations vary in magnitude and seasonality among herds and regions. The specific objectives of our analyses were to first identify the occurrence of nutritional deficiencies and limitations in western elk herds. We also evaluated the severity, seasonality, and extent of variation in nutritional limitations among herds and regions of the West to improve understanding of how summer and winter nutrition influences, and interacts with, reproduction. Finally, we provided a baseline data set as a standard of comparison for future studies of nutritional condition and reproduction of elk in North America. These data also should help identify the need for habitat management models and planning efforts that explicitly account for nutritional limitations on behalf of elk.

Although many of the data were collected opportunistically and in deference to other objectives of the collaborating agencies, our study provides the largest multi-seasonal data set of nutritional condition and reproduction for a large ungulate species. It is also 1 of the few data sets in which individual animals were sequentially sampled over time, such that histories of reproduction, previous nutritional condition, seasonal effects, and carry-over effects across seasons might be analyzed in the context of annual cycles of nutritional condition and reproduction (see also Dale et al. 2008, Monteith et al. 2013).

STUDY AREAS

We collected nutritional condition data from 21 elk herds in 5 western states (Washington, Oregon, Wyoming, Colorado, South Dakota). Studies occurred in 4 ecological regions based on climate, landform, and vegetation: coastal plains and mountains, west-slope Cascade range, inland Northwest, and the Rocky Mountains (Fig. 1, Table 2).

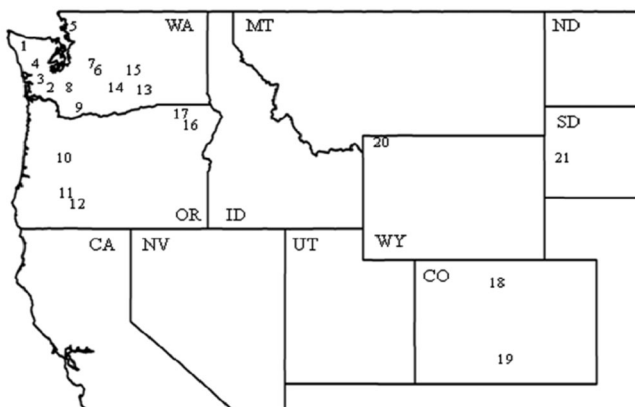


Figure 1. Locations of 21 elk herds in Washington, Oregon, Wyoming, Colorado, and South Dakota, USA, from which we collected nutritional condition and reproduction data during 1998 through 2007. Herd numbers presented on this map correspond to the herd numbers presented in all figures and tables.

Coastal Plains and Mountains (coastal)

We collected data from 4 elk herds west of Interstate Highway 5 in western Washington: herd #1, Forks (10 km north of Forks on the Olympic Peninsula [$-124^{\circ}22'W$, $48^{\circ}00'N$]); herd #2, Wynoochee (50 km west of Olympia [$-123^{\circ}38'W$, $47^{\circ}15'N$]); herd #3, Chehalis Valley (30 km southwest of Olympia [$-123^{\circ}20'W$, $46^{\circ}50'N$]); and herd #4, Willapa Hills (75 km south of Olympia [$-123^{\circ}10'W$, $46^{\circ}30'N$]). In general, elk herds in this region were presumed to be the Roosevelt subspecies (*C. e. roosevelti*), although elk of the Rocky Mountain subspecies (*C. e. nelsoni*) were transported and released near the coast, at least in western Oregon, just after the turn of the century (Harper 1987). The elk we sampled in these herds were non-migratory to slightly migratory among seasons.

Elevation ranged from 50 to 450 m at Forks, 100 to 500 m at Wynoochee, 20 to 200 m at Chehalis Valley, and 75 to 950 m at Willapa Hills. Topography at Willapa Hills was rugged, with steep canyons and mountains but was flat to gently rolling with occasional ridge systems at the other 3 study areas. Climate was maritime in all 4 coastal study areas, with annual precipitation averaging 180–250 cm. Average minimum January temperature ranged from 0 to $2.5^{\circ}C$ and average maximum July temperature ranged 20 to $23^{\circ}C$ at the lower elevations of each of these study areas (Daly et al. 1994). Snow was normally absent in winter except at higher elevations of Willapa Hills and in hills surrounding the other 3 study areas. At all 4 study areas, temperate rainforest in various seral stages primarily supporting Douglas fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) dominated across this region. Western red cedar (*Thuja plicata*) and red alder (*Alnus rubra*) also were common. At the highest elevations of Willapa Hills, forests often contained substantial amounts of Pacific silver fir (*Abies amabilis*) and noble fir (*A. procera*). Franklin and Dyrness (1988) described the plant communities of these study areas in detail.

West-Slope Cascades Range (Cascades)

We sampled 8 elk herds along the west slope of the Cascades range, including 5 herds in Washington: herd #5, Nooksack (50 km east of Bellingham near Mount Baker [$-122^{\circ}20'W$, $48^{\circ}35'N$]); herd #6, White River (60 km east of Tacoma [$-121^{\circ}30'W$, $47^{\circ}10'N$]); herd #7, Green River (50 km east of Tacoma [$-121^{\circ}40'W$, $47^{\circ}15'N$]); herd #8, South Rainier (near Packwood [$-122^{\circ}29'W$, $46^{\circ}30'N$]); and herd #9, Mount St. Helens (50 km north of Vancouver [$-122^{\circ}30'W$, $46^{\circ}30'N$]) and 3 herds in Oregon: herd #10, Springfield (immediately north of the Mackenzie River 40 km northeast of Springfield [$-122^{\circ}45'W$, $44^{\circ}13'N$]); herd #11, Steamboat (immediately north of the North Umpqua River 45 km east of Roseburg [$-122^{\circ}40'W$, $43^{\circ}20'N$]); and herd #12, Toketee (south of the North Umpqua River 80 km east of Roseburg [$-122^{\circ}25'W$, $43^{\circ}13'N$]). Autumn data collected at Mount St. Helens (MSH) were collected from elk drive-trapped on the Toutle River debris slide, an erosive area still highly affected by the 1980 volcanic eruption. The debris slide, a matrix of rock and volcanic ash with vegetated islands dominated by grasses and alders, is used by a modest number of resident elk and a larger number of migratory elk that enter the Toutle River valley bottom during winter months. The MSH elk sampled for nutritional condition during

Table 2. Herd characteristics and details of capture efforts for 21 elk herds in Washington, Oregon, Wyoming, Colorado, and South Dakota, USA, from which we collected nutritional condition and reproduction data during 1998 through 2007. Herd numbers correspond to those in Figure 1.

Herd#/herd	Region ^a	Years	Seasons	Females	Captures ^b	Age ^c	Yearlings	Old ^{b,d}	C:C ^e	Herd status ^f
1/Forks	CS	2000–2003	5	31	98	5.8	1	0	41 _{aut} , 26 _{win}	S/H/Pr
2/Willapa Hills	CS	2000–2002	4	22	66	6.3	4	6	41 _{win}	S/H/Pr
3/Chehalis	CS	2002	1	24	24	4.3	4	2	No data	S/H/Pr
4/Wynoochee	CS	2003–2005	5	40	149	7.1	1	6	36 (25–46) _{aut}	S/H/P, Pr
5/Nooksack	CM	2000–2002	6	21	80	8.4	1	13	65 (60–69) _{aut}	I/U/P, Pr
6/White River	CM	1998–2007	9	72	149	8.4	1	20	35 (9–58) _{win}	D*/M/P, Pr
7/Green River	CM	1998–2006	15	58	275	8.6	1	28	29 (6–43) _{win}	D*/U/P, Pr
8/South Rainier	CM	2000	1	11	11	4.8 ^g	3	0	31 _{win}	D/H/P, Pr
9/Mount St. Helens	CM	2003–2009	4	110	110	6.3	13	1	44 (40–47) _{win}	S/H/P, Pr
10/Springfield	CM	2000–2002	4	23	60	4.0	3	0	46 (42–50) _{win}	S/H/Pr
11/Steamboat	CM	2003–2004	4	24	62	7.6	0	4	24 _{win}	D/H/P
12/Toketee	CM	2003–2004	4	39	65	7.0	0	5	25 (18–31) _{win}	D/H/P
13/Hanford	IN	2000–2001	4	29	70	5.9	2	3	40 _{win}	I/H/P, Pr
14/Yakima	IN	2003–2006	6	65	165	8.7	1	15	39 (29–45) _{win}	S/H/P, Pr
15/Colockum	IN	2009	1	36	36	6.9	2	3	20 _{win}	S/H/P, Pr
16/Sled Springs	IN	2001–2007	13	69	298	8.3	2	17	26 (18–32) _{win}	S/H/P, Pr
17/Wenaha	IN	2002–2007	11	49	196	8.8	1	30	18 (14–30) _{win}	D/U/P, Pr
18/Rocky Mtn. NP	RM	2001	1	29	29	9.8 ^g	0	4	No data	S/U/P
19/San Luis Valley	RM	2005–2006	4	53	115	6.1	3	1	30 (22–38) _{win}	S/H/P, Pr
20/Yellowstone NP	RM	2000	1	38	38	8.0	2	4	23 _{aut}	S/M/P
21/Black Hills	RM	2007	1	18	18	6.0	1	0	No data	D/H/P, Pr

^a CS, coastal plains and mountains; CM, west-slope Cascade range; IN, inland Northwest; RM, Rocky Mountains.

^b Total number of capture events. If the capture events are greater than the number of females, this indicates we used a repeated measures approach.

^c Average age of all females at first capture. Age estimated to the nearest year via counts of cementum annuli in the canine (Hamlin et al. 2000; Matson's Laboratory, Milltown, Montana) except where indicated.

^d Number of capture events where the female was ≥ 15 years old.

^e Mean number (with range in parentheses) of calves per 100 cows. Data were collected via surveys in either late summer or early autumn (_{aut}) or late winter or early spring (_{win}). If only 1 year of data were available, we only presented 1 value. We obtained data from the following sources: F. Geyer, Quileute Indian Tribe, unpublished data (Forks); Washington Department of Fish and Wildlife, Game status and trend reports, Wildlife Program, Washington Department of Fish and Wildlife, Olympia, Washington, USA (Willapa Hills, South Rainier, Mount St. Helens); B. Murphie, Washington Department of Fish and Wildlife, unpublished data (Wynoochee); M. Davison, Washington Department of Fish and Wildlife, unpublished data (Nooksack); D. Vales; Muckleshoot Indian Tribe, unpublished data (White River, Green River); Tiller et al., Pacific Northwest National Laboratory, unpublished report (Hanford); B. Johnson, Oregon Department of Fish and Wildlife (Springfield, Sled Springs, Wenaha); D. Imell, Oregon Department of Fish and Wildlife (Steamboat, Toketee); W. Clark, Yellowstone Center for Resources, unpublished report (Yellowstone); Schoenecker, United States Geological Survey, unpublished data (San Luis Valley).

^f Herd status relative to population growth (S = stable, I = increasing, D = declining, D* = declining at start of captures but a predator control program was initiated and the herd started increasing), hunting (H = hunted, U = unhunted, M = mix of hunted and unhunted; refers to National Park animals where a portion of elk left Park Service land and were exposed to hunting), and land ownership (P = public lands, Pr = private lands [commercial timber, agriculture, etc.]).

^g Age estimated by tooth wear (Harder and Kirkpatrick 1994).

autumn most likely consisted of elk resident to the debris slide and may not be representative of elk on the larger MSH forest landscape. The MSH elk sampled in late winter and spring were from the larger forested landscape. These 2 seasonal samples were likely derived from elk groups that experienced different habitat-mediated nutritional constraints.

Elk along the west-slope of the Cascade Range in western Oregon and Washington were considered to be Rocky Mountain elk, although Roosevelt elk from near the coast were translocated to the Cascades (Harper 1987) and several herds were established from transplanted stock from Yellowstone National Park early in the 20th century. Many elk in the Cascade herds were migratory, particularly in White River where elk moved to high elevations in Mount Rainier National Park during summer.

Topography in all ranges of these herds was mountainous. Radio-marked elk occupied habitats at elevations from 100 to 1,400 m (Nooksack), 350–1,200 m (Green River), 400–2,200 m (White River), 300–2,100 m (South Rainier), 350–1,500 m (Mount St. Helens), 350–900 m (Springfield), 500–1,800 m (Steamboat), and 900–3,000 m (Toketee). In Washington, climate in the western Cascades also is maritime, with annual precipitation of 150 cm at lower elevations and ≥ 250 cm at higher elevations. Mean minimum January temperature ranged

from -2.5°C to 0°C , and mean July maximum temperature was 25°C at the lower elevations (Daly et al. 1994). Below 800 m in Washington, temperate rainforests supported primarily Douglas fir and western hemlock with red cedar and red alder in this region. With increasing elevation, forests transitioned into the Pacific silver fir zone where western hemlock typically co-dominated with silver fir, to the mountain hemlock (*Tsuga mertensiana*) zone, where Pacific silver fir and mountain hemlock usually co-dominated (Franklin and Dyrness 1988, Henderson et al. 1992). At the highest elevations, subalpine and alpine communities were uncommon but occasionally were used by elk in this region.

Climate of the Oregon Cascade study areas tended to be drier and warmer with declining latitude than in Washington. Annual precipitation ranged from about 100 cm to 160 cm at Springfield, 70 cm to 100 cm at Steamboat, and 80 cm to 120 cm at Toketee. Mean minimum January temperatures ranged from -2.5°C to 0°C , and mean maximum July temperature from 27°C to 29°C for these 3 herds (Daly et al. 1994). Forests of the Springfield study area were in the western hemlock zone, but cooler-moister species that were codominant in our Washington sites (red cedar, red alder, western hemlock) were less common in much of this study area except on wetter sites. The southernmost extension of

the western hemlock zone occurred at Steamboat and Toketee areas, where forests were largely dominated by Douglas fir, occasionally with ponderosa pine (*Pinus ponderosa*), incense-cedar (*Libocedrus decurrens*), and a variety of sclerophyllous shrubs (Franklin and Dyrness 1988).

Inland Northwest

We collected data from 3 elk herds in central Washington: herd #13, Hanford (U.S. Department of Energy, Fitzner/Eberhardt Arid Lands Ecology Reserve 20 km northwest of Richland [$-119^{\circ}35'W$, $46^{\circ}25'N$]); herd #14, Yakima (spread along the east-slope of the Cascades just west of Yakima north to Ellensburg [$-120^{\circ}35'$ to $-121^{\circ}20'W$, $46^{\circ}30'$ to $47^{\circ}00'N$]); herd #15, Colockum (northeast of Ellensburg [$-120^{\circ}3'W$, $45^{\circ}7'N$]); and 2 herds in northeastern Oregon, herd #16, Sled Springs (75 km northeast of La Grande [$-117^{\circ}40'W$, $45^{\circ}45'N$]); and herd #17, Wenaha (70 km north of La Grande [$-117^{\circ}50'W$, $48^{\circ}29'N$]). These elk were Rocky Mountain subspecies, with genetic stock translocated from Yellowstone National Park (although indigenous elk were never completely eliminated in extreme northeast Oregon; Cliff 1939, Irwin et al. 1994). Elk at Yakima, Colockum, Wenaha, and Sled Springs were migratory, although migration distances were variable depending on local elevation gradients. Elk at Hanford were non-migratory.

Elevations ranged from 500 m to 1,600 m (Yakima), 200 m to 3,000 m (Colockum), 200 m to 1,000 m (Hanford), 700 m to 1,600 m (Wenaha), and 700 m to 1,350 m (Sled Springs). Topography at Yakima and Colockum ranged from gentle, long slopes as elevation gradually increased from the Yakima valley west to the crest of the Cascades, but with rugged terrain primarily along river corridors interspersed throughout. Topography at Hanford was gently sloping with prominent ridges adding diversity to the landscape. Very steep V-shaped canyons interrupted an otherwise flat to gently rolling plateau at higher elevations of the Wenaha and Sled Springs areas.

Climate varied greatly across the Yakima and Colockum study areas, from very wet and cold along the Cascade crest to very dry with hot summers in the Yakima valley on the east side. Annual precipitation varied from 20 cm to 250 cm, mean January minimum temperature from $-9^{\circ}C$ to $-5^{\circ}C$, and mean July maximum temperature from $22^{\circ}C$ to $31^{\circ}C$ along the elevational gradient of this area. At Hanford, annual precipitation averaged 20 cm, mean January minimum temperature was $-3^{\circ}C$, and mean July maximum temperature was $33^{\circ}C$. At Wenaha and Sled Springs, annual precipitation was 75 cm, mean January minimum temperature was $-7^{\circ}C$, and mean July maximum temperature was $28^{\circ}C$ to $29^{\circ}C$ (Daly et al. 1994).

Vegetation was considerably more diverse across our inland Northwest study areas than across coastal and Cascade study areas. At the lower elevations of each of our inland areas and throughout Hanford, various xeric grassland or shrub-steppe rangeland plant communities served as elk winter ranges. With increasing elevation, forested habitats predominated, with ponderosa pine and Douglas fir forest common in the xeric forestlands, mixed coniferous forest consisting of ponderosa pine, Douglas fir, grand fir (*Abies grandis*), western larch (*Larix occidentalis*), Engelman spruce (*Picea engelmannii*), and lodgepole pine (*Pinus contorta*) at moderate to high elevations in the forest

zone, and at the highest elevations of the Yakima study area, subalpine fir (*Abies lasiocarpa*) and mountain hemlock were common (Franklin and Dyrness 1988). At Hanford, a 113,000-ha fire (Fluor Hanford 2002) burned most native vegetation in June 2000, and no regrowth was evident until mid-autumn 2000. The fire markedly reduced forage available to these elk in early autumn 2000 across much of their core range.

Rocky Mountain Region

We collected data from 4 herds of the northern and central Rocky Mountains: herd #18, Rocky Mountain National Park (elk were captured from 2 relatively distinct winter range areas [Horseshoe and Moraine] located northwest and west of Estes Park, Colorado [Lubow et al. 2002]) that we combined for analysis herein [$-105^{\circ}45'W$, $40^{\circ}20'N$]); herd #19, San Luis Valley (elk were captured from winter range in the San Luis Valley and adjacent foothills of the Sangre De Cristo Mountains on the Great Sand Dunes National Monument about 20 km northeast of Alamosa, Colorado north to Poncho Pass [$-105^{\circ}45'W$, $37^{\circ}45'N$]); herd #20, Yellowstone (elk were captured from the winter range of the northern herd of Yellowstone National Park near Gardiner, Montana south into northwestern Wyoming [$-110^{\circ}35'W$, $44^{\circ}55'N$]); and herd #21, Black Hills (south and east of Interstate 90 at Sturgis, South Dakota [$-103^{\circ}35'W$, $44^{\circ}25'N$]). All elk were Rocky Mountain subspecies, and herds varied from strongly migratory (Yellowstone, Rocky Mountain National Park) to mixed or migratory (San Luis Valley, Black Hills).

Elevation ranged from 1,650 m to 3,200 m (Yellowstone), 2,400 m to 4,000 m (Rocky Mountain National Park), 2,400 m to 4,000 m (San Luis Valley), and 900 m to 1,600 m (Black Hills). Topography was flat to gently rolling in large, wide valleys across the winter ranges where elk were captured. At Black Hills, elk occupied forest communities on relatively flat to gently rolling plateaus and surrounding plains at lower elevations, although occasional steep canyons added topographic diversity to this landscape. Annual precipitation averaged 43 cm, 41 cm, 24 cm, and 65 cm; mean minimum January temperatures were $-14.3^{\circ}C$, $-9.5^{\circ}C$, $-16.5^{\circ}C$, and $-10.4^{\circ}C$; and mean maximum July temperatures were $25.7^{\circ}C$, $25.5^{\circ}C$, $29.6^{\circ}C$, and $28.8^{\circ}C$, respectively, for each area (Daly et al. 1994).

The majority of the Yellowstone winter range supported grasslands and sagebrush-grasslands that transitioned into Ponderosa pine-Douglas fir forests at moderately high elevations. Beyond the winter range, lodgepole pine, spruce-fir and alpine communities were common (Despain 1990). Winter ranges at Rocky Mountain National Park included flat valley bottoms with wet meadows and mesic grasslands, whereas communities of ponderosa pine and big sagebrush dominated south-facing slopes and Douglas fir and lodgepole pine forests dominated on north-facing slopes. At higher elevations off the winter range, aspen (*Populus tremuloides*), lodgepole, subalpine spruce-fir, and alpine communities dominated (Singer et al. 2002). Plant communities of the valley floor at San Luis Valley included active sand dunes with sparse grass communities and occasional cottonwood (*Populus angustifolia*) stringers in wet areas and ephemeral wetlands. Large areas of sand sheet communities usually dominated by greasewood (*Sarcobatus vermiculatus*) and rabbit-brush (*Chrysothamnus viscidiflorus*) also occurred in San Luis

Valley (Schoenecker et al. 2006). Woodland communities of pinyon (*Pinus monophylla*) and juniper (*Juniperus* spp.) were common along the valley floor–foothill interface. At Black Hills, short- and mixed-grass rangeland communities dominated at lower elevations, and mixed coniferous forest of Ponderosa pine, Douglas fir, and lodgepole pine dominated at higher elevations of the study area.

METHODS

Animal Capture and Handling

We captured female elk using 4 techniques: 1) helicopter pursuit and chemical immobilization using projectile syringes; 2) helicopter pursuit and net gunning without chemical restraint (San Luis Valley, Yellowstone National Park); 3) drive-capture operations using helicopters (Mount St. Helens); and 4) chemical immobilization with projectile syringes delivered from the ground (Rocky Mountain National Park). For chemical immobilization of elk, we used a mixture of carfentanil citrate (3.6 mg) and xylazine hydrochloride (100 mg) and reversed anesthesia with naltrexone hydrochloride (360 mg) and either tolazoline hydrochloride (1,000 mg) or yohimbine hydrochloride (25 mg). Generally, we captured females twice per year, usually in late February–early April and November–early December in a repeated measures design. We fitted each female with a radiotelemetry collar at first capture, which provided for subsequent recaptures for ≥ 2 years. However, females in 6 of the elk herds were captured only once (Mount St. Helens, South Dakota, Chehalis Valley, South Rainier, Rocky Mountain National Park, and Yellowstone National Park). We conducted this research in accordance with approved animal welfare protocol (Starkey Experimental Forest and Range Animal Care and Use Committee Protocol #92-F004; Wisdom et al. 1993).

Two experienced investigators (R.C.C., J.G.C.) collected a rump body condition score (rump BCS) developed for elk (Cook et al. 2001a, b) and measured maximum subcutaneous rump fat thickness (MAXFAT; Stephenson et al. 1998; Cook et al. 2001a, b) using a Sonovet ultrasound with a 5.0 MHz, 7.0-cm probe (Universal Medical Systems, Bedford Hills, NY). We measured chest-girth circumference to estimate body mass.

We estimated the percent of ingesta-free body fat (IFBF) using the scaled LIVINDEX for elk, an arithmetic combination of the rump body condition score and maximum rump fat thickness allometrically scaled to surface area (see method 3 for elk, Appendix A in Cook et al. 2010). We converted girth circumference measurements taken on hobbled females (x) to a sternally recumbent basis (y) using the equation $y = 0.88x + 15.39$ (Cook et al. 2003), before calculating body mass, because the position of the front legs when hobbled inflates the circumference measurement. We calculated body mass 3 ways depending on the analytical objectives. For all females >1 year-old when using body mass as a primary condition index for analysis, we used the best predictive equation available for estimating mass from girth circumference and body fat levels (Table 3 in Cook et al. 2003; $r^2 > 0.65$). However, to avoid a potential bias in the spring between pregnant and non-pregnant females, we used only those equations for non-pregnant animals (Cook et al. 2003) to remove the influence of products of

conception on body mass (BM_{NP} = non-pregnant body mass). For 1-year-old females, we calculated BM_{NP} using yearling equations presented in Table 2 of Cook et al. (2003). We also calculated body mass adjusted to an ingesta-free, fat-free basis (BM_{IFF}) that would be representative of the mass of the animal independent of body fat. We removed ingesta mass using equations presented in Appendix C of Cook et al. (2001a), and we removed fat mass by multiplying percent IFBF by body mass and subtracting the product from ingesta-free body mass.

We extracted a vestigial upper canine from each animal during the initial capture and estimated age to the nearest year via counts of cementum annuli (Hamlin et al. 2000; Matson's Laboratory, Milltown, MT). We determined pregnancy status through ultrasonography via rectal entry or analysis of Pregnancy-Specific Protein B (PSPB; Biotracking, Moscow, ID; Noyes et al. 1997) in serum samples collected at each capture. We classified females as lactating when milk could be extracted from the udder (milk indicated either a female is still nursing a calf, or had been nursing a calf within 3–11 days [Flook 1970, Fleet and Peaker 1978, Noble and Hurley 1999]). We classified females as non-lactating if the udder contained no milk. Thus, our non-lactating category included a mix of females that were not pregnant the previous spring, were pregnant but lost their calves very soon after parturition, those that lactated an unknown portion of the season, and those that ceased lactating within a few weeks before capture. We classified females as true non-lactating (or spring non-pregnant) if sequential capture data were available indicating they were not pregnant the previous spring.

Statistical Analysis

Our evaluation of nutritional condition was based on 3 variables. Our primary variable was IFBF, but we also evaluated BM_{NP} and BM_{IFF} . Although body mass has been used frequently as a surrogate for nutritional condition (Hudson et al. 1991, Harder and Kirkpatrick 1994), our analyses of body mass was supplemental. It is poorly correlated with nutritional condition (Torbit et al. 1985, Cook et al. 2001a) because it is affected by frame size, gut fill, hydration, or pregnancy. Also, because elk are very difficult to weigh in field settings, our estimates of body mass were based on girth measurements, which is only a moderately precise measure of body mass (Cook et al. 2003; $r^2 < 0.83$ for adults and yearlings).

Our analysis centered on point estimates of the 3 variables in autumn and spring and the change in condition across summer and across winter. For analyses of point estimates (e.g., autumn IFBF, spring IFBF), we included data collected from all individuals and all capture events. When analyzing seasonal changes in nutritional condition, we included only individuals for which sequential data were available (i.e., spring and subsequent autumn, autumn and subsequent spring). A majority of our analyses involved comparing among individual herds, but we were limited to regional comparisons in some cases, mainly for those analyses requiring consecutive data points of individual elk (e.g., change in condition across seasons), because sample sizes of these sequential data were inadequate for some herds and not collected for other herds. Where we were able to conduct herd-level comparisons, data were presented by herd but separated according to region to maintain consistency.

We analyzed the majority of our data with repeated measures analysis of variance (ANOVA) or analysis of covariance (ANCOVA) in PROC MIXED (SAS Institute 1993) to avoid inflating degrees of freedom and potential autocorrelation associated with collecting multiple samples from the same elk. We used Akaike's Information Criterion, corrected for small sample size (AIC_c), to select the best fitting error structure from those deemed biologically appropriate (see Verbeke and Molenberghs 2000); error structures considered were simple or variance component, compound symmetry, spatial power, spatial Gaussian, and spatial exponential, and, unless noted otherwise, we used compound symmetry in all cases. However, regression techniques (PROC REG, PROC LOGISTIC; SAS Institute 1993) provide no basis for using repeated measures and thus we could not account for potential autocorrelation when using these techniques. More details on specific analyses are provided below. For all analyses of statistical hypotheses, we used a significance level of $\alpha = 0.05$.

Preliminary analyses: accounting for age, lactation status, and year.—We explored influences of age on pregnancy status and IFBF, and lactation status and year on IFBF. Our primary goal with these analyses was to reduce the number of covariates and simplify subsequent analyses.

Our first preliminary analysis was intended to identify prime-aged and old-aged categories. We used logistic regression of pregnancy status in relation to IFBF and age for different age ranges to define these age categories (PROC LOGISTIC, SAS Institute 1993). We included IFBF as a covariate in this analysis because body fat may influence pregnancy status as much as or more than age (Cook et al. 2004a). We conducted this analysis with data from all females ≥ 9 years old, to ensure that older females and prime-aged females were approximately equally represented in the data set (thereby making the test for an age effect more liberal). We ran the logistic regression iteratively, first including females 9–12 years old, then 9–13 years old, and so on until all older animals were included. We selected our prime age category as the age range at which we found no significant effect of age on pregnancy status. To determine whether the age categories applied to females in both the coastal region (*C. e. roosevelti*) and the rest of their range (*C. e. nelsoni*), we repeated the logistic regression using autumn IFBF, age, subspecies, and the interaction of age and subspecies for all animals ≥ 9 years old but < 15 years old. If the interaction term of age and subspecies was significant, we ran the iterative analysis with females from each subspecies separately. We also ensured that nutritional condition was not influenced by age within our prime-age category by conducting repeated measures ANCOVA on autumn condition (IFBF and BM_{NP}; lactating females only) and spring condition (IFBF and BM_{NP} using only females that were lactating the previous autumn) with 3 covariate predictor variables: age at capture, herd, and their interaction.

We used a second preliminary analysis to determine if lactation status masked relations between IFBF and other variables, such as herd or season. Substantial evidence indicates data for each elk would need to be stratified by lactation status during the summer-autumn seasons because fat accretion of lactating females and non-lactating females varies substantially despite identical levels of nutrition (i.e., IFBF of non-lactating females might be less

sensitive to their nutritional environment; Clutton-Brock et al. 1982, Gerhart et al. 1997b, Landete-Castillejos et al. 2003, Cook et al. 2004a). We checked to ensure this pattern held in wild elk and throughout the herds we sampled. We categorized females as lactating or non-lactating at time of autumn capture, and then we used individual repeated measures ANCOVAs to analyze the relationship of change in IFBF over summer to previous-season IFBF, herd, lactation status, and the interactions as independent variables. We used prime-age animals in this analysis.

We also evaluated whether lactation throughout winter affected body fat dynamics such that it would need to be included as a covariate in all winter analyses. We performed the same analysis for winter except we used change in IFBF over winter as the dependent variable. In addition, Robbins et al. (1981) suggested that past some point in the autumn, lactation has more value for calf-mother bonding than nutrient transfer. Therefore, lactation may have little influence on energy balance and IFBF of the mother over winter. Although some analyses required using only elk that lactated the previous autumn, we did not want to group animals into a physiological category unless biological evidence indicated that doing so would be appropriate. Thus, to address the effect of lactation on condition change over winter more accurately, we compared IFBF dynamics of elk that were either 1) lactating at capture in the autumn but not lactating at capture in the subsequent spring; or 2) lactating at capture in autumn and still lactating the subsequent spring. We used repeated measures ANOVA with change in IFBF over winter as the dependent variable and herd, lactation status, and the interaction as independent variables. Only prime-age animals were included in this analysis.

We evaluated the effect of herd year on IFBF to determine if pooling across years within herds was justified or whether including herd year as a covariate would be necessary in our analyses. We conducted individual repeated measures ANCOVA for autumn IFBF (lactating females only), spring IFBF (previous autumn lactating females only), change in IFBF over summer (lactating females only), change in IFBF over winter (previous autumn lactating females only) with 3 covariates: year of capture, herd, and the interaction of the 2. Only the interaction term was relevant for this analysis because we were interested only in annual variation within herds. We used least-squares means (LSMEANS, SAS Institute 1993) to identify which herds had significant year effects.

Autumn and spring nutritional condition.—Using prime-age females only, we evaluated herd-level differences in nutritional condition between spring and autumn and tested for differences among herds. As an initial screening to identify differences in nutritional condition among herds, we used a 1-way, fixed effects ANOVA with Duncan's multiple range test for each condition variable (IFBF and BM_{NP} as dependent variables) with herd as the independent variable. We ran separate ANOVAs for autumn and spring, and for this analysis only, we averaged condition estimates for individual animals across years so that no single female would be represented more than once in the data. We used this approach because post hoc multiple range tests to compare among herds in a repeated measures mixed model is not currently possible. Our approach retains all elk, but eliminates undue influence by data from individual elk that were repeatedly sampled among years. Because lactating females are more sensitive to their

nutritional environment over summer and early autumn than are non-lactating females (Clutton-Brock et al. 1982, Gerhart et al. 1997b, Landete-Castillejos et al. 2003, Cook et al. 2004a), we used nutritional condition data only from lactating females in both the spring and autumn analysis. Thus, non-lactating females captured in spring but not captured the previous autumn were censored from the spring ANOVA because we did not know their lactation status the previous autumn.

We also evaluated the relation between autumn fat level of lactating females and body size of females to examine whether summer nutrition levels have long-term effects on adult animal size (Skogland 1983). We hypothesized that summer ranges providing good nutrition should support larger elk than summer ranges of relatively poor nutrition. Using a herd-level approach, we used linear regression to examine the relationship between BM_{IFF} and autumn IFBF of lactating females because they are more indicative of summer nutrition levels.

Seasonal changes in nutritional condition.—We evaluated herd-level trends in changes of nutritional condition across summer and winter. We only included animals for which we had paired samples (autumn and subsequent spring or spring and subsequent autumn) in these analyses. Because the number of days between sequential captures among herds was not always the same, we analyzed change-in-condition expressed as daily change (which would account for differences in number of days between sequential samples) and total change over the season. Our intention was to present only the latter results if the 2 methods were significantly and biologically equivalent.

We first evaluated the relationship between changes in condition over winter versus changes in condition over summer to determine if individual females were able to recover in summer what they had lost the previous winter. Using ANOVA, we performed separate analyses for each condition index (change in IFBF [percentage points] and change in BM_{NP} [kg] as dependent variables) with herd, season (winter, summer) and their interaction as independent variables. We repeated the analysis substituting region in place of herd. For this analysis, the dependent variable was the absolute value of seasonal change either in winter or summer; an insignificant result for season would indicate that winter losses approximately equaled summer gains. We restricted the sample for statistical analysis to prime-age elk and excluded Hanford (herd #13) from this analysis. We also restricted the analysis to include only those elk that lactated 2 years in row and for which we had 3 sequential captures, either 1) were lactating upon capture in autumn, recaptured the next spring, lactated again that summer, and were recaptured that second autumn or 2) were lactating in spring at capture, were lactating upon capture the following autumn, and were recaptured the following spring. This approach was necessary to avoid comparing winter losses of previously non-lactating elk to their summer gains while lactating, a potentially invalid comparison.

Second, we evaluated the relationship between starting condition and ending condition to evaluate potential carry-over effects across seasons on condition levels. Expecting that winter weather (temperature and precipitation) may influence IFBF dynamics over winter, we evaluated effects of winter on the relationship between spring IFBF and previous autumn IFBF, and between change in IFBF over winter and previous autumn

IFBF by including winter weather variables as covariates. We used either a minimum convex polygon for all animal relocations within a herd from December to February ($n = 10$ herds) or we asked biologists associated with each herd to delineate winter range boundaries based on their knowledge of herd movements ($n = 4$ herds). We obtained weather data for December–February for the winter range of each herd for each year that we collected nutritional condition data from PRISM (Parameter-elevation Regressions on Independent Slopes Model), a climate analysis system that uses point data, a digital elevation model, and other spatial datasets to project spatial grids of annual and monthly weather parameters (Daly et al. 1994). The PRISM weather metrics are spatially explicit on a 4-km² grid across North America. We randomly selected 6–15 pixels (number of pixels depended on winter range polygon size; average = 9) within the winter-range polygon to obtain representative winter weather data. Our winter variables were average December–February precipitation (mm), the sum of December–February precipitation (mm), and average December–February minimum temperature (°C).

We evaluated the relationship between spring IFBF with each individual weather variable and previous autumn IFBF using multiple regression (PROC REG, SAS Institute 1988) and with each herd $\times$ year combination as an independent sample ($n = 32$). We ran the same regressions using change in IFBF over winter as the dependent variable. We plotted relations between both spring IFBF and change in IFBF over winter with each independent variable and identified significant nonlinear relations between those variables and spring IFBF and overwinter change in IFBF (CurveExpert 1.37; Daniel Hyams, Hixson, TN). If winter weather was not significant, it was dropped from subsequent analyses.

To evaluate the direct effect of previous nutritional condition on current condition, we used repeated measures ANCOVA to evaluate the relation of autumn condition (IFBF or BM_{NP}), herd, and the interaction on subsequent spring condition and change in condition over winter. We repeated the analysis using region instead of herd. We conducted a similar analysis to evaluate autumn nutritional condition as a function of previous spring condition for lactating females to see if animals starting summer in poorer condition could compensate by the breeding period. We used repeated measures ANCOVA to evaluate the effect of previous spring condition (IFBF or BM_{NP}), herd, and the interaction on both autumn condition and the change in condition across the summer.

Pregnancy, fetal loss, and lactational infertility.—Pregnancy rates could differ across herds as a function of their autumn nutritional condition, which would be indicative of a prior nutritional constraint in summer. To compare herds in this regard, we calculated herd-level pregnancy rates (number of pregnant females/total number female captures) across years based on both spring and autumn samples. We calculated rates separately by lactation status and included prime-age females only. In 1 herd (Wynoochee), we removed 5 females from the analysis because we found no evidence of pregnancy ≥ 2 consecutive years despite having high IFBF levels each year ($>12\%$; we suspected these elk were permanently infertile). We classified females that were not pregnant in autumn, but pregnant in spring, as late-breeding. Similarly, we assumed that any

females pregnant in autumn and not pregnant the subsequent spring based on both PSPB and ultrasonography results suffered embryonic or fetal loss. Such elk were excluded from pregnancy rate calculations and further analyses.

We used logistic regression to evaluate the probability of breeding relative to autumn IFBF for both individual herds and regions. Because we did not conduct captures in some herds in the spring, thus reducing sample size using spring pregnancy determinations, we ran this analysis separately for autumn and spring pregnancy determinations. We used all data from prime-age females without adjusting for repeated measures because, to our knowledge, such an adjustment cannot be incorporated with logistic regression. We also evaluated probability of breeding relative to spring IFBF to assess whether nutritional condition data collected during late winter or early spring could be related to either current reproductive success (breeding the previous autumn) or future reproductive success (breeding the subsequent autumn) using females for which we had successive data. We used logistic regression for both analyses and including herd and its interaction with IFBF as covariates.

Using the same data sets (with spring and autumn evaluated separately), we tested for lactational infertility by including autumn lactation status and herd with autumn IFBF and all 3-way and 2-way interactions in the logistic regression model. If interactions were not significant, we removed them from the model and evaluated simple effects. We defined lactational infertility as a reduction in probability of breeding primarily due to the interaction of physical stimulus of being nursed and changes in reproductive hormones (Loudon et al. 1983, Gerhart et al. 1997a). We assumed that significantly lower pregnancy rates of lactating versus non-lactating elk at any given level of body fat in autumn would provide evidence of lactational infertility (Gerhart et al. 1997a).

We also evaluated factors influencing pregnancy in older, senescent females. Using logistic regression, we assessed the probability of breeding relative to autumn IFBF and 2 age categories, prime (2–14 years old) and old (>14 years old). Because so few animals were included in the old age category, we did not include region or location as a covariate when analyzing their data. We ran separate analyses for spring pregnancy and autumn pregnancy status. We focused on the interaction between age class and condition, which, if significant, would suggest that the best predictor of the probability of pregnancy in younger females may be different than for older females. Given our small sample sizes for older females and the effect of small sample size on logistic regression results (Kutner et al. 2005), we also used ANOVA to determine if autumn body fat varied by pregnancy status (pregnant or not; autumn only) and age category. Again, the interaction term (age $\times$ pregnancy status) was of interest.

Condition and pregnancy of sub-adults.—We provide descriptive statistics for body mass of calves and body mass and body fat of yearlings in spring and autumn among herds. We did no formal statistical comparisons because we only had data on calves from 3 herds, and for yearlings, sample sizes were too small within herds for meaningful comparisons. Using logistic regression, we evaluated the probability of pregnancy in yearlings relative to BM_{NP} based on spring data only (sample sizes in autumn were too limited for an analysis).

Causes of year-to-year variation.—Using only autumn-lactating females, we performed individual ANOVAs for each herd to first identify year effects on autumn IFBF, spring IFBF, change in IFBF over summer, and change in IFBF over winter. Although previously we had performed a preliminary global analysis on year effects to determine whether pooling across years was justified, this more liberal analysis by individual herd allowed us to identify those factors that might induce annual variation in body fat levels within those herds that exhibited significant year effects.

For any herd exhibiting a year effect, we then added previous-season IFBF and its interaction with year to an ANCOVA as covariates. If the year effect remained significant, previous-season IFBF was not inferred to be the cause of the year effect and something else (e.g., differences in weather among years) had likely caused the year effect. Thus, if year was still significant, we replaced year with weather (precipitation and temperature in winter, precipitation in summer) and ran the ANCOVA again. We conducted these analyses for each herd individually, such that if year (or weather effects) were local, our chance of detecting these local effects might be enhanced compared to our global analyses using all herds.

RESULTS

We estimated nutritional condition and pregnancy on at least 1 capture event in each of 21 elk herds (Table 2). We captured 861 individual elk over 2,114 captures during autumn (from early Nov to mid-Dec) and spring (late-Feb through early Apr). We censored data collected outside these 2 periods from the analysis ($n = 106$ capture events from 2 herds).

Preliminary Analyses: Accounting for Age, Lactation Status, and Year

Elk pregnancy rates tended to decline after 15 years of age for the Cascades, inland Northwest, and Rocky Mountain herds (Fig. 2). Although pregnancy rates seemed to decline at age 13–14 years in coastal herds, sample sizes for these older age classes were ≤ 4 (Fig. 2). Age had an effect on the relationship between autumn IFBF and probability of pregnancy for all females >1 year of age ($\chi^2 = 12.59$, $n = 729$, $P < 0.001$) and for all females ≥ 9 years of age ($\chi^2 = 4.59$, $n = 389$, $P = 0.03$). Using this latter subset iteratively, age was not significant with animals ≥ 12 years of age removed ($\chi^2 = 0.07$, $n = 239$, $P = 0.80$), ≥ 13 years of age removed ($\chi^2 = 0.12$, $n = 286$, $P = 0.12$), ≥ 14 years of age removed ($\chi^2 = 1.39$, $n = 349$, $P = 0.24$), but approached significance when females ≥ 15 years of age were removed ($\chi^2 = 3.6$, $n = 324$, $P = 0.059$). Therefore, we classified females ≥ 2 and <15 years as prime-age for our subsequent analyses. We found no interaction between subspecies and age on the relationship between IFBF and pregnancy ($\chi^2 = 0.60$, $n = 324$, $P = 0.44$), thus our prime-age category was the same for both Roosevelt and Rocky Mountain females.

Within our prime-age category, we found no effect of age or age $\times$ herd on IFBF of lactating females in autumn (age: $F_{1, 85} = 1.53$, $P = 0.22$; age $\times$ herd: $F_{16, 85} = 1.33$, $P = 0.20$) or BM_{NP} (age: $F_{1, 77} = 1.21$, $P = 0.27$; age $\times$ herd: $F_{16, 77} = 1.47$, $P = 0.13$). We also found no effect of age or age $\times$ herd on spring IFBF (age: $F_{1, 51} = 0.08$, $P = 0.77$; age $\times$ herd: $F_{16, 51} = 1.87$, $P = 0.06$) or BM_{NP} (age: $F_{1, 46} = 0.06$, $P = 0.81$; age $\times$ herd:

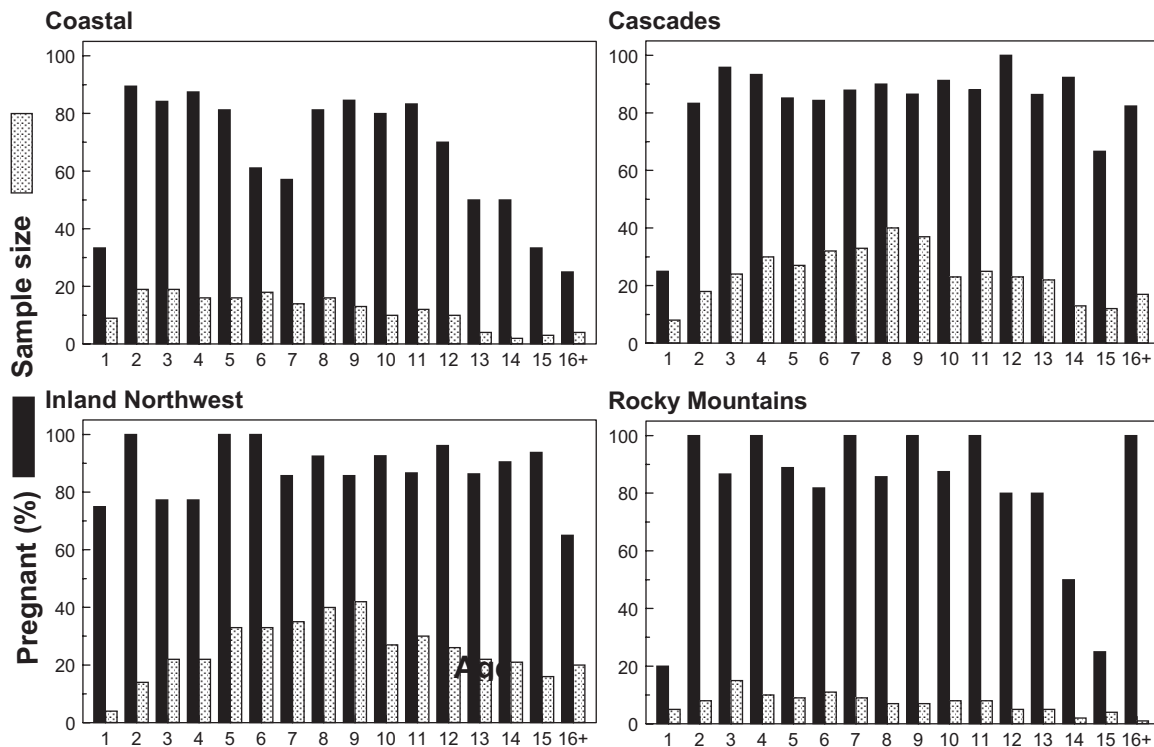


Figure 2. Percent pregnant and sample size (frequency) by age of elk in 4 regions of the western United States: 1) coastal areas west of Interstate 5 in Oregon and Washington (*Cervus elaphus roosevelti*); 2) Cascades east of Interstate 5 and west of the Cascades crest in Oregon and Washington (*C. e. nelsoni*); 3) inland Northwest east of the Cascades crest in Washington and Oregon (*C. e. nelsoni*); and 4) Rocky Mountains of Wyoming, Colorado, and South Dakota (*C. e. nelsoni*). We collected data during 1998–2007.

$F_{16, 46} = 0.91$, $P = 0.56$). Therefore, we used only prime-aged animals and did not include age as an independent variable in subsequent analyses unless otherwise noted.

We found that change in IFBF over winter was not affected by lactation status ($F_{1, 44} = 0.71$, $P = 0.40$), herd ($F_{12, 232} = 1.66$, $P = 0.08$) or the 2-way or 3-way interactions of herd, lactation status, and autumn IFBF on change in IFBF over winter ($P > 0.14$). Only IFBF of females in autumn was significant in predicting change in IFBF over winter ($F_{1, 142} = 211.00$, $P < 0.001$). When we used only females that were lactating the previous autumn, we found no effect of lactation status in spring on change in IFBF over winter ($F_{1, 29} = 1.11$, $P = 0.384$), indicating that overwinter declines in IFBF of females that lactated until spring were similar to declines in females that did not continue to lactate through the winter. Furthermore, the result was consistent among herds (herd $\times$ lactation interaction; $F_{9, 29} = 0.00$, $P = 0.978$). Therefore, we conducted subsequent analyses of changes in nutritional condition over winter without respect to overwinter lactation status.

We found that lactation status affected change in IFBF over summer ($F_{1, 62} = 47.96$, $P < 0.001$), and lactating females were in poorer condition than their non-lactating counterparts by autumn. Spring IFBF ($F_{1, 186} = 364.67$, $P < 0.001$) and herd ($F_{12, 295} = 20.91$, $P < 0.001$) each influenced the change in IFBF over summer, but none of the 2-way or 3-way interactions were significant ($P > 0.08$), suggesting that the depressing effects of lactation on IFBF were the same among herds. Therefore, for all

subsequent analyses using autumn or change in summer variables, we classified females according to lactation status at the time of autumn capture and limited all subsequent analyses for autumn condition levels and change in nutritional condition over summer to lactating females only. We restricted analyses in this manner because females not lactating in autumn are a heterogeneous group of elk that either were not pregnant the previous spring or had lost their calf sometime between parturition and the autumn capture, thus, greatly complicating interpretation of this group's data.

Including only lactating females in our analyses, we found no year $\times$ herd interaction effect on autumn IFBF ($F_{26, 61} = 1.46$, $P = 0.11$), on change in IFBF across summer ($F_{18, 25} = 1.48$, $P = 0.18$), or on spring IFBF ($F_{11, 38} = 0.90$, $P = 0.59$). However, we did find a year $\times$ herd effect on change in IFBF over winter ($F_{11, 23} = 2.62$, $P = 0.02$). Significant yearly variation was evident for both the Green and White River herds (Cascade region) and the Yakima herd (inland Northwest region). However, when we included autumn IFBF as a covariate in the analysis (assuming previous IFBF influences overwinter change in IFBF [Dale et al. 2008]), autumn IFBF was significantly related to change in IFBF over winter ($F_{1, 22} = 87.76$, $P < 0.001$), but the herd $\times$ year interaction was not ($F_{11, 22} = 1.67$, $P = 0.15$). Given these results and given that sample sizes were generally too small to support a more robust year analyses within herd, we subsequently pooled each herd's data across years and excluded herd-year as a covariate for the remaining analyses.

Autumn and Spring Nutritional Condition

Although sample sizes were small for several herds (10–40 elk per sampling period; Table 2), IFBF estimates for most herds were relatively precise within the lactating category, having standard errors of ± 0.5 to 1.5 percentage points of the estimated IFBF (Fig. 3). In every herd, lactating females were in poorer condition than non-lactating females in both autumn and in spring.

Substantial variation in nutritional condition was evident among regions and among herds within regions for prime-age, lactating females in both autumn and in spring (Figs. 3 and 4). We found an effect of herd on autumn IFBF ($F_{16, 300} = 15.59$,

$P < 0.001$) and BM_{NP} ($F_{16, 276} = 11.73$, $P < 0.001$). We also found an effect of herd on spring IFBF ($F_{16, 206} = 7.99$, $P < 0.001$) and BM_{NP} ($F_{16, 201} = 14.15$, $P < 0.001$).

Average autumn IFBF levels of lactating females varied among herds, ranging from 5.5% to 6.2% in the coastal plains and foothills, 5.5% to 12.4% in the Cascades, 5.7% to 7.3% in the inland Northwest, and 5.9% to 9.6% in the Rocky Mountains (Fig. 3A). In general, nutritional condition was highest in northern Cascade herds (including Nooksack and White River) and some portions of the Rocky Mountains, and lowest along the coastal foothills, southern Cascade Mountains and inland Northwest herds. Herd averages for spring IFBF of females

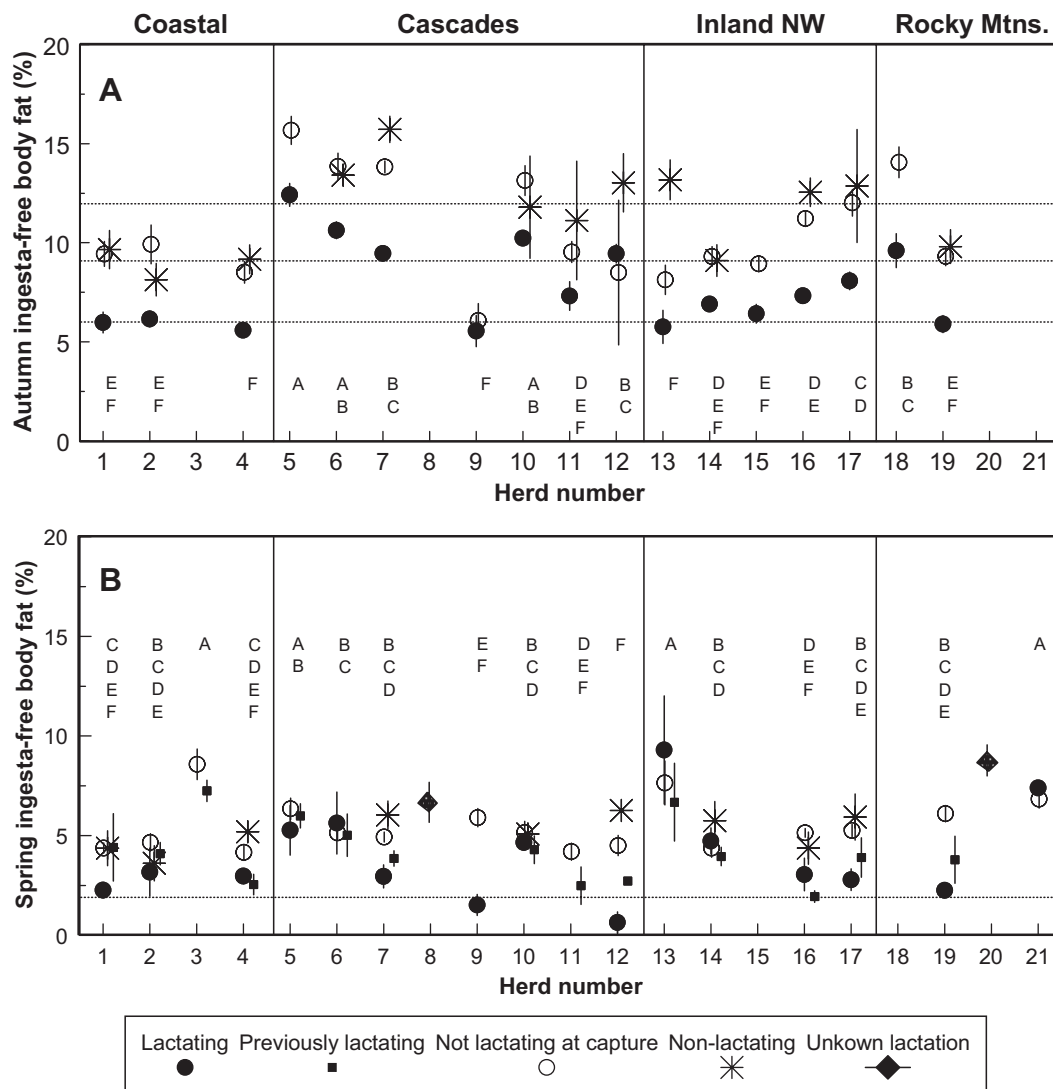


Figure 3. Average percent ingesta-free body fat (IFBF) in late autumn (A) and early spring (B) for female elk in 21 herds (see Table 2 and Fig. 1 for herd numbers) across 4 regions of the western United States: 1) coastal areas west of Interstate 5 in Oregon and Washington (*Cervus elaphus roosevelti*); 2) Cascades east of Interstate 5 and west of the Cascades crest in Oregon and Washington (*C. e. nelsoni*); 3) inland Northwest (NW) east of the Cascades crest in Washington and Oregon (*C. e. nelsoni*); and 4) Rocky Mountains (Mtns.) of Wyoming, Colorado, and South Dakota (*C. e. nelsoni*). Data are grouped according to lactation status: lactating = milk present at time of capture; previously lactating applies to spring females only and indicates females that were lactating the previous autumn but had ceased by spring capture; non-lactating indicates no evidence of milk at capture but were pregnant the previous spring; spring non-pregnant indicates females that were not pregnant the previous spring. We collected data during 1998–2007 and typically obtained 2 years of sampling (range 1–7) and 40 sampled elk (range 11–160) per herd. Error bars represent the standard error of the mean. Different letters among herds denote significant differences in IFBF for females lactating in autumn only. Horizontal lines indicate nutrition-performance thresholds from Cook et al. 2004a): >12% body fat = little or no summer nutritional limitations; >9% body fat = high probability of pregnancy; <6% body fat = high probability of reproductive pause and suggestive of strongly inadequate summer nutrition; <2% body fat (in B) = level of condition in which chance of death in late winter is probably elevated.

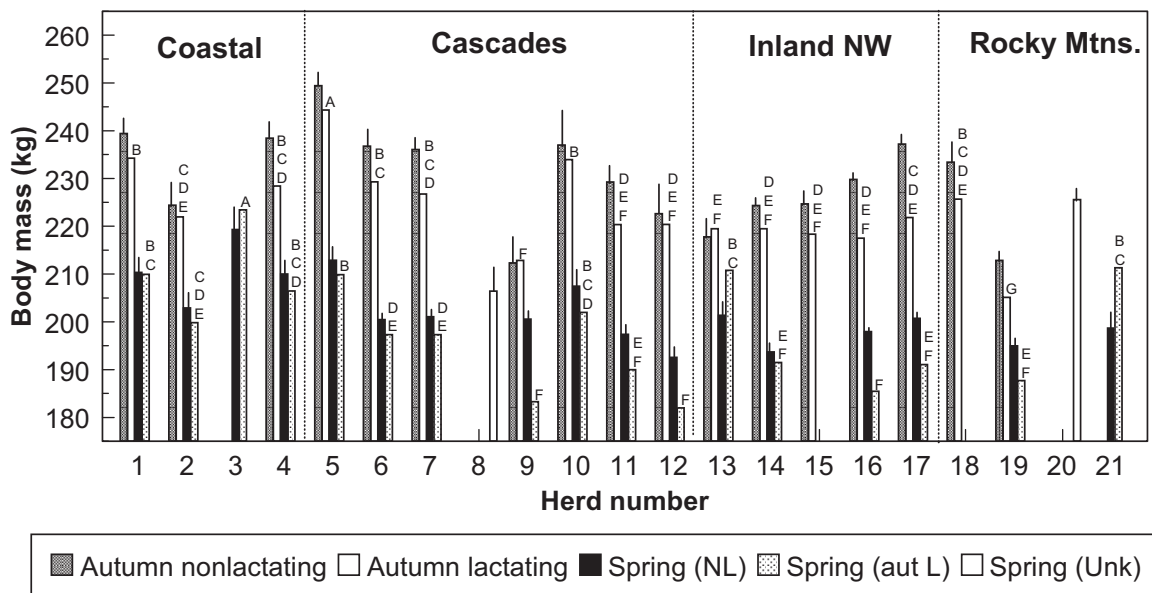


Figure 4. Average body mass (BM_{NP} ; estimated via girth circumference with products of conception excluded) in late autumn and early spring for female elk in 21 herds (see Table 2 and Fig. 1 for herd numbers) across 4 regions of the western United States: 1) coastal areas west of Interstate 5 in Oregon and Washington (*Cervus elaphus roosevelti*); 2) Cascades east of Interstate 5 and west of the Cascades crest in Oregon and Washington (*C. e. nelsoni*); 3) inland Northwest (NW) east of the Cascades crest in Washington and Oregon (*C. e. nelsoni*); and 4) Rocky Mountains (Mtns.) of Wyoming, Colorado, and South Dakota (*C. e. nelsoni*). We grouped data according to lactation status and season: autumn lactating indicates milk present at time of capture; autumn non-lactating indicates no evidence of milk at capture and thus the elk may or may not have experienced the demands of lactation for a portion of the growing season; spring (NL) indicates no evidence of milk at capture; spring (aut L) indicates either milk was present at capture or had milk in the autumn; and spring (Unk) indicates lactation status was unknown. We collected data during 1998–2007 and typically obtained 2 years of sampling (range 1–7) and 40 sampled elk (range 11–160) per herd. Error bars represent the standard error of the mean. Different letters among herds denote significant differences in BM_{NP} across herds within seasons for females lactating in autumn only.

that had lactated through the previous growing season ranged from 2.2% to 3.2% in the coastal plains and foothills, 0.6–5.6% in the Cascades, 2.8–9.3% in the inland Northwest, and 2.3–7.4% in the Rocky Mountains (Fig. 3B). In general, spring IFBF was highest in the northern Cascades of Washington and some parts of the Rocky Mountain region and lowest in the coastal plains and foothills, the inland northwest, and the southern Cascades in Washington and Oregon. However, 2 herds showed exception: 1) spring fat levels at Chehalis Valley (herd 3, Fig. 3B) were markedly higher than the other coastal herds likely because we captured elk from agricultural pastures; and 2) spring fat levels at Hanford (herd 13, Fig. 3B) were markedly higher the second year of data collection, which occurred after the fire.

We found similar patterns among and within regions for BM_{NP} . Herd averages of autumn BM_{NP} of lactating females ranged from 222 kg to 234 kg in the coastal plains and foothills, 213–244 kg in the Cascades, 217–222 kg in the inland Northwest, and 205–226 kg in the Rocky Mountains (Fig. 4). Herd averages of spring, BM_{NP} levels of females that lactated through the previous summer ranged from 203 kg to 219 kg in the coastal plains and foothills, 192–213 kg in the Cascades, 194–204 kg in the inland Northwest, and 195–199 kg in the Rocky Mountains (Fig. 4).

Fat-free, ingesta-free body mass (BM_{IFF}) declined significantly across Rocky Mountain herds as the autumn condition of their lactating females declined ($t_{1, 12} = 2.65$, $P = 0.021$). Each percentage point change in autumn IFBF corresponded to a 1.13 kg change in BM_{IFF} (Fig. 5). Thus, herd ranges that support fatter elk in autumn also support larger elk.

Seasonal Change in Nutritional Condition

In all herds except 1, females that lactated 2 years consecutively gained condition in summer and lost condition in winter (Fig. 6A,B); the exception was San Luis Valley, Colorado (herd #19). Gains in nutritional condition over summer and losses over winter varied among herds (IFBF: $F_{11, 132} = 4.47$, $P < 0.001$; BM_{NP} : $F_{10, 114} = 8.23$, $P < 0.001$) and regions (IFBF: $F_{3, 150} = 21.84$, $P < 0.001$; BM_{NP} : $F_{3, 128} = 17.48$,

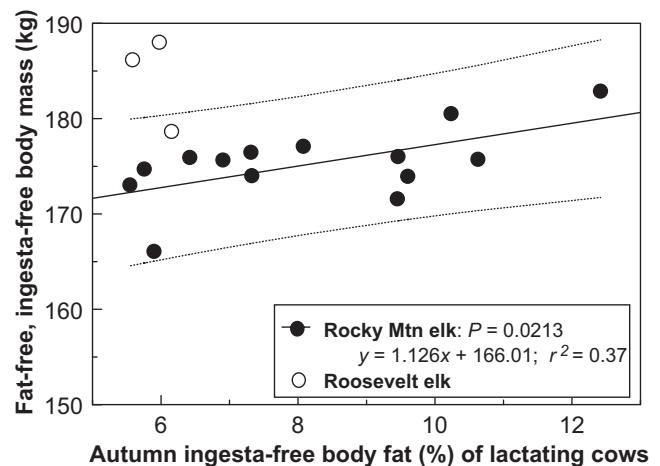


Figure 5. Relationship between the average fat-free, ingesta-free body mass (BM_{IFF}) and average ingesta-free body fat in autumn of lactating females for 21 elk herds in Washington, Oregon, Wyoming, Colorado, and South Dakota, USA, collected during 1998 through 2007. Dotted lines indicate 95% confidence intervals for Rocky Mountain (Mtn) elk (*Cervus elaphus nelsoni*).

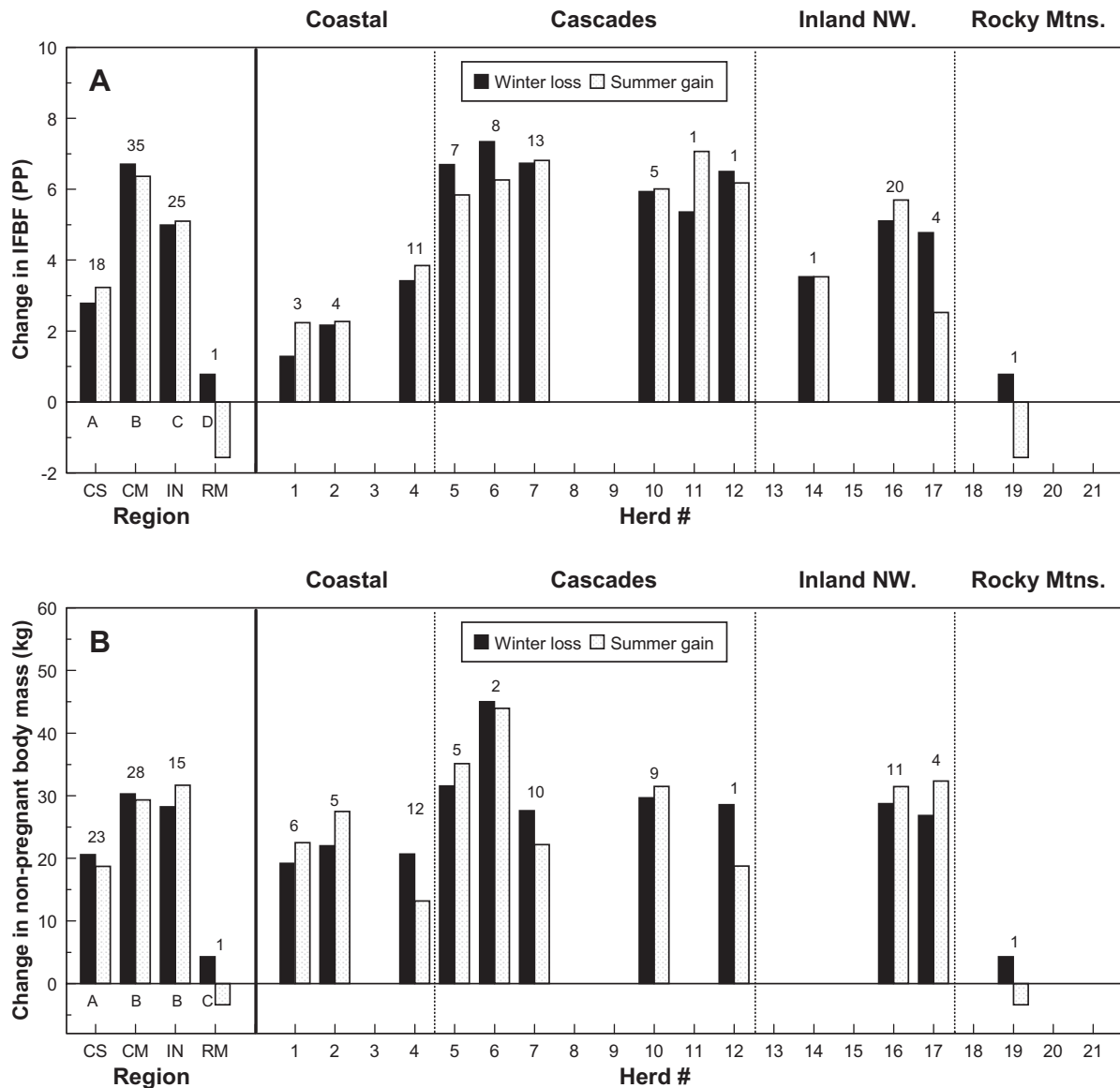


Figure 6. Average loss of ingesta-free body fat (IFBF on a percentage-point [PP] basis); (A) and body mass (with products of conception removed; BM_{NP} [kg]) (B) over winter paired with average gain of IFBF and BM_{NP} over summer for female elk in 21 herds (see Table 2 and Fig. 1 for herd numbers) across 4 regions of the western United States during 1998–2007: 1) the coastal plains and mountains west of Interstate 5 in western Oregon and Washington (CS; *Cervus elaphus roosevelti*; herds 1–4); 2) the hills and Cascades mountains east of Interstate 5 and west of the crest of the Cascades in western Oregon and Washington (CM; *C. e. nelsoni*; herds 5–12); 3) the inland Northwest (NW.) from the crest of the Cascades east across Washington and Oregon (IN; *C. e. nelsoni*; herds 13–17); and 4) the northern and central Rocky Mountains (Mtns.) of Wyoming, Colorado, and South Dakota (RM; *C. e. nelsoni*; herds 18–21). We only included data from elk lactating 2 years in a row and with consecutive spring, autumn, spring data values in this analysis. We report sample sizes above the bars for each herd and region. Different letters denote differences in condition gains or losses for regions.

$P < 0.001$), but did not vary with respect to season (IFBF: $F_{1, 132} = 0.00$, $P = 0.94$; BM_{NP}: $F_{1, 114} = 0.07$, $P = 0.79$) or the interaction of season with herd (IFBF: $F_{11, 132} = 0.31$, $P = 0.98$; BM_{NP}: $F_{10, 114} = 1.0$, $P = 0.44$) or season with region (IFBF: $F_{2, 150} = 0.29$, $P = 0.75$; BM_{NP}: $F_{3, 128} = 0.59$, $P = 0.62$). These results indicate that for lactating females, winter losses equaled summer gains in condition, but how much loss or gain occurred varied across herds and regions.

Average herd-level improvement of nutritional condition during summer of lactating females ranged from 2.2 to 3.9 percentage points IFBF (13.2–27.5 kg BM_{NP}) gained in the coastal plains and foothills herds, 5.8–7.1 points IFBF (18.8–43.98 kg BM_{NP}) gained in the Cascades, 2.5–5.7 points IFBF

(31.5–32.4 kg BM_{NP}) gained in the inland Northwest, and 1.6 points IFBF (3.4 kg BM_{NP}) lost in San Luis Valley (Fig. 6A,B).

Herd averages for nutritional condition lost during winter by females that were lactating the previous autumn ranged from 1.3 to 3.4 percentage points IFBF (19.2–22.0 kg BM_{NP}) lost in the coastal plains and foothills, 5.4–7.3 points IFBF (27.6–45.1 kg BM_{NP}) in the Cascades, 3.5–5.1 points IFBF (26.9–28.7 kg BM_{NP}) in the inland Northwest, and 0.8 points IFBF (4.3 kg BM_{NP}) lost in San Luis Valley (Fig. 6A,B).

Although winter conditions varied dramatically among herds and among years within herds (Fig. 7A,B, Appendix), we found no significant influence of winter weather on either spring IFBF ($F_{1, 28} > 0.13$; $P > 0.36$) or change in IFBF over winter

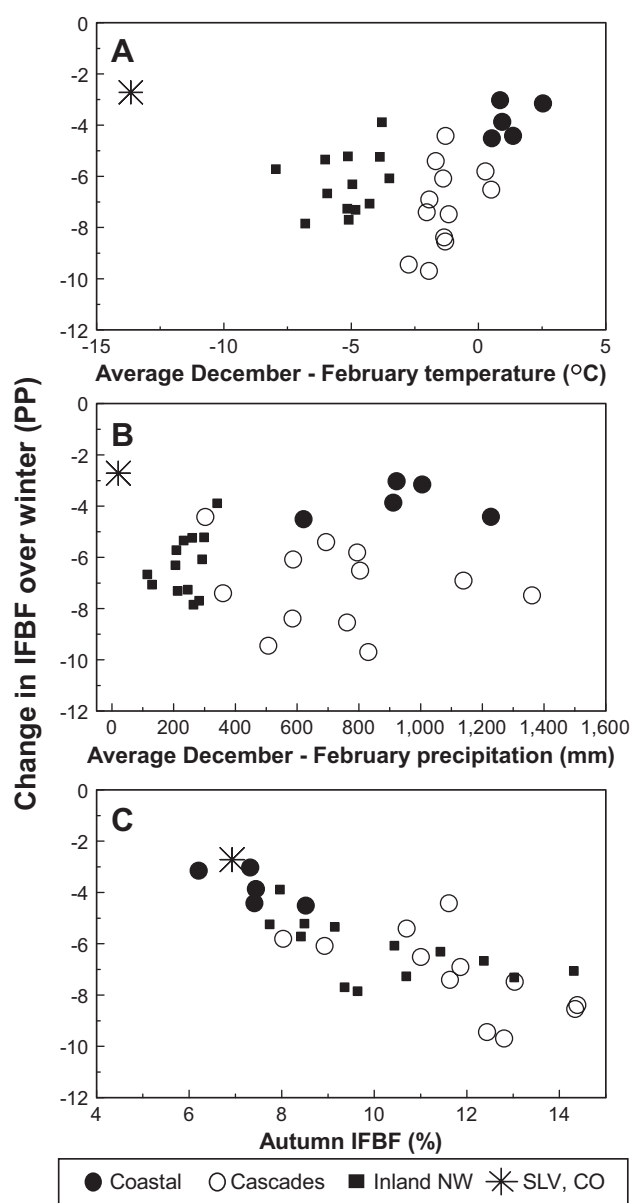


Figure 7. Relationship between average change in ingesta-free body fat (IFBF; on a percentage-point [PP] basis) for lactating female elk over winter with average minimum temperature during December through February (panel A); average precipitation during December through February (panel B); and average autumn IFBF (panel C) for 13 elk herds across 4 regions of the western United States: 1) the coastal plains and mountains west of Interstate 5 in western Oregon and Washington (*Cervus elaphus roosevelti*); 2) the hills and Cascades mountains east of Interstate 5 and west of the crest of the Cascades in western Oregon and Washington (*C. e. nelsoni*); 3) the inland Northwest (NW) from the crest of the Cascades east across Washington and Oregon (*C. e. nelsoni*); and 4) San Luis Valley, Colorado (SLV, CO) in the northern and central Rocky Mountains (*C. e. nelsoni*). We only included those herds with IFBF data from autumn and the subsequent spring in this analysis (Appendix), and presented each herd year of data ($n = 32$) separately. We collected all data during 1998–2007.

($F_{1, 28} > 0.12$; $P > 0.35$) when we also included previous-autumn IFBF as an independent variable (Fig. 7C). Thus, the principal driver of spring IFBF was more related to autumn condition than to winter weather. Consequently, we found no compelling rationale for including winter weather in subsequent analyses.

We found a positive and significant linear relationship (slope of 0.32) between spring IFBF as a function of previous-autumn

IFBF for all herds combined ($P < 0.001$) and for each region (slopes ranged from 0.24 to 0.47; $P < 0.04$; Fig. 8A). This positive relation with slope significantly > 0 but < 1 indicates that thinner females compensated over winter, but they nevertheless ended winter in poorer condition than their fatter counterparts (Fig. 8A; a horizontal line would indicate complete convergence of nutritional condition, whereas a slope of 1 would indicate no compensation [i.e., all animals, regardless of autumn condition, would lose the same absolute amount of condition over winter]).

We found no evidence of a herd, herd $\times$ autumn IFBF interaction effect ($F_{12, 201} \leq 1.39$, $P \geq 0.17$), region, or region $\times$ autumn IFBF interaction effect ($F_{12, 201} \leq 1.64$, $P \geq 0.180$) on spring IFBF. The lack of a region $\times$ autumn IFBF interaction on spring IFBF suggested that the rate of IFBF loss was relatively consistent across regions, indicating that winter fat loss, for any given level of previous-autumn body fat, was similar among regions, despite considerably different winter weather regimes among them.

We obtained a similar result using overwinter change in IFBF as the dependent variable (Fig. 8B). Change in IFBF over winter was negatively related to previous-autumn IFBF ($F_{1, 131} = 37.71$, $P < 0.001$), but did not vary by herd ($F_{12, 232} = 1.10$, $P = 0.36$) or the interaction of herd and previous-autumn IFBF ($F_{12, 131} = 1.37$, $P = 0.19$). Using region in place of herd produced similar results. These findings, in particular those showing no difference among herds and regions with widely variable winter conditions, again provide evidence of the overriding effect of autumn body fat on loss of fat over winter.

Similar patterns existed for changes in BM_{NP} over winter (Fig. 9A). We found no evidence of an interaction between autumn BM_{NP} with herd or region ($P > 0.20$) or a main effect of herd ($P = 0.27$) or region ($P = 0.35$) on BM_{NP} in spring. However, spring BM_{NP} was significantly related to previous-autumn levels ($P < 0.001$) whether using herd or region as a covariate. A regression of spring BM_{NP} on autumn BM_{NP} produced positive slopes < 1 (ranges: 0.53–0.79) indicating heavier or bigger females in autumn, though losing body mass more rapidly, were still heavier or bigger in the spring for each region (Fig. 9A).

IFBF of lactating females in autumn, however, was not related to IFBF the previous spring ($F_{1, 216} = 3.02$, $P = 0.084$). Females were able to compensate during summer for being relatively thin in spring (Fig. 10A). Autumn IFBF also was unrelated to the interaction of herd and spring IFBF ($F_{12, 216} = 0.79$, $P = 0.659$), but was related to herd ($F_{12, 216} = 4.53$, $P < 0.001$). As a check, we evaluated spring and autumn IFBF relations within regions, and found a weak but positive relationship between autumn IFBF and previous spring IFBF only in the Cascade region ($r^2 = 0.03$; $P < 0.027$; Fig. 10A). Separating this analysis for North and South Cascades (Fig. 10A) suggested a similar pattern (parallel regression lines) in the 2 sub-regions. Our results indicated very little advantage of having higher IFBF levels in spring in terms of IFBF levels in autumn, at least under the weather and forage conditions that predominated during our study.

Using change in IFBF over summer in a similar analysis illustrated the considerable ability of thin elk in spring to compensate over summer while raising a calf (Fig. 10B). Change

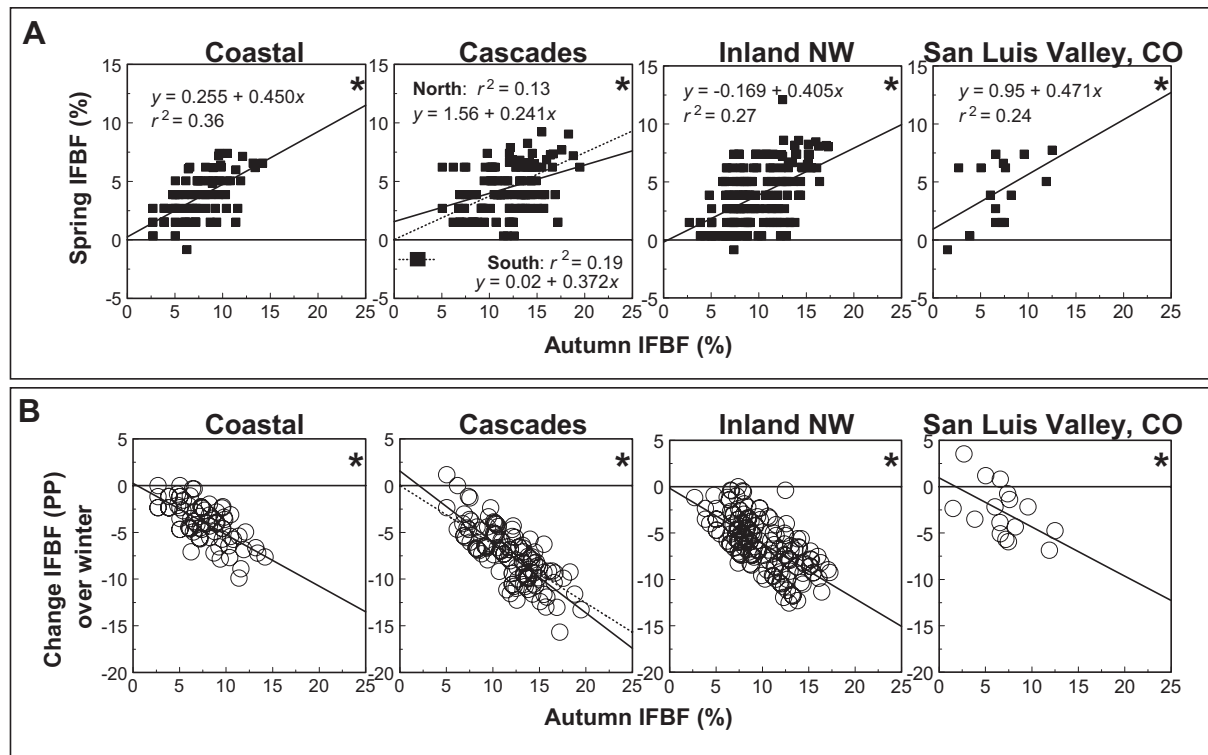


Figure 8. Relations of starting (autumn) ingesta-free body mass (% IFBF) and either (A) ending (spring) IFBF (closed squares) or the (B) change in IFBF (on a percentage-point basis [PP]; open circles) over winter. We collected data from 21 herds across 4 regions of the western United States: 1) the coastal plains and mountains west of Interstate 5 in western Oregon and Washington (*Cervus elaphus roosevelti*); 2) the hills and Cascades mountains east of Interstate 5 and west of the crest of the Cascades in western Oregon and Washington (*C. e. nelsoni*; North Cascades herds [Nooksack, WA, and Green and White River, WA] are shown with a solid line and South Cascades herds are shown with a dotted line); 3) the inland Northwest (NW) from the crest of the Cascades east across Washington and Oregon excluding Hanford, WA (*C. e. nelsoni*); and 4) San Luis Valley, CO, the only herd from the Rocky Mountain region with repeated sampling (*C. e. nelsoni*). We collected data during 1998–2007 and included all females, regardless of lactation status. All regression relations significant at $P \leq 0.05$ are marked (*) in the upper right corner of each graph.

in IFBF over summer was negatively related to previous spring IFBF ($F_{1, 216} = 146.94$, $P < 0.001$), and to herd ($F_{12, 216} = 2.72$, $P = 0.002$), but over-summer change was not related to the interaction of herd and spring IFBF ($F_{12, 216} = 0.89$, $P = 0.559$). Using region in place of herd produced similar results. The slope of the relationship between spring and autumn IFBF in lactating elk was similar among regions (coastal: $y = 4.85 - 0.779x$, $S_{y,x} = 1.65$, $P < 0.001$, $r^2 = 0.49$; north Cascades: $y = 10.07 - 0.800x$, $S_{y,x} = 2.52$, $P < 0.001$, $r^2 = 0.34$; south Cascades: $y = 7.95 - 0.814x$, $S_{y,x} = 2.26$, $P < 0.001$, $r^2 = 0.37$; inland Northwest: $y = 6.75 - 0.842x$, $S_{y,x} = 2.79$, $P < 0.001$, $r^2 = 0.48$; San Luis Valley, CO: $y = 4.11 - 0.711x$, $S_{y,x} = 2.19$, $P < 0.001$, $r^2 = 0.52$; Fig. 10B). However, the intercept of these regressions varied by over 2-fold, indicating that the absolute amount of gain in condition over summer varied significantly among regions, from 4 to 10 percentage points of fat for lactating elk starting summer with virtually no IFBF (Fig. 10B).

In contrast to findings for IFBF, our analysis indicated that across all herds and habitat conditions, lactating females were unable to completely compensate for lower spring mass; females that had lower BM_{NP} measurements in the spring also had lower values in the autumn (Fig. 11A,B). Autumn BM_{NP} was related to previous spring levels ($F_{1, 192} = 50.72$, $P < 0.001$; $F_{1, 190} = 18.59$, $P < 0.001$). Neither herd ($F_{12, 192} = 0.83$, $P = 0.62$) nor the

interaction of herd and spring IFBF ($F_{12, 192} = 0.84$, $P = 0.61$) was related to autumn levels of BM_{NP} .

Pregnancy, Fetal Loss, and Lactational Infertility

Spring pregnancy rates of all prime-age females regardless of lactation status ranged from 69% to 100% across herds (Table 3). The lowest pregnancy rates were found in the coastal herds of Forks (63.6% in autumn, 68.6% in spring) and Wynoochee (63.8% in autumn, 74.6% in spring), the Cascades herds of Toketee (68.4% in autumn, 76.9% in spring) and Mount St. Helens (69.8% in spring), and Rocky Mountain National Park (77.8% in autumn). The spring pregnancy rate for Toketee females was slightly overestimated because we avoided catching known non-pregnant females in spring. Other herds exhibiting depressed pregnancy rates (75–85%) included Springfield, Yakima, Wenaha, and Willapa Hills.

Based on 417 samples for which we identified autumn and spring pregnancy, we found evidence of delayed breeding (i.e., not pregnant in late autumn, but pregnant in spring indicating some females were not breeding until late Oct at the earliest) in 33 females (7.9%) from Willapa Hills ($n = 1$ of 27 capture events), Wynoochee ($n = 10$ of 61 capture events), San Luis Valley ($n = 1$ of 54 capture events), Hanford ($n = 1$ of 35 capture events), Wenaha ($n = 4$ of 60 capture events), Green River

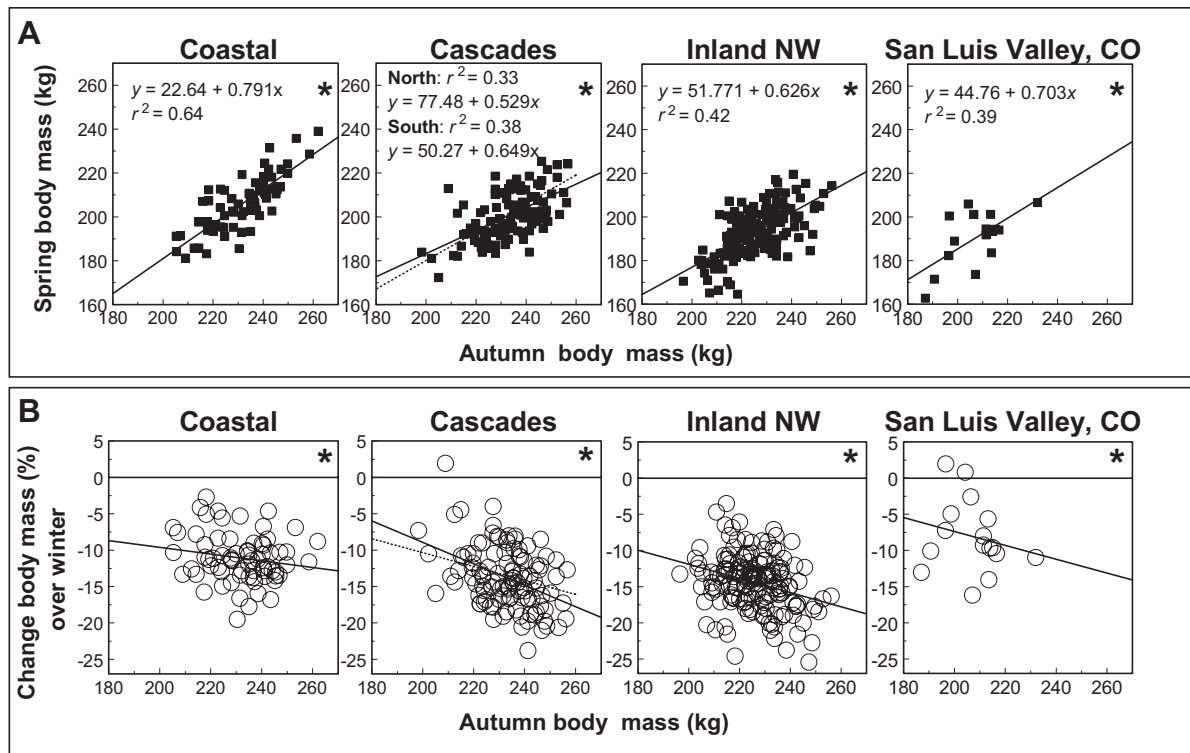


Figure 9. Relations of starting (autumn) body mass (BM_{NP} ; estimated via girth circumference with products of conception excluded) and either (A) ending (spring) BM_{NP} (closed squares) or (B) the change in BM_{NP} (on a percentage basis; open circles) over winter. We collected data from 21 herds across 4 regions of the western United States: 1) the coastal plains and mountains west of Interstate 5 in western Oregon and Washington (*Cervus elaphus roosevelti*); 2) the hills and Cascades mountains east of Interstate 5 and west of the crest of the Cascades in western Oregon and Washington (*C. e. nelsoni*; North Cascades herds [Nooksack, WA, and Green and White River, WA] are shown with a solid line and South Cascades herds are shown with a dotted line); 3) the inland Northwest (NW) from the crest of the Cascades east across Washington and Oregon excluding Hanford, WA (*C. e. nelsoni*); and 4) San Luis Valley, CO, the only herd from the Rocky Mountain region with repeated sampling (*C. e. nelsoni*). We collected data during 1998–2007 and included only those females that we handled during both the fall capture and the subsequent spring capture. We included all females, regardless of lactation status. All regression relations significant at $P \leq 0.05$ are marked (*) in the upper right corner of each graph.

($n = 12$ of 128 capture events), and Sled Springs ($n = 4$ of 137 capture events). Delayed breeding probably was more common, however, because our techniques and our timing for sampling pregnancy were not designed to identify delayed breeding unless it was markedly delayed. Based on this same sample, we found evidence of pregnancy termination in 5 females (1.2%; a 6-year-old from Forks, a 4-year-old who lost her fetus 2 sequential years in Wynoochee, a 7-year-old from Sled Springs, a 17-year-old from Wenaha, and a 5-year-old from Green River).

Probability of current pregnancy among prime-age females was a function of autumn IFBF whether pregnancy was determined in the autumn ($n = 680$; $P < 0.001$) or the spring ($n = 390$; $P < 0.001$). This pattern held within each region (Fig. 12) for autumn pregnancy determination (coastal: $n = 114$, $P = 0.006$; Cascades: $n = 229$, $P = 0.011$; inland Northwest: $n = 267$, $P = 0.007$; Rocky Mountains: $n = 70$, $P = 0.035$). However, reduced sample sizes using spring pregnancy determination (where spring pregnancy could be paired with previous autumn IFBF) produced variable results (coastal: $n = 71$, $P = 0.015$; Cascades: $n = 125$, $P = 0.476$; inland Northwest: $n = 178$, $P = 0.010$; Rocky Mountains: $n = 160$, $P = 0.556$). Lack of significance in the Cascades probably was attributable to autumn IFBF levels exceeding those thresholds at which body fat would

limit pregnancy (i.e., very few unbred elk with low body fat levels were represented in the logistic analysis; Fig. 12). Within individual herds, sample sizes were too small (< 30 animals) to develop a logistic regression model; thus, we generally failed to find an effect of autumn condition on pregnancy within herds ($P > 0.100$ except Forks, where $P = 0.035$).

We found no evidence of lactational infertility on pregnancy status whether pregnancy was determined in autumn or spring (Fig. 13). Neither the 3-way interaction between autumn IFBF, herd, and autumn lactation status (autumn pregnancy: $n = 680$; $\chi^2 = 7.09$; $P = 0.90$; spring pregnancy: $n = 390$; $\chi^2 = 3.42$; $P = 0.99$), nor any 2-way interaction (autumn pregnancy: $n = 380$; $\chi^2 \leq 7.14$; $P \geq 0.098$; spring pregnancy: $n = 390$; $\chi^2 \leq 3.62$; $P \geq 0.318$) were related to pregnancy status. Removing all interactions to evaluate simple effects, autumn IFBF remained significantly related to pregnancy status (autumn pregnancy: $n = 680$; $\chi^2 = 34.10$; $P \leq 0.001$; spring pregnancy: $n = 390$; $\chi^2 = 11.18$; $P \leq 0.001$), but autumn lactation status was not (autumn pregnancy: $n = 680$; $\chi^2 = 3.22$; $P = 0.07$; spring pregnancy: $n = 390$; $\chi^2 = 18.03$; $P = 0.16$). Performing this analysis using only 1 observation/female to remove potential for autocorrelation again provided similar results. Regardless of how we analyzed these data, we found no evidence of lactational infertility on probability of pregnancy.

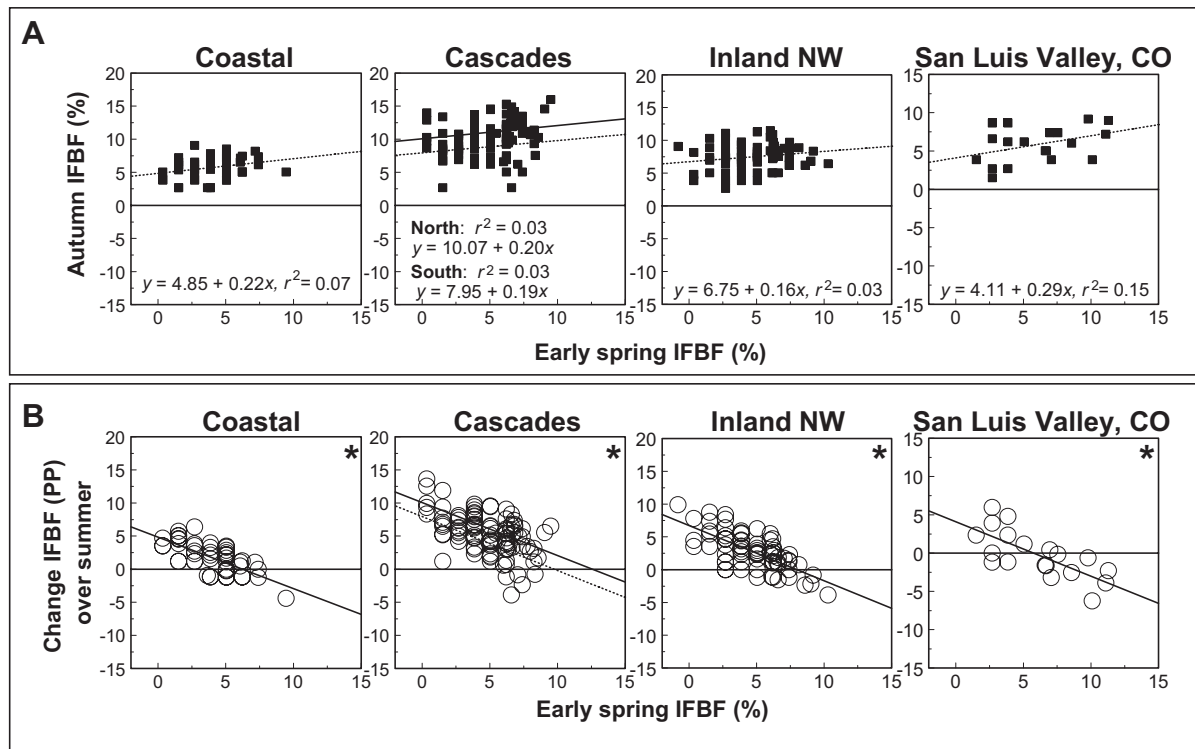


Figure 10. Relations of starting (spring) ingesta-free body fat (%) IFBF and either (A) ending (autumn) IFBF (closed squares) or (B) the change in IFBF (on a percentage-point basis [PP]; open circles) during summer. We collected data from 21 herds across 4 regions of the western United States: 1) the coastal plains and mountains west of Interstate 5 in western Oregon and Washington (*Cervus elaphus roosevelti*); 2) the hills and Cascades mountains east of Interstate 5 and west of the crest of the Cascades in western Oregon and Washington (*C. e. nelsoni*; North Cascades herds [Nooksack, WA, and Green and White River, WA] are shown with a solid line and South Cascades herds are shown with a dotted line); 3) the inland Northwest (NW) from the crest of the Cascades east across Washington and Oregon excluding Hanford, WA (*C. e. nelsoni*); and 4) San Luis Valley, CO, the only herd from the Rocky Mountain region with repeated sampling (*C. e. nelsoni*). We collected data during 1998–2007 and included only those females that we handled during both the spring capture and subsequent fall capture and only those females with milk at capture in autumn. All regression relations significant at $P \leq 0.05$ are marked (*) in the upper right corner of each graph.

Neither spring IFBF ($n = 967$; $\chi^2 = 0.01$; $P = 0.91$) nor its interaction with herd ($n = 967$; $\chi^2 = 25.28$; $P = 0.09$) was related to current-year pregnancy status. Similarly, neither spring IFBF overall ($n = 480$; $\chi^2 = 1.75$; $P = 0.19$) nor its interaction with herd ($n = 480$; $\chi^2 = 9.11$; $P = 0.69$) was related to future (subsequent autumn) pregnancy status.

Sixty-eight percent of females ≥ 15 years old were pregnant ($n = 116$). Average age of non-pregnant females was not different from that of pregnant females (16 years old for both) in our old-age category. We observed pregnancy in animals up to 19 years old; 1 female caught at 20 years old and again at 21 years old was not pregnant in either year. Using all animals and categorizing them as either prime age or old age, we found a marginally significant age category $\times$ autumn IFBF interaction to predict probability of pregnancy only in autumn, but not in spring (autumn pregnancy: $n = 749$; $\chi^2 = 3.49$; $P = 0.06$; spring pregnancy: $n = 422$; $\chi^2 = 1.67$; $P = 0.20$) possibly suggesting a higher IFBF breeding threshold in older animals (Fig. 14). In addition, we found no effect of the age category $\times$ autumn pregnancy status interaction ($F_{1, 745} = 1.98$, $P = 0.16$) or age category ($F_{1, 745} = 2.34$, $P = 0.13$) on autumn IFBF. Pregnant females, however, had greater IFBF levels in autumn than non-pregnant females regardless of age category ($F_{1, 745} = 15.75$, $P < 0.001$; Fig. 15).

Condition and Pregnancy of Sub-Adults

We captured 46 yearlings but estimated BM_{NP} on 39 and pregnancy on 33 (Oct capture efforts on 13 yearlings at Mount St. Helens were too early in the autumn for pregnancy determination; Table 2). Body mass of 11 yearlings in autumn averaged 161.9 kg (range: 146.2–177.4 kg) and 3 of these were pregnant. IFBF averaged 6.1% in autumn (range: 1.5–9.2%). Based on categories described by Cook et al. (2004a), 4.9%, 33.3%, and 100% of yearlings captured in the Cascades, inland Northwest, and San Luis Valley had autumn body mass representing poor summer nutrition (Table 4). The remaining yearlings had autumn body mass levels representing marginal summer nutrition (Table 4). Body mass (BM_{NP}) of 28 yearlings in the spring averaged 163.1 kg (range: 148.4–182.5 kg), IFBF averaged 5.5% (range: 1.5–9.8%), and 34.4% were pregnant. Non-pregnant yearlings averaged 159.1 kg in the spring and 4.8% IFBF (range: 163–193 kg; 1.5–7.4%) versus 170.5 kg and 6.9% IFBF (range: 169–201 kg; 2.7–9.8%) for pregnant yearlings. We found an effect of spring BM_{NP} on probability of pregnancy in yearling females ($n = 28$; $P = 0.009$; Fig. 16).

We obtained weights on calves from 3 herds (Fig. 17A). Average mass of calves weighed during winter on feed grounds near Yakima was 97 kg ($n = 208$ [unknown mix of males and females]; S. McCorquodale, Washington Department of

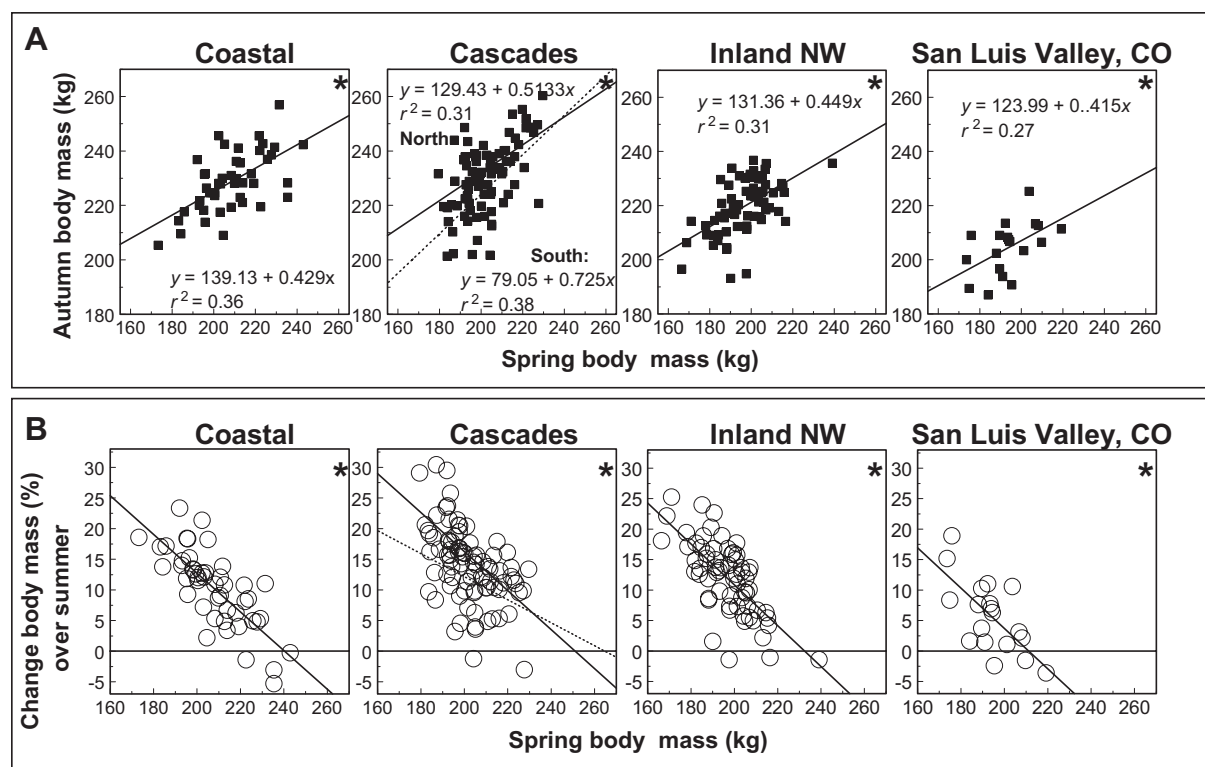


Figure 11. Relations of starting (spring) body mass (BM_{NP} ; estimated via girth circumference with products of conception excluded) and either (A) ending (autumn) BM_{NP} (closed squares) or (B) the change in BM_{NP} (on a percentage basis; open circles) over summer. We collected data from 21 herds across 4 regions of the western United States: 1) the coastal plains and mountains west of Interstate 5 in western Oregon and Washington (*Cervus elaphus roosevelti*); 2) the hills and Cascades mountains east of Interstate 5 and west of the crest of the Cascades in western Oregon and Washington (*C. e. nelsoni*; North Cascades herds [Nooksack, WA, and Green and White River, WA] are shown with a solid line and South Cascades herds are shown with a dotted line); 3) the inland Northwest (NW) from the crest of the Cascades east across Washington and Oregon excluding Hanford, WA (*C. e. nelsoni*); and 4) San Luis Valley, CO, the only herd from the Rocky Mountain region with repeated sampling (*C. e. nelsoni*). We collected data during 1998–2007 and included only those females that we handled during both the spring capture and subsequent fall capture and only included those females with milk at capture in autumn. All regression relations significant at $P \leq 0.05$ are marked (*) in the upper right corner of each graph.

Fish and Wildlife, unpublished data); 75 kg ($n = 9$; 2 males and 7 females) during October at Mount St. Helens; 81 kg ($n = 25$; 15 males and 10 females) during November at San Luis Valley. In general, calf weights were as predicted by Cook et al. (2004a) based on nutritional condition of female elk in the same herds (Fig. 17B). Calves at the Yakima feed-site were an exception in that the proportions of calves in marginal and good categories were higher than would have been predicted (Fig. 17B).

Causes of Year-to-Year Variation

Using a more liberal test for evaluating annual variation within herds (analyzing herds individually rather than with a global test with herd included as a covariate), we found significant differences in IFBF of lactating elk among years during autumn only at Hanford, Washington (herd #13). There, autumn IFBF was depressed following a very large (113,000 ha), early-summer rangeland wildfire that removed vegetation from much of the summer range of this herd (appreciable vegetative growth failed to occur until autumn rains in Oct). We assume that this wildfire accounted for the year effect, and we did no additional analysis on this herd. We found no year effects with respect to spring IFBF ($P > 0.15$).

However, regarding change in IFBF over winter, we found year effects at Yakima (herd #14; $F_{1, 17} = 4.67$; $P = 0.045$),

Wynoochee (herd #4; $F_{1, 22} = 5.79$; $P = 0.025$), and Green River (herd #7; $F_{5, 30} = 3.62$; $P = 0.011$). Including autumn IFBF as a covariate removed the year effect for all 3 herds ($P > 0.29$). With respect to change in IFBF over summer, we found that both the White River (herd #6; $F_{2, 18} = 8.29$; $P = 0.003$) and Sled Springs (herd #16; $F_{5, 31} = 4.50$; $P = 0.034$) herds exhibited a significant year effect. But when we included spring IFBF as a covariate, the year effect was no longer significant in either herd ($P > 0.13$). These data indicate that what first appears to be significant year-to-year variation in nutritional condition in winter and summer was largely due to carry-over effects among seasons that we addressed in our various seasonal analyses, and was not due to extraneous factors, such as weather, which might have confounded our analyses.

DISCUSSION

Our data, consisting of seasonal measures of nutritional condition and reproduction in 21 elk herds in 5 western states, clearly demonstrated that nutritional resources on summer ranges across many of the areas we sampled were inadequate for high levels of growth of juveniles and yearlings, fat accretion in adults during summer and autumn, and pregnancy rates (Table 4; Cook et al. 2004a), and may have reduced probability of overwinter

Table 3. Pregnancy rates (%; number of pregnant females/total number of females $\times$ 100) and sample sizes (n) for 21 elk herds in Washington, Oregon, Wyoming, Colorado, and South Dakota, USA during 1998 through 2007. Herd numbers presented correspond to Figure 1.

Herd#/herd	Region ^a	Spring			Autumn		
		All	Lactating ^b	Non-lactating ^c	All	Lactating	Non-lactating
1/Forks	CS	68.6 (51)	58.8 (17)	73.5 (34)	63.6 (44)	66.7 (21)	60.9 (23)
2/Willapa Hills	CS	93.3 (30)	81.8 (11)	100.0 (19)	80.0 (25)	73.7 (19)	100.0 (6)
3/Chehalis	CS	100.0 (18)	100.0 (11)	100.0 (7)			
4/Wynoochee	CS	74.6 (67)	68.8 (32)	80.0 (35)	63.8 (47)	59.3 (27)	70.0 (20)
5/Nooksack	CM	97.4 (38)	100.0 (14)	95.8 (24)	92.0 (25)	90.0 (17)	87.5 (8)
6/White River	CM	95.5 (67)	90.1 (11)	96.4 (56)	98.1 (53)	97.1 (34)	100.0 (19)
7/Green River	CM	95.1 (122)	91.7 (36)	96.5 (86)	90.7 (108)	88.5 (61)	93.6 (47)
8/South Rainier	CM	100.0 (7)			100.0 (7)		
9/Mount St. Helens	CM	69.8 (43)	0.0 (6)	81.1 (37)			
10/Springfield	CM	80.0 (30)	73.3 (15)	86.7 (15)			
11/Steamboat ^d	CM	90.9 (33)	100.0 (5)	89.3 (28)	87.5 (24)	88.2 (16)	85.7 (8)
12/Toketee ^d	CM	76.9 (39)	22.2 (9)	93.3 (30)	68.4 (19)	73.3 (15)	50.0 (4)
13/Hanford	IN	93.6 (31)	85.7 (7)	95.8 (24)	86.2 (29)	88.2 (17)	83.3 (12)
14/Yakima	IN	84.8 (79)	83.3 (36)	86.0 (43)	87.1 (62)	86.8 (38)	87.5 (24)
15/Colockum	IN				96.9 (32)	100.0 (6)	96.2 (26)
16/Sled Springs	IN	90.7 (151)	85.4 (41)	92.7 (110)	87.5 (128)	86.0 (50)	88.5 (78)
17/Wenaha	IN	92.5 (106)	75.0 (20)	96.5 (86)	84.0 (50)	76.2 (21)	89.7 (29)
18/Rocky Mtn. NP	RM				77.8 (18)	33.3 (6)	100.0 (12)
19/San Luis Valley	RM	92.9 (57)	75.0 (16)	100.0 (41)	94.2 (52)	87.5 (24)	100.0 (28)
20/Yellowstone NP	RM	90.0 (30)		90.0 (30)			
21/Black Hills	RM	82.4 (17)	50.0 (2)	86.7 (15)			

^a CS, coastal plains and mountains; CM, west-slope Cascade range; IN, inland Northwest; RM, Rocky Mountains.

^b Elk that were still lactating at the time of the spring capture or identified as lactating the previous autumn.

^c Elk that were not lactating at the time of the spring capture. This category could include females lactating the previous autumn that had ceased lactating by spring capture if previous autumn data had not been collected.

^d Pregnancy data may represent a slight to severe bias relative to study design and objectives. Autumn captures focused on collecting data from lactating females so captures were biased toward females known to have a calf at heel (based on collaring calves at birth) or females whose lactation status was unknown (calf was not collared). Spring captures focused on deploying vaginal implant transmitters so captures were biased toward females known to be pregnant (based on autumn sampling) or females whose pregnancy status was unknown. During the spring capture, autumn non-pregnant females were avoided.

survival via carry-over effects of summer-autumn nutrition (Hobbs 1989, Gerhart et al. 1996, Monteith et al. 2013). These data also failed to support the common assumption that winter forage and weather are the primary limiting bottom-up factors of elk productivity. Although adult elk in our study areas typically lost substantial nutritional condition during winter, nutrition during summer (as indexed by autumn body fat) influenced reproduction and juvenile growth, and consequently exerted greater influences than winter nutrition on population dynamics. Evidently because of a variety of physiological or behavioral adaptations, adult elk were able to reduce the rate of decline in fat and lean tissue as winter progressed, despite relatively harsh winters in some areas, and those elk that exited winter in unusually poor nutritional condition effectively compensated and caught-up with their fatter counterparts by autumn. These results support findings from captive elk nutrition research that indicated inadequate summer nutrition, primarily low digestible energy content of food, has inordinate effects on virtually all aspects of reproduction and influences subsequent probability of overwinter survival (Cook 2002:321, Cook et al. 2004a).

Our data indicated effects of inadequate summer nutrition are rarely catastrophic and obvious; instead, the influence of nutrition on elk populations largely occurred through subtle, but cumulative, effects on nutritional condition, pregnancy rates, adult body size, yearling body size and pregnancy rates, and calf body size. Annual cycles of nutritional condition and performance resulted from complex interactions between winter nutritional deficiencies, summer nutritional deficiencies, and

mechanisms by which elk responded to these deficiencies. Our findings that nutrition is inadequate on summer ranges support a growing body of literature that reported limiting effects of summer nutrition, not only for elk (e.g., Trainer 1971, Harper 1987, Merrill and Boyce 1991, Alldredge et al. 2002, Cook et al. 2004a) but also for other ungulates in the northern hemisphere (Table 1). Traditional views that nutrition in winter, rather than that in summer, limits ungulate populations (Wallmo et al. 1977, Houston 1982, Adamczewski et al. 1987, Coughenour and Singer 1996, Christianson and Creel 2007, Bishop et al. 2009) originate from an era when precise and easy-to-obtain repeated measurements of nutritional condition and pregnancy across years were unavailable to compare seasonal effects on herd productivity. The growing evidence from around the northern hemisphere, combined with our data, support the paradigm that nutrition on summer range, to a substantially greater degree than nutrition on winter range, drives the productivity of elk and probably other ungulates in many ecological settings. Below, we consider these interactions in greater detail by season and across the annual cycle, discuss implications for animal performance, and discuss implications of our findings in the context of suitable sampling designs for monitoring free-ranging populations.

Nutritional Condition in Summer and Autumn

The value of estimates of nutritional condition collected in autumn as indicators of the adequacy of summer range can be masked by several factors. In particular, whether females produce a calf and how long it survives during summer greatly affects

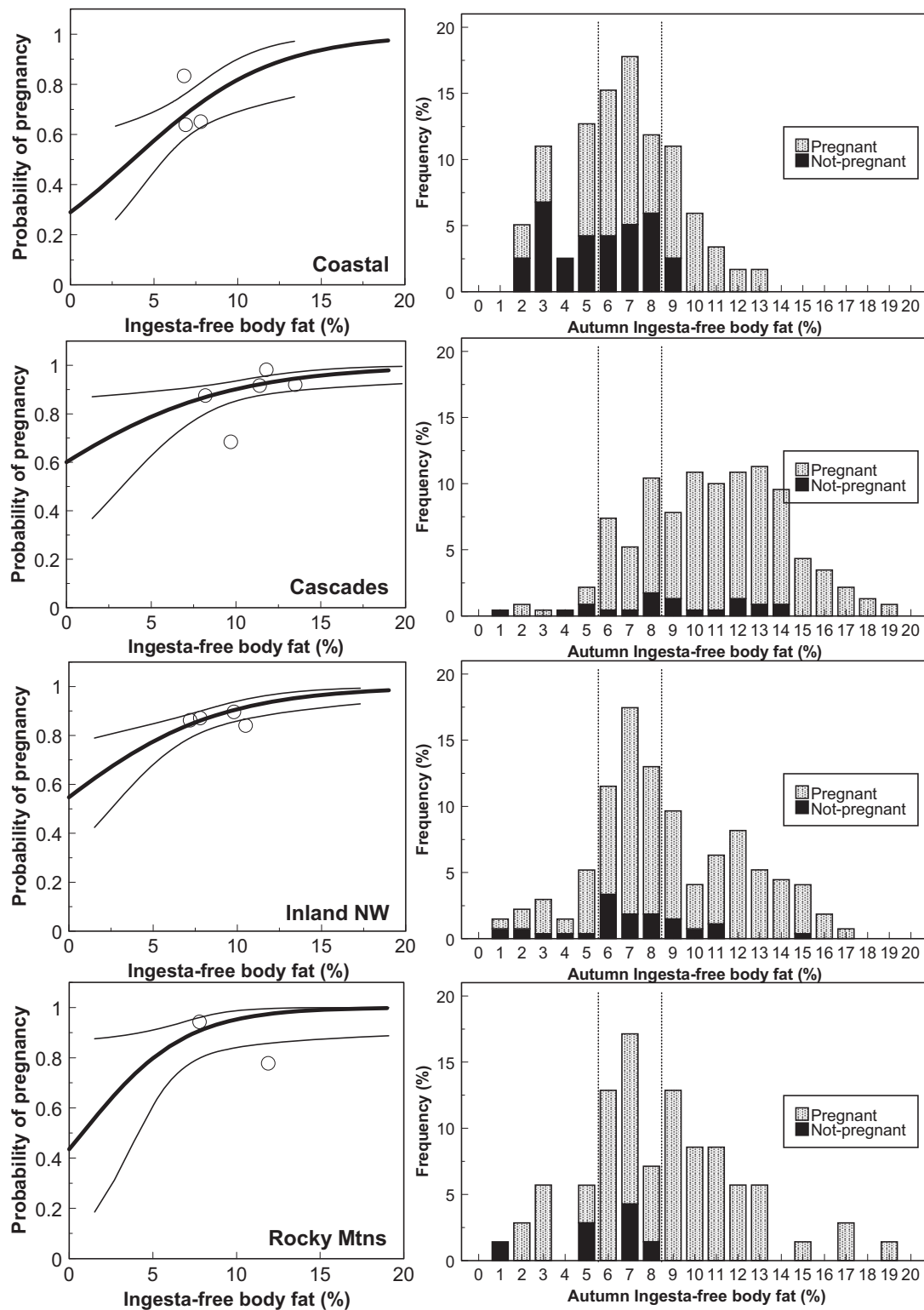


Figure 12. Relationships between probability of pregnancy and ingesta-free body fat (IFBF) in autumn (dotted lines indicate 95% confidence intervals) for prime-age female elk in 15 herds across 4 regions of the western United States: 1) coastal areas west of Interstate 5 in Oregon and Washington (*Cervus elaphus roosevelti*); 2) Cascades east of Interstate 5 and west of the Cascades crest in Oregon and Washington (*C. e. nelsoni*); 3) inland Northwest (NW) east of the Cascades crest in Washington and Oregon (*C. e. nelsoni*); and 4) Rocky Mountains (Mtns) of Wyoming, Colorado, and South Dakota (*C. e. nelsoni*). Pregnancy rates of individual herds are represented by open circles for each region. Matched with each regional probability graph is a frequency histogram (%) of pregnant and non-pregnant females relative to autumn IFBF. Vertical bars delineate the nutritional categories depicted by Cook et al. (2004a; Table 4): IFBF <6% = strongly depressed pregnancy rates; IFBF >6% but ≤9% = some depression in pregnancy rates or evidence of delayed breeding; IFBF >9% = no limitations on pregnancy rates although delays in breeding still possible. We collected all data during 1998–2007.

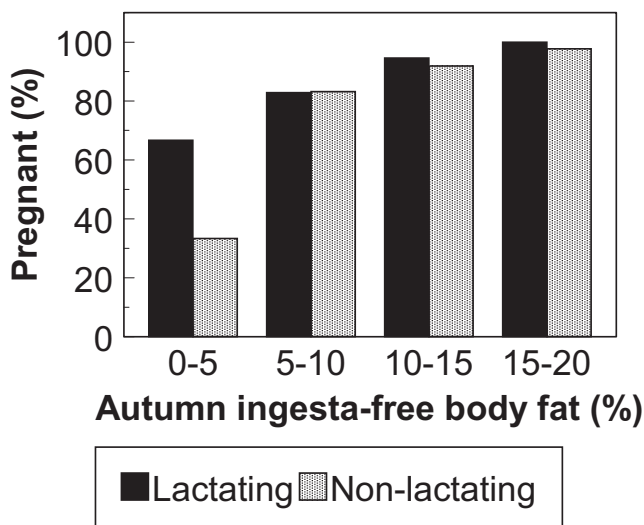


Figure 13. Percent of females pregnant relative to lactation status and ingesta-free body fat (IFBF) in autumn. Data are from 15 herds from Oregon, Washington, and Colorado collected during 1998–2007.

over-summer energy balance and autumn nutritional condition (Clutton-Brock et al. 1982; Gerhart et al. 1996, 1997a, b; Landete-Castillejos et al. 2003; Cook et al. 2004a). For example, lactating elk require about 18,500 kcal/day of metabolizable energy (ME), about 50% more than equivalent non-lactating females (Oftedal 1985, Cook 2002, Cook et al. 2004a). When summer nutrition is high relative to requirements, lactating females are capable of accruing fat to about the same level (i.e., >15% IFBF) as non-lactating females (Adamczewski et al. 1987, Cook et al. 2004a). However, inadequate levels of summer nutrition that reduce accretion of body fat by lactating females may have little such effect on non-lactating females, an effect

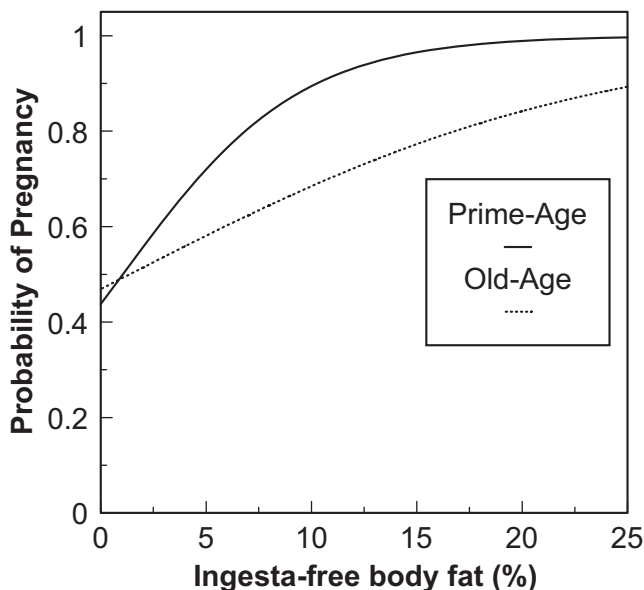


Figure 14. Relationships between probability of pregnancy and ingesta-free body fat (IFBF) in autumn for prime-age female elk (2–14 years old) and old-age female elk (>15 years old). We found a marginally significant age category $\times$ autumn IFBF interaction to predict probability of pregnancy ($P = 0.06$). We collected data from 15 herds across 4 regions of the western United States during 1998–2007.

clearly illustrated experimentally by Cook et al. (2004a). Hence, females escaping the energetic costs of lactation are relatively insensitive to nutrition, and nutritional condition data collected from them provide substantially less insight of the nutritional adequacy of their summer range (Gerhart et al. 1997b).

Estimates of nutritional condition of non-lactating females also are confounded because no validated approach exists to identify lactation history over the previous 5–6 months before autumn capture without intensive and costly calf-capture approaches. Therefore, females deemed non-lactating at the time of capture are likely to be a heterogeneous group of animals in terms of their nutritional demands and expenditures over the previous months, and inferences from their condition data could be both ambiguous and potentially misleading (e.g., Piasecke et al. 2009).

Estimates of nutritional condition may also be influenced by condition in previous seasons, depending on the nutritional measure being used. If spring IFBF significantly influences subsequent autumn IFBF, then change in IFBF over summer is a more appropriate index to summer range quality than a mere point estimate of IFBF in the autumn. However, spring IFBF was unrelated to subsequent autumn IFBF, regardless of the herd or region (Fig. 10), and thus autumn estimates of IFBF were superior to changes in IFBF over summer as an indicator of summer nutritional adequacy. Renecker and Samuel (1991) and Dale et al. (2008) reported similar patterns relative to juvenile growth. However, our analysis showed that spring levels of BM_{NP} in adults were related to subsequent autumn levels (Fig. 11); thus, having sequential data (spring and autumn) may be more important for variables reflecting status of lean mass during summer.

Adult females were capable of compensating during summer for their low nutritional condition in spring despite the nutritional demands of pregnancy and subsequent lactation. Compensatory growth improves reproductive success and winter survival in variable, stochastic environments (Renecker and Samuel 1991, Dale et al. 2008). Compensatory responses during summer by animals in low condition, particularly those still growing, are well documented in captive (Verme 1963, Hudson et al. 1985, Renecker and Samuel 1991, Watkins et al. 1991, Wairimu and Hudson 1993) and, less frequently, in wild settings (Dale et al. 2008). Although reported for body mass in adult elk (Watkins et al. 1991) and red deer (*C. elaphus*; Suttie et al. 1983, 1984; Adam and Moir 1985), we present a novel data set illustrating strong spring-summer compensation of nutritional condition in elk in wild settings. Hyperphagia is a commonly documented strategy of compensation in large ungulates (Wairimu and Hudson 1993), but large mammals may use a variety of strategies for compensation, such as substantial reductions in organ size and skeletal muscle mass to reduce maintenance energy requirements (Ramsey and Hagopian 2006). Those females that exit winter at relatively low levels of condition therefore are primed to outperform better-conditioned females when nutrition improves, because fewer nutrients are required for maintenance and thus a greater portion of consumed nutrients can be shunted to anabolic processes in these animals.

Compensatory growth in spring-summer, however, may occur at the expense of perinatal viability and growth and development

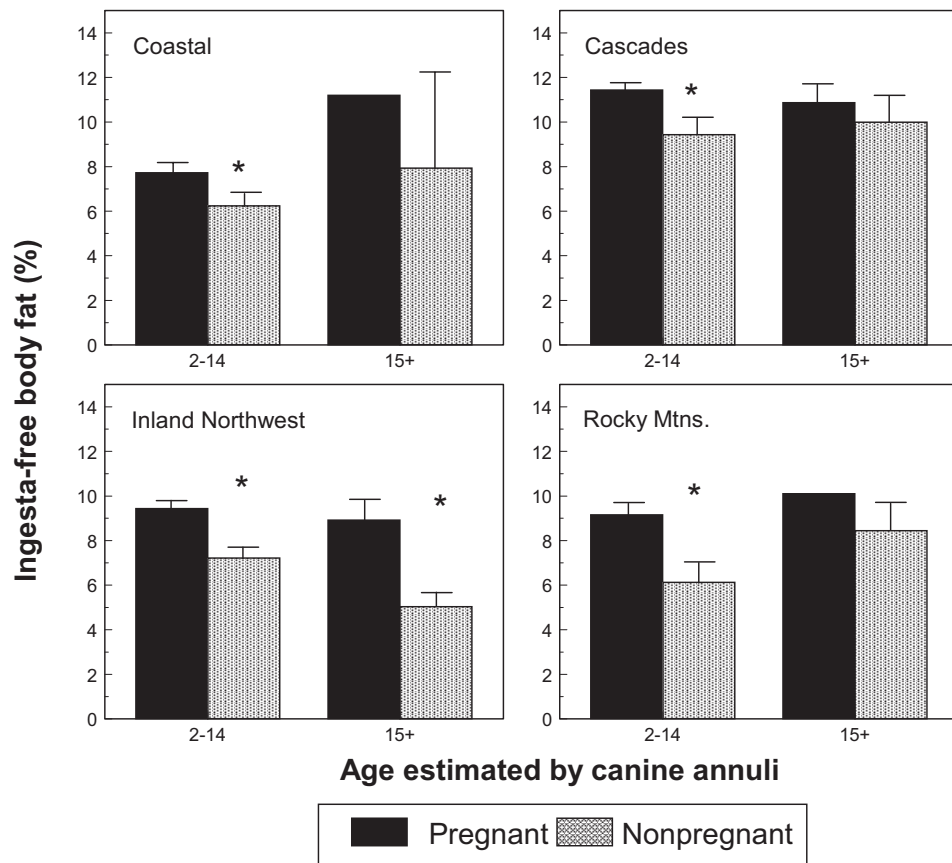


Figure 15. Average ingesta-free body fat (IFBF) in autumn for pregnant and non-pregnant females grouped according to age (prime-age or old-age). Error bars = standard error of the mean and asterisks indicate significant differences in IFBF between pregnant and non-pregnant females within age category. We collected data from 15 herds across 4 regions of the western United States during 1998–2007: 1) coastal areas west of Interstate 5 in Oregon and Washington (*Cervus elaphus roosevelti*); 2) Cascades east of Interstate 5 and west of the Cascades crest in Oregon and Washington (*C. e. nelsoni*); 3) inland Northwest east of the Cascades crest in Washington and Oregon (*C. e. nelsoni*); and 4) Rocky Mountains (Mtns.) of Wyoming, Colorado, and South Dakota (*C. e. nelsoni*).

of offspring. We found up to 50% of females within herds and years exited winter with IFBF <2%, suggesting that pregnant females may enter the birthing and neonatal nursing period in relatively poor condition. Numerous studies have shown that nutrition of females affects milk yield or composition, nursing bouts, and juvenile performance (Landete-Castillejos et al. 2003, Cook et al. 2004a, Tollefson 2007), but the literature

does not clarify the extent to which female nutritional condition may influence calf performance independently of nutritional plane (i.e., will calves from fatter females on a nutritional plane perform better than calves from skinnier females given the same nutrition?). For example, Keech et al. (2000) found that calf birth mass and calf birth date were positively related to nutritional condition of female moose in March. In contrast,

Table 4. Levels of performance expected for elk in temperate ecosystems as a function of nutritional status over summer and autumn.^a Estimates are based on late-October measurements. For adult females, we assume lactating and prime-age (3–10 years of age). This table was developed from captive elk under controlled experimental conditions in a penned setting (Cook et al. 2004a); the energetic demands of free-ranging existence may reduce animal performance at any given level of nutrition.

Summer-autumn nutrition ^b	Calf body mass (kg)	Yearling F body mass (kg)	Ad F body fat (%)	Yearling pregnancy (%)	Ad pregnancy (%)	Ad F breeding date
Excellent	125–145	195–230	17–21	≥90	≥90	≤30 Sep
Good	105–125	180–195	13–17	30–90	≥90	≤5 Oct
Marginal	90–105	160–180	8–13	0–30	70–90	≤10 Oct
Poor	<90	<160	<8	<5	40–70	>10 Oct

^a These levels of performance should be robust across a reasonable range of winter conditions (see caveats of Cook et al. 2004a).

^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 capabilities of elk. Dietary digestible energy levels >2.90 kcal/g of forage through summer until mid-autumn are required for this level of performance. Good is defined as summer-autumn nutrition levels that exert some limitations on performance, but the magnitude of this effect generally will not impede reproduction and reduce survival. Corresponding digestible energy levels after mid-summer are 2.75–2.9 kcal/g. Marginal pertains to nutrition levels that may influence reproduction and survival (enhanced probability of death in winter, delayed breeding, delayed puberty). Corresponding dietary digestible energy levels after mid-summer are 2.45–2.75 kcal/g. Poor pertains to nutrition levels that markedly affect reproduction and reduce survival probability. Corresponding dietary digestible energy levels after mid-summer is <2.45 kcal/g.

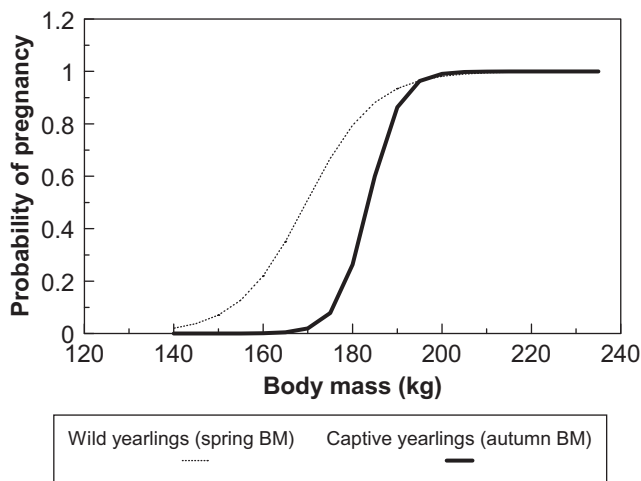


Figure 16. Probability of pregnancy relative to body mass (BM_{NP} ; estimated without products of conception included) for 1) 29 yearlings captured during spring 1998–2007; and 2) captive Rocky Mountain yearlings during 1997 (captive data are from Cook et al. 2004a). Pregnancy probabilities from wild elk are based on body mass (BM) in spring, whereas these probabilities for captive elk are based on body mass in autumn; winter mass loss of wild elk shift the curve to the left relative to that for captive elk.

Adams (2005) reported that female condition in autumn rather than spring was related to subsequent birth mass in caribou calves. Rearden (2005) found no relation of female condition in early spring with birth date or birth mass of elk calves. Regardless of the mechanism by which females compensate for low nutritional condition, compensation over summer was a powerful attribute that greatly enhanced recovery of thin elk in our study.

Several thresholds of autumn body fat for adult elk are relevant to survival and reproduction (Cook et al. 2004a). For females that raise calves through the autumn, good summer nutrition supports body fat >12% to 20% by autumn. The probability of breeding in autumn declines and timing of breeding is delayed as autumn body fat declines below about 9%, markedly so when IFBF <6% (Cook et al. 2004a; see also Testa and Adams 1998). Captive work suggested that the probability that females can survive moderate or average winter conditions begins to decline at pre-winter fat levels <8%, although under severe winter conditions, probability of overwinter survival may decline even for animals having substantially higher autumn IFBF levels (Cook et al. 2004a).

The level of IFBF that lactating females achieved in autumn, varied 2-fold among herds and regions and averaged 30–75% of levels that elk are capable of achieving if digestible energy in summer-autumn forage is not limiting. Only 1 herd in our sample (Nooksack in the Northern Cascades) averaged body fat levels (12–13%) indicating no substantial nutritional limitations. In contrast, 11 of 17 herds for which we had autumn data averaged $\leq 8\%$ body fat, levels suggesting depressions in pregnancy probability and possibly some increase in probability of winter mortality. Our fattest elk were Rocky Mountain elk in the Northern Cascade herds and the thinnest were Roosevelt elk in the coastal ranges and Rocky Mountain elk at San Luis Valley, Colorado. However, body fat varied nearly as much within

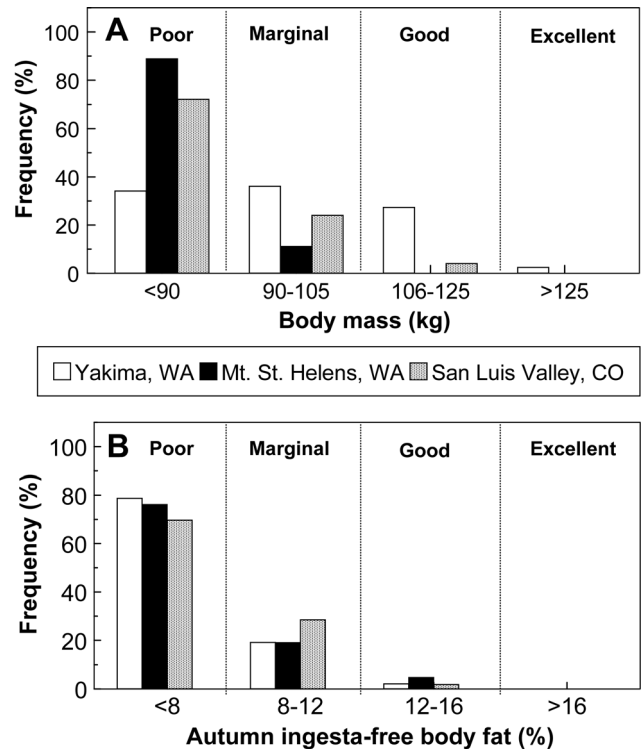


Figure 17. Distribution of body mass (kg) of 242 calves ($n = 208$ in early winter at Yakima, WA; $n = 9$ in October at Mount St. Helens, WA; and $n = 25$ in November at San Luis Valley, CO) relative to nutritional categories depicted by Cook et al. (2004a; Table 4; panel A). We collected data during 1998–2007. Categories reflect adequacy of the summer range: excellent = settings with virtually no nutritional limitations in summer and autumn; good = summer-autumn nutrition levels that exert some limitations on performance, but the magnitude of this effect generally will not impede reproduction and reduce survival; marginal = nutrition levels that may influence reproduction and survival (enhanced probability of death in winter, delayed breeding, delayed puberty, and reduced growth); and poor = nutrition levels that markedly affect reproduction, reduce survival probability, and limit growth of sub-adults. For comparison, we include the distribution ingesta-free body fat (%) of prime-age females in autumn for the same herds relative to the same nutritional categories (panel B).

regions as it did among regions, and that result probably reflects substantial differences in vegetation, weather, topography, or possibly density among herds within regions. This pattern was most evident in the Washington and Oregon Cascades where a general trend of declining condition was evident along a north-to-south gradient (Figs. 1 and 3A).

We found similar trends for body mass estimates. In general, autumn BM_{NP} ranged substantially below that which female elk are capable of achieving (Fig. 4). Female Rocky Mountain elk offered good nutrition during most of their early adult life weigh 275–325 kg (Hudson et al. 1991, 1994). None of the adult females in our sample exceeded 275 kg and only 2% of females were >250 kg. The largest elk in our sample were in the North Cascades of Washington and Roosevelt elk in some of the coastal study areas. In contrast, 15% of females in our sample, primarily of inland Northwest herds and the San Luis Valley herd, had autumn $BM_{NP} < 210$ kg, levels expected for yearlings under conditions without summer nutritional limitations (Cook et al. 2004a). Our analysis of BM_{IFF} of lactating elk in autumn indicated a similar pattern. Better summer nutrition enhances

growth and results in larger juveniles, sub-adults and, ultimately, adults (Fig. 5; Clutton-Brock et al. 1982, Festa-Bianchet et al. 1996, Bigersson and Ekvall 1997).

We also found evidence of compensatory recovery of body mass during summer, as we did for IFBF. In contrast with that of IFBF, however, positive relations existed between spring BM_{NP} and subsequent autumn BM_{NP} for lactating females (Fig. 11). Successful recovery of fat combined with only partial recovery of BM_{NP} in a few herds may indicate that summer nutrition was inadequate to support complete recovery of lean mass of lactating females in these herds. If this is true, then our results suggest that summer nutrition was generally inadequate in many herds for complete recovery between spring and autumn of lean mass lost the previous winter. Thus, exiting winter with higher body mass might provide benefits to lactating elk the subsequent summer in some settings. As with IFBF, however, BM_{NP} in spring was largely a function of BM_{NP} the previous autumn (and thus previous-summer nutrition levels), rather than winter weather (Fig. 9).

Nutritional Condition in Winter and Early Spring

The value of nutritional condition estimates collected in spring for indexing the nutritional adequacy of winter range may be masked by several factors including overwinter lactation status and the interplay between previous autumn nutritional condition and winter weather. Our data show that lactation over winter imposed no detectable effects on nutritional condition (Robbins et al. 1981), and so stratifying condition data by lactation status for analysis of winter condition data was unnecessary. However, IFBF and BM_{NP} in spring were significantly related to IFBF and BM_{NP} the previous autumn, indicating these in turn were affected by nutritional adequacy of summer range and lactation status the previous summer. Thus, nutritional condition in late winter or early spring, without concurrent data of autumn nutritional condition, was an incomplete and potentially misleading indicator of nutritional adequacy of summer or winter ranges, under the bioclimatological regimes of our sample populations.

We think that our findings of the strong influence of summer on elk performance has more to do with the sequential sampling approach (data on individuals across seasons) than the relatively small number of winter ranges with harsh winter weather conditions in our sample. Coupling estimates of nutritional condition in autumn and spring is crucial for identifying winter effects on nutrition and reproduction. This approach has rarely been used, but when it has, similar findings were reported. Dale et al. (2008) reported minor effects of winter but significant effects of summer range on growth and body mass of sub-adult caribou in Alaska. Using multi-seasonal samples from shot caribou, Huot (1989) in northeast Canada and Gerhart et al. (1996) and Cameron et al. (2005) in northern Alaska documented greater influences of summer nutrition than winter nutrition on caribou body fat and pregnancy. Using the same techniques, however, Adamczewski et al. (1987) concluded that winter nutrition was considerably more limiting to caribou than summer nutrition on Coats Island in northern Hudson Bay. Regardless of results, each study employed a sequential sampling scheme that enabled discrimination of seasonal contributions to

nutritional condition dynamics that sampling solely in late winter or early spring cannot do.

We were surprised to find virtually no evidence that nutritional condition in spring was influenced by winter weather or, more generally, by herd or region. The relationships between autumn and spring nutritional condition, and importantly, autumn condition and the rate of condition loss over winter, were remarkably similar among regions (Figs. 8 and 9), which varied widely in winter temperature and precipitation (Fig. 7A,B, Appendix).

That winter weather had little influence on winter fat loss and pregnancy rates in our study is inconsistent with long-held points of view (e.g., Wallmo et al. 1977, Houston 1982, Coughenour and Singer 1996, Loison and Langvatn 1998, DelGiudice et al. 2002). We acknowledge that winter weather and nutrition may have greater influence on nutritional condition in areas further north where snow cover is more persistent and spatially continuous, particularly during unusually harsh winters. Also, our analysis of winter weather based on precipitation and temperature, rather than the more traditional winter severity indexes, may be inadequate to detect the intricacies of winter weather effects (Knappe and de Valpine 2010), especially the effects of deep snow. All winter severity indices incorporate some measure of snow depth or density with the idea that travel and foraging will be hindered by these factors (Leckenby and Adams 1986, Cederlund et al. 1991, Farnes, 1996, Mech et al. 2001, DelGiudice et al. 2002). Unfortunately, we did not measure snow depth at our study sites, and data on snow depth, available only from weather stations or SNOTEL (an automated system of snowpack and related climate sensors operated by the Natural Resources Conservation Service) were not useful. Weather stations typically are in towns at low elevations and SNOTEL sites are located at very high elevations, whereas elk wintering areas tend to be located somewhere in between. Thus, data on snow depth were unavailable for most of our wintering areas. Nevertheless, because snow depth results from interactions of temperature and precipitation, we would expect that our analyses using these variables would at least be correlated to snow depth.

We add that winter severity indices used for North American ungulate studies exclude solar radiation flux. The effects of solar flux on energy balance can be quite large for elk (Parker and Robbins 1984, Parker and Gillingham 1990, Cook et al. 1998). We did not measure solar flux in this study, but we expect that solar flux was much lower in the maritime climate regime of our coastal region and higher in the colder continental region of the northern and central Rockies. Greater solar radiation possibly compensated for the colder temperatures in the inland Northwest and particularly in the Rocky Mountain region, such that overwinter nutritional condition dynamics among our regions of study were similar despite markedly colder winter weather in the non-coastal areas.

In contrast, our data indicated an overriding and consistent effect of nutritional condition in autumn on rate of loss of condition over winter (see also Monteith et al. 2013 who showed similar trends in mule deer [*Odocoileus hemionus*]). Although our data perhaps suggest a slight positive effect of milder temperatures on the body fat dynamics of coastal elk over winter (Fig. 7A), these animals were also some of the thinnest going into

winter (Fig. 7C). In comparison, elk at San Luis Valley endured much harsher winter weather yet ended winter with similar levels of IFBF as coastal elk because they also started winter with similar levels of IFBF (Fig. 7A,C). We could not include Yellowstone elk in our winter analysis because we did not have autumn data or lactation state on these elk, but they were among the fattest at the end of winter of all our herds (Fig. 3B), despite having the harshest winter weather of any herd in our study (Appendix).

Our identification of autumn nutritional condition as a significant covariate across multiple regions and the lack of any year, region, or winter weather effect on nutritional condition in spring indicated that winter plays a relatively minor role in determining the annual pattern of nutritional condition in females, and thus productivity and perhaps probability of survival, than previously thought. Under unusual circumstances, however, winter nutrition can affect overwinter loss in condition. Elk in our Hanford sample gained fat during winter (Fig. 3A,B). However, those elk were very thin in autumn, likely because of the wildfire that blackened much of their summer range, and had access to what was probably very high-quality forage that began growing in late autumn in response to autumn precipitation. Bishop et al. (2009) demonstrated that supplementation of wild mule deer in winter with a high-quality pellet ration improved survival of both fawns and adults in Colorado. Certainly, elk are also capable of maintaining or even improving nutritional condition in winter when fed an artificially high quality diet of alfalfa hay or pelleted rations, based on 20 years of our (R.C.C. and J.G.C.) experience feeding captive elk in winter.

The ability of some of the thinnest elk in our study to tolerate winter with virtually no loss in condition attests to the adaptability of adult elk to poor food and harsh weather in winter (see also Monteith et al. 2013). This adaptability evidently results from a variety of compensatory physiological responses to declining energy intake and increasing weather severity. For example, whole-body metabolic rates fluctuate with seasonal changes in forage availability (Silver et al. 1969, McEwan and Whitehead 1970, Lieb 1981, Argo and Smith 1983, Hudson et al. 1994). Declines in organ size are an initial response to declining energy intake. Organs account for about 70% of resting energy expenditure despite comprising only 10% of body mass, so changes in organ size have very large effects on whole-body energy needs (Ramsey and Hagopian 2006). In mammals, the body dynamically adjusts the amount of metabolically active tissue, mainly organs (e.g., liver, viscera, kidneys, heart) and skeletal tissue, to match energy intake levels (Kleiber 1947, Burrin et al. 1990, Robbins 1993, Fluharty and McClure 1997, Ramsey and Hagopian 2006). Energy expenditure at the cellular level probably declines (Ramsey and Hagopian 2006). Cervids also may compensate by increasing forage intake if forage conditions allow (Wairimu and Hudson 1993) or by reducing activity levels (Verme and Ozoga 1980). Whatever the strategy, our data indicate that winter compensatory responses play an important role in the nutritional ecology of elk.

Probability of starvation mortality in late winter will vary with winter weather and duration of harsh winter conditions. Cook et al. (2004a) identified mortality thresholds in a captive setting by inducing nutritional deficiencies that simulated very harsh

winter weather: adults below 2% IFBF and calves losing >17–18% body mass in late winter were susceptible to mortality. However, elk at moderately low levels of condition may also be predisposed to mortality (Bender et al. 2008) because of reduced vigilance, reduced likelihood to flee perceived dangers, and increased susceptibility to parasites or disease (Davidson and Doster 1997; Fortin et al. 2004, 2005).

Many elk sampled, primarily those that lactated the previous season, exited winter in poor condition, suggesting a carry-over effect of inadequate summer nutrition. Mean herd-level IFBF was >3% in all years (Fig. 3B), but these averages may incompletely portray late-winter risk of starvation. Pooling all spring captures across years within herds, we found a relatively high frequency of elk with low body condition. For example, in 10 herds (Forks, Green River, Mount St. Helens, San Luis Valley, Sled Springs, Steamboat, Toketee, Wenaha, Willapa Hills, and Wynoochee), between 14% and 33% of prime-age females had $\leq 2\%$ body fat at spring capture; 3 of these herds had up to 50% of females exiting winter with $\leq 2\%$ body fat in individual years. Among individual elk, the range in body mass change was -25% (up to 63 kg lost) to $+2\%$. More than 50% of the females in our sample ended winter at $BM_{NP} < 200$ kg and only 8% ended winter with $BM_{NP} > 220$ kg. Whether animals in this range of nutritional condition can survive winter depends on a number of factors, particularly late winter-early spring weather severity and forage phenology. Substantial mortality from winter starvation has been reported for 2 of our herds: resident and migratory elk in the Mount St. Helens area that enter the Toutle River valley during winter months (Washington Department of Fish and Wildlife 2006); and, during very harsh winters, elk in Yellowstone National Park (Houston 1982, Coughenour and Singer 1996). Regardless, females in our study that successfully raised a calf the previous summer-autumn were typically those in the poorest nutritional condition (i.e., $< 2\%$ IFBF) in late winter (Figs. 3B and 4), and these elk evidently were at elevated risk of dying during late winter. Because of tradeoffs between reproduction (i.e., successfully raising a calf) and winter mortality (i.e., dangerously low winter nutritional condition) in areas with inadequate summer ranges, predation on juveniles in summer may improve overwinter survival of adult females (Gerhart et al. 1997b), a compensatory mechanism between predation and nutrition.

Annual Cycles in Nutritional Condition

Understanding influences of each season on nutritional condition, reproduction, and survival is fundamental to developing effective conservation strategies (Skogland 1983, Post and Klein 1999, Cook 2002). These interactions are particularly complex because of the interplay among pregnancy, lactation, nutritional condition, the ability of animals to physiologically compensate for seasonal variation in their nutritional environment, and carry-over effects (e.g., body fat levels) from 1 season to the next (Cameron 1994, Cook 2002, Parker et al. 2009). Where nutritional resources are inadequate, endogenous energy levels will decline and at some point females forego breeding for a year (i.e., reproductive pause; Festa-Bianchet and Côté 2008), allowing nutritional condition to recover, perhaps the ultimate compensatory response.

At least 3 possible hypotheses have been proposed to explain the influences of nutrition on summer range, winter range, or interactions of both, on productivity of females. The first, which we term the sledging hypothesis, was probably first proposed for white-tailed deer (*Odocoileus virginianus*) by Mautz (1978) and recently discussed by Parker et al. (2009:61). This scenario suggests that each animal, regardless of starting condition, will lose a given amount of condition over winter, and gain a given amount of condition during summer, where the extent of both loss and gain is set mainly by the environmental conditions available to them (e.g., forage, weather, and density that can vary year to year). Therefore, starting nutritional condition will greatly affect condition at the end of the season, but would not affect rate of change in condition over the season. A regression of either autumn condition with the previous spring condition within a herd, or of spring condition with the previous autumn condition, would have a slope of 1 (e.g., if 2 animals started summer at 2% and 6% IFBF and the nutritional potential of the resources available to them is a 6% gain in IFBF, then they would end summer at 8% and 12% IFBF). However, this hypothesis does not account for the ability of elk to compensate in body condition within seasons (Figs. 8–11).

A second hypothesis, or winter convergence hypothesis, suggests that complete convergence of nutritional condition occurs over winter, resulting in all animals in a herd having the same nutritional condition at the end of winter. Therefore, spring condition is unrelated to previous autumn condition, even if autumn condition varies widely among animals (i.e., a regression of autumn condition with subsequent spring condition would have a slope of 0). This hypothesis is supported by Clutton-Brock et al. (1983), who found that rump fat and kidney fat converged over winter among lactating and non-lactating red deer hinds such that the 2 groups were in equivalent condition by late spring. This hypothesis accounts for reproductive pauses when nutrition is inadequate on summer range, but fatter animals in autumn would have only a minimal advantage in terms of survival to early spring or fetal development during the third trimester. This latter is a challenge in northern settings where vegetation growth is relatively late in spring (Parker et al. 2005). Our data unambiguously refute the hypothesis that nutritional condition of elk completely converges by early spring in our study region (Figs. 8 and 9). The complete winter convergence observed by Clutton-Brock et al. (1983) occurred in late spring and may have been influenced by interactions of spring nutrition and compensatory responses of thinner animals at that time. Evidence of complete convergence of body condition in spring observed in other studies (e.g., Piasecke 2006) may be an artifact of using condition indices that can predict body condition only over a limited range (e.g., subcutaneous fat indices) or analyses conducted on herd averages by season or lactation state, rather than changes in condition across seasons of individual animals.

The third hypothesis, the step-down hypothesis, was first suggested by Reimers (1983) and later mentioned by Cameron (1994) and Parker et al. (2009:61). The step-down hypothesis is similar to the sledging hypothesis in that it assumes no convergence of nutritional condition through winter (i.e., a regression slope of 1 for either autumn condition with the previous spring condition or of spring condition with the previous

autumn condition). However, it differs from either of the above hypotheses by suggesting nutritional condition will decline an approximately equal amount each summer the female raises young until she fails to breed or dies in winter. This hypothesis applies to summer ranges where nutrition is inadequate to simultaneously support lactation demands and recovery of all tissue catabolized the previous winter. Female elk, at least, have no difficulty providing milk and completely replenishing endogenous reserves lost the previous winter in time to ovulate early in the breeding season, when summer nutrition is adequate (Cook et al. 2004a). Although this process was suspected in wild reindeer herds where females lost 10–13% of body fat in years they successfully raised a calf (Reimers 1983), it excludes the compensatory capabilities of very thin females in winter (Fig. 8) and summer (Fig. 10) observed in our region.

Because all 3 hypotheses fail to account for the seasonal dynamics in condition we observed in elk, we offer a fourth hypothesis, the summer convergence hypothesis. It merges ideas of the above hypotheses but is modified in 2 ways. First, it includes compensation of relatively thin elk in winter (Figs. 8 and 9; regressing autumn condition on subsequent spring condition produces a slope between 0 and 1) and summer (Fig. 10; regressing autumn condition on previous spring condition produces a slope of 0). This compensatory capability prevents elk from continuing to decline in condition during sequential years of lactation as per the step-down hypothesis. Second, the summer convergence hypothesis suggests lactating female elk within herds converge to achieve similar nutritional condition levels by autumn regardless of starting spring condition (Fig. 10). On ranges providing low levels of summer nutrition, lactating females that end winter in good condition may actually lose condition over summer (Figs. 10 and 11), a response well documented in captive elk studies (Cook et al. 2004a), yet females on the same range that end winter relatively thin compensate by improving condition over summer while lactating (Figs. 10 and 11). The level of nutritional condition at which females within herds converge by autumn is set by the adequacy of their summer nutritional resources, which depends on forage quality and quantity, herbivore density, micro-habitat use by individual animals, and stochastic summer weather events, particularly in dry ecosystems. The convergence level is found at the intercept of the relation between spring IFBF (x -axis) and autumn IFBF (y -axis; Fig. 10). Thus, the y intercept of this relationship for a particular herd is approximately synonymous with the average level of IFBF that is achieved by lactating elk by autumn as a function of the nutritional resources available to them. These levels ranged from a low of approximately 5.5% in 4 herds (Forks, Wynoochee, Mount St. Helens, and San Luis Valley) to 12.4% in the extreme north Cascades (Nooksack; Figs. 3 and 10).

To better illustrate how the summer convergence hypothesis accounts for dynamics of elk herds in our region, we present individual elk data from 2 herds for which we had a reasonable sample size of the autumn, spring, and autumn sequence of IFBF data (Fig. 18A): 1 herd with the fattest elk in our sample (herd #5, Nooksack) and the other among the thinnest (herd #4, Wynoochee). A wide variety of body fat levels existed in the first autumn within each herd because some animals failed to

lactate the previous summer (either because of reproductive pauses or loss of calf) and thus had accrued high body fat by autumn. These data clearly show that 1) autumn differences carried through such that there was still variation in animal condition by spring; 2) how fat elk were that spring was unrelated to how fat they were the second autumn thus illustrating different points of summer convergence in IFBF for lactating females of the 2 herds; and 3) those elk that were fat in spring failed to gain or even lost body fat over summer, whereas those elk which were

thin in spring gained fat over summer, with approximate convergence of the 2 extremes by autumn, particularly for the Wynoochee herd. Over the next annual cycle for these same elk, the process would be expected to repeat such that lactating elk would end the second summer at roughly the same level of fat that they had in the first summer. Data from 1 elk from the Sled Springs herd that successfully raised a calf 5 consecutive summers showed consistency in autumn condition regardless of spring condition (Fig. 18B). Likewise, the level of spring body fat

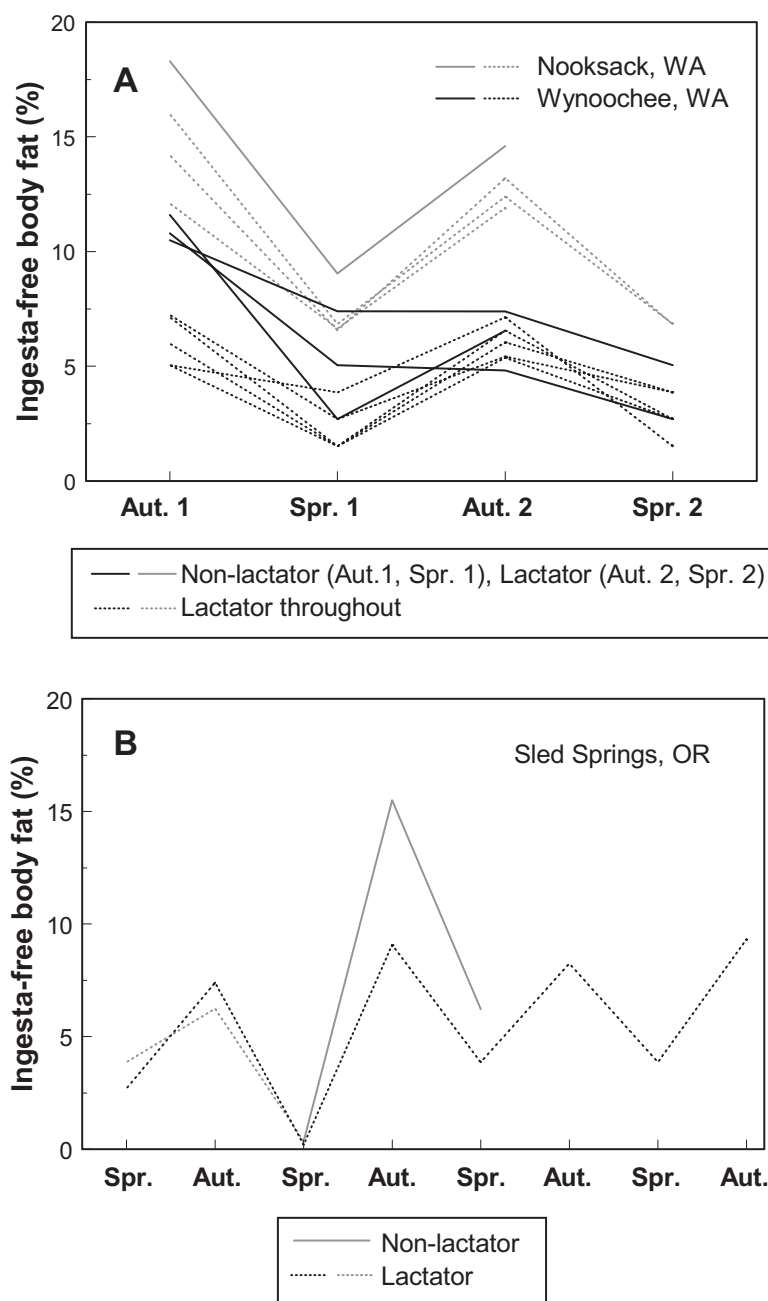


Figure 18. In panel A, seasonal levels of ingesta-free body fat (IFBF) of individual female elk at Nooksack, WA (relatively high summer nutrition) and Wynoochee, WA (relatively low summer nutrition). Solid lines represent non-lactating females the first autumn (Aut. 1) and spring (Spr. 1) but were lactating the second autumn (Aut. 2) and spring (Spr. 2), and dotted lines represent females that lactated the summer prior to Aut. 1 and Aut. 2. Panel B presents data from 1 elk at Sled Springs, OR that successfully raised a calf 5 consecutive summers (black dotted line) and data for 1 elk that lactated 1 year (gray dotted line), failed to become pregnant, and subsequently accrued high levels of IFBF the next summer (gray solid line). We collected data during 2001–2007.

stabilized after 2 years. Given the relation of autumn condition to spring condition, this stabilization is expected (see also Fig. 10), and illustrates how little winter conditions affected the change in condition over winter, despite substantial annual variation in winter weather for this herd (Appendix). However, elk that either failed to breed because of inadequate summer nutrition (Table 3) or lost their calf early in summer could attain relatively high body fat levels during the next summer (Fig. 18B).

Distinguishing between the 4 hypotheses is important for understanding and predicting how productivity (e.g., probability of pregnancy, overwinter survival, calf growth) is influenced by nutrition across the annual cycle. In nutritionally inadequate environments, each hypothesis predicts that reproductive pauses may occur. But the summer convergence hypothesis differs from the others in 2 ways regarding pregnancy probability: 1) pregnancy probability of lactating elk in autumn primarily depends on nutrition in summer and early autumn; and 2) exiting winter in relatively good condition fails to compensate for inadequate summer nutrition. If summer nutrition largely dictates annual cycles of body fat of lactating elk, as our data indicate, then measuring autumn body fat in lactating females (i.e., the summer convergence point) provides valuable insights regarding how nutrition affects a variety of animal performance attributes. The level of nutrition that affects accretion of body fat in summer similarly affects pregnancy probability, growth and development of juveniles, and may carry over to influence overwinter survival probability (Table 4; Cook et al. 2004a:55). For example, nutrition has little influence on the productivity of herds with autumn body fat of lactating elk >12%, but in herds with ≤7% body fat, lactating females often fail to breed and performance of young animals is greatly diminished (Cook et al. 2004a). The autumn convergence points of body fat from the wild herds in our study conform well to these guidelines determined with captive elk. For example, in the northern Cascades where autumn body fat ranged from 10% to 13%, pregnancy rates of lactating elk exceeded 90%, whereas in the coastal herds where body fat ranged from 5% to 7%, pregnancy rates were only 50% to 70%. Our data for calves and yearlings were limited, but nevertheless also indicated substantial reductions in their growth and development which could influence survival (Parker and Robbins 1985, Cook et al. 2004a) and adult body size (Fig. 5; Dale et al. 2008).

Finally, all but the summer convergence hypothesis suggest that variation in winter nutrition or weather contributes substantially to late-winter and early-spring nutritional condition, which may in turn influence late-winter starvation mortality. However, our data indicated little influence of winter conditions on late-winter body fat, and thus, the probability of winter starvation would be largely determined by summer nutrition and autumn IFBF (except under exceptionally harsh winters; Houston 1982, Coughenour and Singer 1996). Data from the radio-collared elk for several herds in our study indicated that late winter–early spring starvation mortality was rare (see Evans et al. 2006, Bender et al. 2008), except in the elk sub-herd we sampled at Mount St. Helens along the Toutle River. Here, late-winter starvation mortality was common and well documented (Washington Department of Fish and Wildlife 2006), but our body fat data from autumn suggested that those mortalities

occurred principally because body fat in October of many of these elk was very low (<5%), not because winter at the Mount St. Helens area was particularly harsh (Appendix). However, we note that interactions between timing of vegetation regrowth in spring during the third trimester, along with late winter and spring weather, may affect neonatal viability and survival (Mech et al. 1995, Valkenburg et al. 2002, Pettorelli et al. 2005).

Other Evidence of Summer Limitations

Pregnancy rates of prime-aged females.—Positive relationships between body fat levels and pregnancy rates are well documented across a variety of ungulate species (e.g., Trainer 1971, Gerhart et al. 1997a, Heard et al. 1997, Testa and Adams 1998, Cook et al. 2004a). In addition, inadequate nutrition in the months before the breeding season may delay conception and desynchronize the birth pulse the following spring, perhaps increasing susceptibility of late-born calves to predation (Adams et al. 1995, Singer et al. 1997, Smith and Anderson 1998, Keech et al. 2000, Rearden 2005). Nutrition-mediated delays in ovulation or breeding have been documented for red deer (Mitchell and Lincoln 1973, Guinness et al. 1978), elk (Trainer 1971, Kohlmann 1999, Cook et al. 2004a), white-tailed deer (Verme 1969), and reindeer (Reimers 1983).

For prime-aged elk, Cook et al. (2001c, 2004a) demonstrated that elk with at least moderate summer and early autumn nutrition (specifically, summer digestible energy levels that satisfy maintenance needs of lactating elk) will have >90% probability of breeding. Thus, pregnancy rates of <90% in prime-aged elk should normally indicate inadequate summer nutrition. Our data indicated at least 2/3 of the herds that we sampled had depressed pregnancy rates (Table 3) and we found evidence of delayed breeding in several herds from the coastal, southern Cascades, and inland Northwest regions. These findings corroborate conclusions from our data of nutritional condition that summer nutritional limitations are widespread.

Although body fat levels generally predict these declines in pregnancy in captive elk (Table 4; and see Cook et al. 2004a), we observed pregnancy rates higher and lower than predicted based on body fat in many of our free-ranging elk herds (Fig. 12). Body fat is an imperfect predictor of pregnancy because a variety of physiological mechanisms influence ovulation and breeding (National Research Council 1985, Bronson and Manning 1991, Gerhart et al. 1997a). Thus, the use of herd-level pregnancy data alone as an indicator of habitat nutritional adequacy is fraught with problems for at least 4 reasons. First, nutrition can contribute to ovulation either via a static component (i.e., body fat levels) resulting from long-term nutrition over the 2 to 3 months prior to breeding, or a dynamic component involving short-term nutrition ranging from a few days to 3 weeks prior to the normal breeding time (National Research Council 1985, Molle et al. 1995, Martin et al. 2004). Variation in either may independently or interactively affect ovulation. Several of the herds we sampled in drier communities of the inland Northwest and Rocky Mountains (e.g., Sled Springs and San Luis Valley) had higher pregnancy rates than predicted by their late-autumn body fat levels. Given adequate precipitation, these landscapes can periodically experience vegetative re-growth events in

autumn (Westenskow-Wall et al. 1994) that may provide a caloric boost and enable thinner females to breed when they otherwise would not do so.

More generally, the relation between body fat and pregnancy is indirect. No strong causal physiological relation between body fat and pregnancy has been found in any species (Bronson and Manning 1991), although leptin, a hormone primarily produced in adipose tissue, may signal nutritional status to the central reproductive axis of mammals (Zieba et al. 2005). Plasma levels of metabolic substrates such as glucose, insulin, leptin, and insulin-like growth factor play the main modulatory roles (Scaramuzzi et al. 2006). Thus, quantitative relations among nutrition levels in the summer, resultant body fat levels in late summer and autumn, and probability of pregnancy are imperfect and might be inconsistent across space and time (Gerhart et al. 1997a). The oft-cited relation between pregnancy and body mass in adult females probably occurs primarily because weight and body fat are inter-related, not because weight per se controls ovulation (Cook 2002:296).

Second, lactation before or during the breeding season may confound the relation between nutrition and pregnancy in 2 ways: 1) elevated nutritional demands required to support lactation greatly hinder fat accretion before breeding (Cook et al. 2004a); and 2) at any given level of body fat during breeding, the physical stimulus of being nursed may affect reproductive hormones, thereby reducing probability of ovulation (i.e., lactational infertility; Loudon et al. 1983, Gerhart et al. 1997a). We found no evidence that lactating females had a lower probability of breeding at any level of condition than their non-lactating counterparts (our data actually suggested the opposite [Fig. 13]). In herds where calf mortality is high (e.g., high predation), particularly during the months before breeding, a large proportion of mothers are released from the nutritional demands of raising a calf, allowing them to recover condition more rapidly than they would with a calf at heel. Thus, overall herd fat levels may be higher in herds hard-hit with predation than those experiencing little predation, an effect that effectively masks the effects of nutrition on reproductive performance (Verme 1962, Verme and Ullrey 1984, Gerhart et al. 1997b).

Third, breeding occurred as much as 3 months before our autumn nutritional condition data were collected; thus, females possibly lost IFBF between the breeding season and when captured in our study. Reviewing available data sets, Cook (2011) found that elk typically lost IFBF over autumn in our region (see also Kohlmann 1999). Thus, variable sampling dates over autumn may confound IFBF-pregnancy relations because IFBF declines in many herds over autumn and because the rate of change in IFBF over autumn can be quite variable (Table 5 in Cook 2011).

Fourth, nutrition levels that are just adequate to maintain high pregnancy rates are nevertheless inadequate to support optimal performance in other ways, such as juvenile growth and adult fat accretion rates (Table 4; Cook et al. 2004a). Pregnancy rates, though easy to measure, may not influence population dynamics as much as calf survival (Raithel et al. 2007). However, depressed pregnancy rates are indicative of summer range conditions that are sub-par for calf growth and subsequent winter survival, yearling growth and productivity, age at first breeding, delayed

breeding, accretion rates of fat and lean muscle, and probability of adult survival. Pregnancy rates are less sensitive to nutritional deficiencies than many of these other performance attributes (Gaillard et al. 2000; Cook et al. 2001c, 2004a; Bonenfant et al. 2002). Thus, for the purpose of evaluating nutritional adequacy of ungulate ranges, pregnancy rate may be a misleading indicator, especially in those herds with high juvenile losses in summer (see above discussion of herds affected by heavy predation on calves). Barring disease or other such effects, low pregnancy rates clearly indicate nutritional deficiencies, especially in summer, but high pregnancy rates do not necessarily signal superior nutrition in summer or any other season (Gerhart et al. 1997b, Cook et al. 2001c).

Fetal loss either from resorption early in pregnancy or abortion later in the term was virtually non-existent in our data, as was reported in captive elk studies where pregnant females were fed highly deficient winter rations (Cook et al. 2001c, 2004a). Fetal loss only accounted for 1% of our sample and most notably, no evidence of fetal loss between the time of capture in March or early April and calving were documented for herds where vaginal implants were used ($n = \text{approx. } 220$ females from Toketee, Steamboat, Sled Springs, Wenaha, and White River herds; B. Johnson and D. Immell, Oregon Department of Fish and Wildlife, and D. Vales, Muckleshoot Indian Tribe, unpublished data). Despite growing belief alleging that nutritional condition, predation risk (Creel et al. 2007, 2009; Cunningham et al. 2009), and capture drugs may cause fetal loss in elk, we found no evidence to support these hypotheses in our herds despite repeated capture using drugs, abundant large predators in their ranges, and many elk in poor condition by late winter.

Pregnancy rates of old-age females.—Our data indicated that IFBF exerted greater influence than chronological age on pregnancy status of elk ≥ 15 years old (Figs. 14 and 15). Cook et al. (2004b) found similar patterns for older animals in Yellowstone National Park and concluded that older animals were less capable of recovering condition in years they lactated, and this resulted in more frequent reproductive pauses, compared to younger animals. Combined, these results suggest an interaction between age and nutritional condition (i.e., possibly suggesting a higher IFBF breeding threshold in older animals) may be more responsible for declining pregnancy rates in animals ≥ 15 years old. At some point, age may preclude ovulation but our data suggest that inability to maintain condition terminates reproduction before chronological age per se.

Juvenile growth and development.—Cook et al. (2004a) demonstrated that summer nutrition greatly affected growth, development, and probability of pregnancy among yearlings (see also Gaillard et al. 1996). Despite near starvation feeding levels in winter that forced body mass losses of 15–25%, good to excellent nutrition during their first 2 summers of life resulted in autumn body mass of captive yearling females typically 185–225 kg, and pregnancy rates approaching 100% (Cook et al. 2004a; Table 4). In our study, body mass for yearlings in autumn were 65–80% of mass attained if summer-autumn nutrition is not limiting (Cook et al. 2004a). Our data were similar to body mass for yearlings reported by Dean et al. (1976) during early-winter ($\bar{x} = 162$ kg) on feed grounds in western Wyoming and for 261 yearlings sampled during early- to mid-winter in the 1990s and 2000s at

Starkey Experimental Station in northeast Oregon ($\bar{x}$ = 158 kg; M. Wisdom, United States Forest Service, unpublished data). Our estimates ($\bar{x}$ = 161.9 kg) were slightly lower than the average late autumn body mass reported for yearlings ($\bar{x}$ = 177 kg) in an increasing elk population in Michigan (Piasecke et al. 2009) and lower than the 220 kg reported by Blood and Lovaas (1966) for 1 yearling female in Manitoba. Dale et al. (2008) also concluded that winter weather and habitat had relatively little influence on growth and subsequent body size in caribou over the next summer, and indicated that growth rates during summer were limited by summer nutrition levels.

Our pregnancy rates fell within the ranges reported for yearlings in other herds (Greer 1968, Piasecke et al. 2009) but were higher than would have been predicted from their body mass based on experiments in captive trials (Fig. 16; Cook et al. 2004a). Because of an inadequate autumn sample size, we generated our curve on spring body mass rather than the autumn body mass used by Cook et al. (2004a); as females lose weight over winter, the probability curve would be expected to shift to the left. Adjusting our spring BM_{NP} estimates to reflect previous autumn BM_{NP} by adding a conservative 10% to spring BM_{NP} , to account for winter mass loss, produced predictions similar to Cook et al. (2004a); probability of yearling pregnancy began to decline when BM_{NP} in autumn was lower than 200 kg, and approached zero when BM_{NP} of yearlings in autumn was lower than 160 kg. However, like adults, yearling pregnancy probably is affected as much or more by energy balance than body mass or body fat per se. Thus, comparing differences among herds using logistic regression based on body mass or IFBF can be misleading or flawed depending on sample sizes, influential data points, and patterns of body mass or IFBF change between the breeding season and time of capture later in autumn or early winter (see Table 5 in Cook 2011). Regardless, low body mass of yearlings relative to their potential and reduced pregnancy rates provide further evidence of summer nutritional limitations.

Our body mass estimates of calves provided some of the most striking evidence of summer nutritional limitations, particularly because juvenile growth is highly sensitive to nutrition (Price and White 1985; Jiang and Hudson 1994; Cook et al. 1996, 2004a). Thirty to 90% of calves in our sample weighed <90 kg, and nearly all calves were <110 kg (Fig. 17; Table 4; Cook et al. 2004a). Captive studies demonstrated that elk calves can obtain an October mass of 120–140 kg in the absence of summer nutritional limitations (Hudson et al. 1994, Jiang and Hudson 1994, Cook et al. 2004a). Blood and Lovaas (1966) reported mean body mass of 2 wild calves (1 male collected in October and 1 female collected in January) of 133 kg in Manitoba, but body mass normally range substantially below their potential. In Northwest Wyoming, Dean et al. (1976) reported elk calf body mass of 101 kg in females and 110 kg in males during December and January on winter feed grounds. In northeast Oregon at the Starkey Experimental Station, calf body mass was 102 kg in 332 females (range 43–136 kg) and 109 kg (range 48–140 kg) in 287 males collected during early- to mid-winter in the 1990s and 2000s (M. Wisdom, unpublished data). In Colorado, Freddy (1997) reported elk calf body mass of 106 kg in females and 115 kg in males in December over 4 years, with up to 16% of the calves <85 kg in any given year and up to 84% of the calves <110 kg.

Captive experiments to identify relationships between body mass of calves in autumn and their survival probability during harsh winters indicated highly significant linear to slightly nonlinear influences, rather than thresholds (Cook et al. 2004a). Nevertheless, the experiments indicated that calves of <85 kg in autumn were highly susceptible to overwinter starvation mortality during severe winter conditions and reduced nutrient intake, and calves >110 kg exhibited far greater probability of surviving harsh winter conditions (Cook et al. 2004a, see also Taillon et al. 2006). This threshold was generally corroborated with wild elk in Colorado; calves <110 kg in December were more susceptible to mortality (starvation or predation) than were larger calves (Freddy 1997).

Caveats Regarding Analyses and Interpretations

Several additional issues have potential to influence aspects of our analyses and conclusions, or future interpretations of nutritional condition of free-ranging elk. First, we note that estimates of body condition, pregnancy, and other such measures provide little evidence of what environmental factors directly influenced these measures in our samples. Our conclusion that inadequate nutrition is largely responsible for depressed condition is an assumption, but one that reflects a long history of captive animal research using native ungulates and livestock that illustrated the fundamental influences of nutrition on reproduction and other aspects of animal performance. Elk are no exception—detailed studies illustrated considerable effects of inadequate digestible energy of food on fat accretion, juvenile development, and pregnancy dynamics in summer (Cook et al. 1996, 2001c, 2004a).

In a review of studies of dietary quality (i.e., dietary digestible energy and crude protein) of large ungulates in western North America, Cook (2002:324) found that levels of digestible energy in diets typically were inadequate for lactating females in summer, suggesting widespread occurrence of summer nutritional deficiencies as we report herein. Alldredge et al. (2002) arrived at a similar conclusion based on digestible energy content of elk forages in Idaho as did Beck and Peek (2005) in Nevada. All 3 reported that protein content of forage generally satisfied requirements in summer. Skogland (1991) stated “digestibility of food is more critical than ... protein content” and cited 7 studies that showed a “narrow balance between digestible energy availability, spatial dynamics and resource limitation ... among large ruminant grazers and browsers ...” Nevertheless, studies that have attempted to identify direct linkages between forage quality and quantity and nutritional condition and performance are rare, probably because these studies are logistically challenging, but they do exist (Sæther and Heim 1993; Crête and Courtois 1997; Moen et al. 1997; Hjeljord and Histol 1999; Herfindal et al. 2006a, b; Hutchins 2006). The preponderance of evidence indicates that low levels of nutritional condition, depressed pregnancy rates, and small body mass of juveniles are in fact a result of inadequate nutrition—a perception that underlies a multitude of studies that reported nutritional condition and animal performance (e.g., Trainer 1971, Merrill and Boyce 1991, Crête and Huot 1993, Gerhart et al. 1996, Testa and Adams 1998, Dale et al. 2008).

Furthermore, inadequate nutrition often is considered a result of intra-specific competition via density dependent mechanisms

(Leopold 1943, Klein 1968, Caughley 1970, Crête and Huot 1993, Manseau et al. 1996, Vucetich and Peterson 2004). K-selected species such as elk are thought to be controlled by density-dependent mechanisms such that reproduction and survival decline mainly when populations approach carrying capacity (Skogland 1986, Fowler 1987). We suspected that 3 herds in our study had populations at or near carrying capacity, including Rocky Mountain National Park (Lubow et al. 2002), Yellowstone National Park before wolves were introduced (Coughenour and Singer 1996), and Mount St. Helens (Washington Department of Fish and Wildlife 2006). Nevertheless, most herds in our sample were subjected to at least moderate levels of hunting and predation, mainly by black bears (*Ursus americanus*) and mountain lions (*Puma concolor*), and most herds were not likely at nutritional carrying capacity.

On the other hand, the classical views of density dependence do not address the potential for density-independent nutritional limitations on nutritional condition, reproduction, and population dynamics. Certainly, because of variation in climate, soils, and vegetation across broad geographic areas, considerable variation likely exists in forage quality and quantity and thus variation in the level of nutrition that herbivores can acquire from the plant communities available to them (Hjeljord and Histol 1999; Herfindal et al. 2006a, b). Thus, under some conditions, the distribution of forage nutrient concentrations (Hobbs and Swift 1985) of some plant community mosaics may be inadequate to satisfy nutritional needs in summer even at low herbivore densities. Although such studies are quite rare, Crête and Courtois (1997) demonstrated density-independent nutritional limitations of plant communities on very sparse moose populations in the boreal forests of Quebec in summer and winter. Krebs (2002) and Berryman et al. (2002) recently criticized strong emphasis on detecting density-dependent population regulation in various herds, noting that such influences are rarely important in practical settings, and Krebs (2002) noted that limiting, instead of regulating factors, have far more value for management purposes. For our data sets, we suspect that both density-independent and density-dependent nutritional limitations account for the levels of condition and performance that we documented. Either way, summer nutritional limitations for the elk densities encompassed in our study were widespread and affected nutritional condition and reproduction for most of the herds we sampled.

Second, summer and autumn precipitation and temperature, especially in drier ecosystems, may have a large effect on vegetation among years and thus on performance and condition of lactating females (Coe et al. 1976, Vavra and Phillips 1980, Douglas and Leslie 1986). We found no significant effect of year on autumn IFBF levels within herds, which should reflect differences in summer weather if they occurred. However, our data for individual herds in drier settings tended to be limited in terms of sample size of lactating females in autumn and number of years of data with which to evaluate influences of annual variation in summer weather. At Sled Springs, the herd with the largest number of years of data (7 years) in a drier climate, we found a positive trend (albeit insignificant with $n = 7$) between autumn IFBF and April through October cumulative precipitation (Fig. 19).

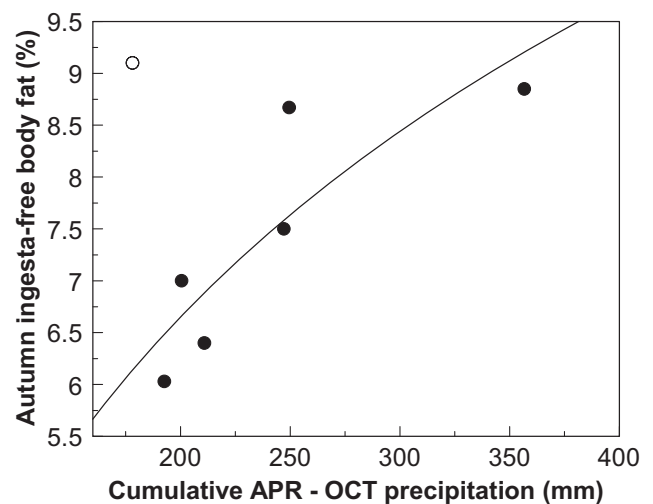


Figure 19. Relationship between cumulative precipitation from April through October and ingesta-free body fat in elk in autumn for Sled Spring, OR during 2001–2007. An apparent outlier is represented by the open circle (we did not calculate statistics on these data).

Finally, we pooled our data across years (within seasons) because we typically had insufficient years of data to support analysis of year effects. Traditionally, a significant year effect might reflect differences in weather among years or perhaps changes in range use patterns. For example, an early summer wildfire blackened a large portion of the range used by elk in the Hanford study area, and this event evidently altered range use and nutritional condition patterns (Fig. 3). The literature provides many examples of weather effects on large ungulate performance metrics, but we stress that without repeated measures data and suitable covariates, results that indicate a significant effect of year on performance may reflect a variety of influences. For every herd in which we found a significant influence of year on winter nutritional condition dynamics, the effect disappeared with addition of autumn nutritional condition as a covariate. Such a result illustrates that significant year effects, particularly in the absence of repeated measures data, should be interpreted with caution.

Sampling Nutritional Condition

Nutritional condition data from live animals, when collected accurately and with adequate sample sizes, provide valuable insight of the influence of nutrition on herd productivity. However, such data are expensive and time-consuming to obtain, require extensive training to collect accurately, and require detailed sampling designs to maximize their value. Research projects often only have enough funding for a single capture effort for the duration of the project, or 1 capture effort per year. Traditionally, ungulate biologists schedule this sampling in mid-to late winter to minimize heat stress during captures and to avoid stress to fetuses in spring.

Our results demonstrate limitations of these single-sample operations. The approach does not allow differentiation between winter and summer nutrition effects on nutritional condition and reproductive performance nor does it allow evaluation of reproductive and condition histories of animals for testing

hypotheses. Finally, it does not allow identification and focus on lactating females, a class of animals that are most sensitive to their nutritional environment. Correctly documenting lactation status of females is critical to understanding summer range limitations and carry-over effects through winter. Classifying animals by lactation status after late autumn has the potential to introduce bias. Although elk in our study sometimes nursed their calves through winter (see Table 3), they were less likely to do so if they bred that previous autumn. Thus, lactation status determined in mid-winter or later should not be used as an indicator of all elk that raised a calf the previous summer. For example, none of the Mount St. Helens elk ($n=6$) that were lactating at capture in February were pregnant, which resulted in an improbable pregnancy rate of 0% for lactating females. At Toketee, pregnancy rate of lactating elk in autumn was 73% but was only 22% in March. Repeated-measures data were difficult to collect on this herd so the spring sample primarily included elk captured for the first time. Our repeated-measures approach also revealed that 6 females continued to nurse their yearling offspring through autumn. Nursing yearlings, never before reported for elk, can lead to incorrectly classifying a female as having raised a calf that year. Thus, considerably less understanding of nutrition's influences can be obtained from traditional single-sample studies conducted in winter or early spring, in most circumstances.

Even with our repeated measures approach, we may have missed influential relationships because of the frequency and timing of sampling in our study. For example, monthly lethal sampling of barren-ground caribou revealed marked declines in body fat between March and the end of spring during the third trimester (Adamczewski et al. 1987, Huot 1989). We assume but cannot prove that such declines did not occur in our data because initiation of vegetation growth was apparent for most herds during our spring captures. Also, scheduling of our autumn captures often reflected policies to minimize complications with hunting. Hence, unanswered questions in our data sets remain regarding changes in nutritional condition over spring and autumn and the best time to sample animals in light of research objectives.

Based on our experiences, we offer some suggestions regarding sampling protocol for nutritional condition and pregnancy in elk. Collecting condition data as a supplement to operations with other primary goals, such as deploying radio-transmitters in winter, typically will provide limited data for study of nutritional ecology. If understanding of nutritional ecology is a primary goal, then sampling methods should be designed accordingly. Repeated-measures designs are crucial for developing reproductive histories of individuals that can have large influences on single-season estimates of nutritional condition and to differentiate relative influences among seasons. Useful data still can be gathered if repeated measures are not an option, but sampling should be conducted in both spring and autumn, at least in our ecological setting. If only a single capture operation can be conducted, the most valuable data will be gained during mid- to late autumn mainly because lactation status can be incorporated into data analysis and because of the demonstrated links between summer and autumn nutrition and productivity. Data collected only once per year in mid- to late winter perhaps may serve as a screening exercise to identify the need for further nutritional

research. Nevertheless, such data will be ambiguous at least under the climatological and biogeographical settings of our study unless nutritional condition levels are unusually low, which probably signals a serious nutritional limitation originating on summer range. In areas with autumn hunting of female elk, collecting samples for condition evaluation from organs or carcasses is a useful option (Cook et al. 2001*b, c*) that can permit evaluation of lactation status. However, this sampling scheme precludes repeated-measures designs and precludes accurate estimates of pregnancy rates if hunting seasons occur relatively early in autumn (e.g., before mid-November).

Finally, reliable inferences of nutritional condition require that estimates are collected accurately. Bias of just 2–3 percentage points of IFFB, for example, can greatly alter conclusions regarding nutrition's influences. Many of the techniques are not user-friendly, and variation of >2 to 3 percentage points can be expected when used by inadequately trained and inexperienced personnel particularly with, but not limited to, ultrasound and body scoring techniques (Cook et al. 2001*a*, 2007). Use of ultrasound and body scoring techniques is proliferating in North America (Cook et al. 2010) with no means in place to certify or evaluate quality and accuracy of data collection. Continuing advances in the realm of nutritional ecology requires that methods to measure nutritional condition are accurate and repeatable. The proliferation of data sets collected without adequate quality control risks doing more to harm than enhance future advances in the realm of nutritional ecology.

MANAGEMENT IMPLICATIONS

Our results provide a broad-scale illustration of the extent to which western elk populations are subject to nutritional limitations. Furthermore, they illustrate that those limitations are primarily mediated by elk summer ranges rather than by winter ranges in most cases, are geographically widespread and substantial in some areas, and suggest that nutritional effects are among the greatest of the various potential influences of habitat on elk population dynamics in many settings across western North America. Our results indicate that a paradigm shift is appropriate regarding how management agencies reconcile their goals for habitat management with their goals for elk production. Of course, past management issues such as roads, cover, and disturbance remain salient. However, the notion is not credible that reproduction, in particular, can be managed through manipulation of those factors alone, without explicit regard to the underlying nutritional potential of elk habitat and elk density.

Our results also should have implications for how managers treat the competing views of bottom-up and top-down regulation. Declining elk populations have generated increasing research and management focus on predation effects (Keister and Van Dyke 2002, Johnson et al. 2005, White et al. 2011). Nevertheless, continued competition between these concepts is rather pointless and unproductive (Gustine et al. 2006). One does not preclude the other, and the importance of providing adequate nutritional resources is just as great in areas with high predator populations as those with low populations.

Additionally, detecting predation effects with field studies is typically simpler than identifying nutrition effects for several reasons, thus perhaps contributing to a relative under emphasis of

nutrition's influences in the current literature. First, predation can mask nutrition effects, because predation on neonates may improve nutritional condition and pregnancy probability of their mothers by autumn (Gerhart et al. 1997b). Thus, thoroughly identifying nutritional effects may require reduction or removal of predation effects. Second, in contrast to predation effects, nutritional influences are subtle, often difficult to detect, and typically operate via relatively minor effects on many facets of reproduction and survival (e.g., pregnancy rates, fetal survival, neonatal vigor and survival, juvenile growth, susceptibility to predation and overwinter starvation, and delays in age at first breeding). The magnitude of nutrition effects on any 1 attribute may be quite small, but the cumulative effects across all may be substantial. Consequently, mensurative field studies intended to compare influence of nutrition versus predation may fail to fully identify nutrition's overall influences. Manipulative studies wherein predation is controlled and rigorous monitoring of responses in nutritional condition, reproduction, and survival of the prey population may be required in many instances to reliably compare the effects of predation and nutrition. After all, removal of dominant predators does not always result in appreciable responses in large ungulate populations because of a variety of complicating factors (Valkenburg et al. 2004, Hurley et al. 2011).

Design of broad-scale land management strategies that effectively account for the nutritional needs of elk and other ungulates is hampered by a lack of knowledge showing how to do so effectively. At the White House Conference on North American Wildlife Policy in 2008, however, attendees concluded that 1 of the main threats to viable and huntable ungulate populations in the West was a region-wide decline of early-successional habitats, particularly on federal lands (Sporting Conservation Council 2008). The conference called for better understanding of how active land management could help conserve disturbance-dependent habitats. It also recommended integration of management for nutritional resources with management for reducing wildfire potential, production of biofuels, alteration of forest density, and other similar activities that can contribute to restoring forest health (Sporting Conservation Council 2008:38–39).

Those recommendations were based on an understanding that early seral habitats, whether the result of natural or anthropogenic disturbance, are required for maintaining productive ungulate populations. Several examples on western landscapes demonstrated dramatic increases in ungulate populations after very large-scale disturbances, including the Tillamook fires of 1933 and 1939 in Oregon (Einarsen 1946), the eruption of Mount St. Helens in Washington (Merrill 1987), and the vast fires in northern Idaho and western Montana early in the 20th century (Pengelly 1963). In each of these cases, ungulate populations now are in various states of decline as forest succession has advanced. Peek et al. (2001, 2002) clearly illustrated that forest succession in central Oregon has reduced, by 60–75%, the amount of forage on higher elevation summer ranges over the last half century, and their retrospective analyses correlated that change to the decline of the region's mule deer herds. Bomar (2000) reported similar significant relations between forest change and elk populations in Idaho, as did Gill et al. (1996) for roe deer (*Capreolus capreolus*) in England.

The depressing effect of advanced forest seral stages on forage for ungulates is well documented across western North America (Irwin and Peek 1979, 1983; Collins and Urness 1983; Riggs et al. 1996; Peek et al. 2001; Keane et al. 2002). Consequently, fire suppression since the 1930s and subsequent succession have and continue to increase prevalence of large areas of mid-seral, dense forests in western North America (Alabeck 1982, Gruell 1983, Peek et al. 2001, Keane et al. 2002). Ungulate herds in many areas persist on landscapes that have less forage production than in the past. Apparent declines in ungulate populations may be more related to successional dynamics than is usually recognized because detecting these long-term relations with short-term research (Hobbs 2003) is difficult.

Challenges facing planners and managers include effectively managing habitat to improve and maintain nutritional resources that benefit large ungulate populations, integrating nutrition-explicit habitat management with management of other habitat attributes for elk, and satisfying other natural-resource objectives. From a practical perspective, we believe 2 broad types of information are required for implementing nutrition-based habitat management programs. First, for any given ecological setting, managers should identify if nutritional limitations influence the population and, if so, on which seasonal ranges the limitations are influential. We recommend that wildlife agencies consider developing monitoring programs to track nutritional condition of their large ungulate herds. Existing programs usually rely on hunter-harvested animals in autumn (e.g., Harder and Kirkpatrick 1994, Kohlmann 1999) and thus are timed to provide data for key seasons (summer and early autumn). Nevertheless, sampling to augment hunter-harvest samples may be needed in many situations, mainly to distinguish relative influences among winter, summer, and perhaps other seasons (Cook et al. 2001a, b). Poorly designed monitoring programs may provide little useful information and could be misleading and do more harm than good.

Second, having reliable, large-scale habitat planning and management protocols will require a new research emphasis that links fine-scale nutrition attributes of habitat to dynamics of populations. Nutritional ecology involves frequent decisions made by herbivores at very fine scales; developing protocols that effectively integrate animal nutritional ecology at fine scales and yet are relevant for planning and management across large landscapes is a considerable challenge (Hobbs 2003). Until these protocols are developed and stringently validated, biologists, managers, and planners will be hard pressed to design useful nutrition-explicit habitat improvements. Our findings of the importance of summer nutrition also have implications for the scale of habitat improvements. The wildlife profession has a long history of creating small areas of high-quality food for large ungulates (e.g., Lopez 2006). These small areas are most useful in winter when ungulates typically are concentrated. To affect a high proportion of animals in summer, however, habitat manipulations will have to be large-scale in scope, and thus manipulations of elk habitat to improve nutrition probably will have to occur in conjunction with other land management activities (Cook 2002, Sporting Conservation Council 2008). On public lands at least, the increasing restrictions on manipulation of habitat increases the challenge considerably. Hence, knowing

how to improve habitat in a manner that effectively improves the nutritional status of large ungulate herds is increasingly important.

Finally, our findings highlight the value of summer range, but we emphasize that protection and management of winter ranges remain important objectives. Some areas in North America experience longer winters and deeper snows than for many areas we sampled, and our findings in no way imply that survival in particular is uninfluenced by winter nutrition and winter weather in these areas, particularly during unusually harsh winters (Houston 1982, Mech et al. 1987, Hobbs 1989, Keech et al. 2000). Our data and conclusions support Torbit et al. (1985) that a primary value of winter ranges to elk is as a holding area of relatively moderate weather and snow to slow the loss of nutritional condition until nutritious forage on spring ranges becomes available. Nevertheless, substantial losses in nutritional condition of elk occur on winter ranges, and minimizing disturbance and harassment on these ranges should remain a key goal (Christensen et al. 1993, Bishop et al. 2009). For herds that enter winter in unusually poor condition, maintaining nutritionally productive winter ranges might compensate for inadequate summer ranges.

SUMMARY

- We seasonally measured body condition and reproduction in 21 elk herds in 5 western states.
- Our data demonstrated that nutritional resources on summer range across the study areas led to substantially reduced growth of juveniles and yearlings, fat accretion in adults during summer and autumn, and pregnancy rates relative to optima determined in captivity.
- Body fat levels of lactating females in autumn varied 2-fold among herds, likely because of differences in nutritional resources on summer ranges. Generally, body fat was lowest in the coastal and inland Northwest regions and highest along the west-slope of the northern Cascades.
- For those elk that successfully raised a calf over summer, thinner females in spring compensated by accruing more fat than their fatter counterparts over summer and within herds, had similar body fat levels in autumn.
- Neither body fat in early spring nor change in body fat over winter was significantly related to winter weather, region, or herd. Instead, loss of body fat over winter was primarily a function of body fat levels the previous autumn and that in turn was dependent on nutrition and lactation status the previous summer. Thinner females in autumn lost less body fat and body mass over winter than did fatter females, but still exited winter in lower condition than their fatter counterparts.
- Probability of pregnancy was positively related to body fat in autumn but we found no evidence that winter or nutritional condition in early spring affected pregnancy rates the subsequent autumn.
- We found performance of calves and yearlings to be congruent with poor to marginal nutritional resources on the summer range, although sample sizes were small.
- Our data indicated a strong interaction among adequacy of summer nutritional resources, lactation status, and probability

of breeding that was little affected by a wide range of winter conditions. Adequacy of summer nutrition in our region dictated annual cycles of nutritional condition, because fat levels in spring reflected fat levels the previous autumn, and thus summer nutrition had substantial influences on potential productivity of elk populations.

- Our data support the paradigm that nutrition on summer range drives the productivity of elk and probably other ungulates in many ecological settings. Our findings indicate a need for increasing emphasis on summer habitats in land management planning.
- Explicit integration will be required of ungulate nutritional ecology, vegetation ecology (disturbance and succession), and population ecology across vast landscapes and long time periods if land management is to effectively improve habitat in a way that will enhance population productivity.

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Appendix. Elk herd by year spring body fat (%) and change in body fat over winter (on a percentage point basis) paired with winter weather statistics. We collected data during 1999 through 2007 from herds in Washington, Oregon, and Colorado and included only those herds for which we had a repeated measures design such that females caught in autumn were caught again the following spring. Herd names correspond to Table 2 and Figure 1.

Herd#/herd	Region ^a	Winter ^b	Spring body fat (%) ^c	Winter change body fat ^{c,d}	Precipitation (mm) ^e	Precipitation (mm) ^f	Temperature (°C) ^g
1/Forks	CS	2001	4.01	−4.51	207.01	621.03	0.53
1/Forks	CS	2003	3.06	−3.15	335.20	1005.59	2.54
2/Willapa Hills	CS	2002	3.58	−3.87	303.96	911.88	0.94
4/Wynoochee	CS	2004	2.99	−4.42	409.41	1228.24	1.36
4/Wynoochee	CS	2005	4.30	−3.03	307.49	922.48	0.85
5/Nooksack	CM	2001	6.10	−8.39	195.20	585.59	−1.35
5/Nooksack	CM	2002	5.55	−7.48	453.87	1361.61	−1.16
6/White River	CM	2004	2.99	−9.45	168.89	506.67	−2.73
6/White River	CM	2005	7.19	−4.42	101.01	303.02	−1.29
7/Green River	CM	1999	4.96	−6.91	379.77	1139.30	−1.93
7/Green River	CM	2000	5.80	−8.54	253.91	761.72	−1.30
7/Green River	CM	2001	4.23	−7.40	119.98	359.95	−2.03
7/Green River	CM	2002	3.11	−9.70	277.07	831.20	−1.94
7/Green River	CM	2004	2.84	−6.08	195.71	587.14	−1.39
9/Mount St. Helens ^h	CM	2009	N/A	N/A	210.43	631.29	−1.23
10/Springfield	CM	2002	4.49	−6.52	268.09	804.27	0.50
11/Steamboat	CM	2004	2.23	−5.81	264.99	794.96	0.28
12/Toketee	CM	2004	5.30	−5.41	231.36	694.09	−1.67
13/Hanford	IN	2001	7.50	2.38	10.45	31.35	−2.63
14/Yakima	IN	2004	2.50	−5.24	86.67	260.01	−3.87
14/Yakima	IN	2006	4.08	−3.89	113.52	340.55	−3.79
16/Sled Springs	IN	2002	2.70	−5.71	69.56	208.68	−7.96
16/Sled Springs	IN	2003	3.43	−7.26	81.85	245.54	−5.15
16/Sled Springs	IN	2004	1.79	−7.84	87.99	263.97	−6.80
16/Sled Springs	IN	2005	5.70	−6.66	38.19	114.57	−5.94
16/Sled Springs	IN	2006	3.81	−5.34	77.48	232.43	−6.02
16/Sled Springs	IN	2007	5.12	−6.30	68.51	205.52	−4.95
17/Wenaha	IN	2003	4.36	−6.07	97.47	292.42	−3.50
17/Wenaha	IN	2004	1.67	−7.69	94.16	282.49	−5.10
17/Wenaha	IN	2005	7.25	−7.06	43.31	129.94	−4.28
17/Wenaha	IN	2006	3.28	−5.21	99.44	298.32	−5.13
17/Wenaha	IN	2007	5.72	−7.31	71.04	213.13	−4.83
19/San Luis Valley	RM	2006	4.21	−2.72	6.86	20.59	−13.66
20/Yellowstone NP ^h	RM	2000	N/A	N/A	64.57	193.71	−14.75

^a CS, coastal plains and mountains; CM, west-slope Cascade range; IN, inland Northwest; RM, Rocky Mountains.

^b Winter refers to that associated with January (e.g., Dec 2000 would be part of winter 2001).

^c Females that were lactating in autumn only.

^d Units are percentage points of ingesta-free body fat.

^e Average December through February precipitation.

^f Sum of December through February precipitation.

^g Average minimum temperature December through February.

^h Herds not included in the winter analysis because we did not have autumn and subsequent spring nutritional condition data. They were included in the table as reference points for discussion.



Biologists collecting data on female elk in December 2005 near Yakima, Washington. Photo Credit: Scott M. McCorquodale.