A MULTI-REGIONAL EVALUATION OF NUTRITIONAL CONDITION AND REPRODUCTION IN ELK

By

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A MULTI-REGIONAL EVALUATION OF NUTRITIONAL CONDITION AND REPRODUCTION IN ELK

Abstract

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We examined the role of nutrition on productivity in elk (Cervus elaphus) by estimating nutritional condition of 861 individual female elk in 2114 capture events from 21 herds across Washington, Oregon, Wyoming, Colorado, and South Dakota during 1998 through 2007. For each animal, we measured body fat of the ingesta-free body, body mass, thickness of the longissimus dorsi muscle, age, pregnancy status, and lactation status. When possible, estimates were obtained in both late winter-early spring (late February through early April) and autumn (November or early December) to estimate seasonal changes in animal condition. Pregnancy rates of females 2- to 14-years old ranged from 68 to 100% in coastal populations, 69 to 98% in Cascade populations, 84 to 94% in inland northwestern populations, and 78 to 93% in Rocky Mountain populations. Mean body mass of 242 calves from 3 populations was 75, 85, and 97 kg, 55 to 70% of potential mass for 6 month-old calves. Body fat levels of lactating females were consistently lower than their non-lactating counterparts in autumn, and herd averages ranged from 5.5% to 12.4%, a level only 30-75% of those documented for captive 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. During winter, adult females in most herds lost an average of 30.7 kg or 13.4% (range: 5 – 62 kg or 2.6 – 25%) of their autumn mass, indicating nutritional deficiencies in winter. Spring body fat level was a function of previous-autumn body fat levels; we found no significant relationship between spring body fat or change in body fat over winter with winter weather, region, or herd location. Body fat levels of lactating females in autumn were related to herd location but not to previous-spring body fat levels; the level lactating females could achieve in late autumn significantly varied among herds. Summer ranges of only 3 herds sampled supported relatively high levels of autumn body fat (≥11% body fat) and, concurrently, high probability of pregnancy even of females that successfully raised a calf year after year.
Dedication

This dissertation is dedicated to Rocky ‘Obi-Wan’ Spencer and to ‘the girls’.
Project Introduction and Attribution

This dissertation originated because a small group of researchers were interested in evaluating whether nutritional limitations on productivity were operating in wild elk herds in the west. Research from the 1990’s with captive elk showed, as had been found with livestock and other ungulates, the importance of nutrition to most all aspects of animal health and productivity, from sub-adult growth and productivity, to pregnancy rates and timing of conception, to survival, and to adult body size. This research also presented guidelines such that measuring body fat of adults, body mass of calves, and/or pregnancy rates, rather than vegetative or range characteristics, could supply some indication of the nutritional adequacy of a summer range.

After indices of body fat, in particular ultrasonography of rump fat depth and a body condition score, were validated for elk in the late 1990’s, we had the tools to not only start collecting data on wild elk, but also to interpret what the levels may mean relative to animal productivity. Mainly we were interested in evaluating whether nutrition was influencing the productivity of wild elk herds, how severe these limitations may be, which seasons of the year (e.g., winter versus summer) were most limiting to productivity and survival, and how wide-spread these limitations may be in the western US.

Capturing wild ungulates, however, is expensive, dangerous, and typically conducted by state wildlife agencies rather than non-profit organizations or universities. As such, capture operations most often are limited to a single herd, rarely more than two, and are usually conducted only once or during a single season. Collecting data in this way provides limited insights of nutritional ecology; surveys conducted across regions and seasons are needed to make significant advances regarding nutritional ecology and population dynamics of large ungulates species such as elk.
The captive elk research in the mid-1990s showing nutrition’s effect on elk productivity and the validating of nutritional indices coincided with growing awareness that populations of Rocky Mountain (Cervus elaphus nelsoni) and Roosevelt (Cervus elaphus roosevelti) elk had been declining over the last 2 decades in many areas across their range in the west, and particularly the Northwest. These population declines caused substantial revenue loss for the states and declines in subsistence hunting for tribal communities. Thus, state wildlife agencies and several tribal communities began capture programs to evaluate nutrition’s contribution (among other things) to these declines. Overall, project objectives ranged from simply documenting pregnancy rates and body fat levels to understanding the relative importance of nutrition and predation. We (John Cook and I) were invited to collect body condition and pregnancy data on these projects. This flush of studies across the west allowed an opportunity to collect a large sample of body condition data from multiple regions, seasons, years, and population conditions.

The result is a collection of data originating from quite a number of projects with varying objectives, sample sizes, and execution. Time of capture was often adjusted to avoid hunting seasons and to capitalize on availability of animals on winter and summer ranges, sample size was often limited by funding constraints and considerable difficulty capturing elk particularly in heavily forested areas of the Cascades and Coast ranges of western Oregon and Washington. Selection of elk herds for sampling was based on scientific or political interest of the agency funding and conducting the capture operation, and in many cases our own needs regarding experimental design were secondary to the lead agency.

Nevertheless, body fat and pregnancy of every animal were measured consistently by the same people (primarily me, but also J. Cook). We excluded data collected in late December, January, and early February to increase comparability among herds. These approaches allowed us
to integrate data from studies with substantially different designs and objectives and include them in a comprehensive, cohesive analysis.

In addition, agreements were made with each individual, tribe or agency that the body condition data we collected could be used for their purposes and could also be included in a region-wide assessment of nutrition’s influence on wild elk productivity, the topic of this dissertation. Although I was responsible for most of the data collection and all of the data entry, analysis, and writing of this dissertation, the submitted manuscript will have a number of deserving co-authors reflecting the large number of individual projects and biologists involved with logistics, funding, and capture efforts. Each either contributed substantially via vision or logistics/funding for the captures themselves, and each will be involved with editing before the manuscript is submitted. Thus, this dissertation is formatted to be submitted to Wildlife Monographs and co-authors for that submission are:

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# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACKNOWLEDGEMENTS</td>
<td>iii</td>
</tr>
<tr>
<td>ABSTRACT</td>
<td>v</td>
</tr>
<tr>
<td>DEDICATION</td>
<td>vii</td>
</tr>
<tr>
<td>PROJECT INTRODUCTION AND ATTRIBUTION</td>
<td>viii</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>xv</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>xvi</td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>STUDY AREA</td>
<td>6</td>
</tr>
<tr>
<td>1. Coastal Plains and Mountains</td>
<td>7</td>
</tr>
<tr>
<td>2. West-slope Cascades Range</td>
<td>8</td>
</tr>
<tr>
<td>3. Inland Northwest</td>
<td>9</td>
</tr>
<tr>
<td>4. Rocky Mountain Region</td>
<td>11</td>
</tr>
<tr>
<td>METHODS</td>
<td>13</td>
</tr>
<tr>
<td>1. Animal Capture and Handling</td>
<td>13</td>
</tr>
<tr>
<td>STATISTICAL ANALYSIS</td>
<td>15</td>
</tr>
<tr>
<td>1. Preliminary Analyses: Confounding Influences of Age, Lactation, Year, and Body Size</td>
<td>17</td>
</tr>
<tr>
<td>a. Selecting age categories</td>
<td>17</td>
</tr>
<tr>
<td>b. Influences of lactation status</td>
<td>18</td>
</tr>
<tr>
<td>c. Annual variation within herd location</td>
<td>19</td>
</tr>
<tr>
<td>d. Adjusting LOIN for body frame size</td>
<td>19</td>
</tr>
<tr>
<td>2. Autumn and Spring Nutritional Condition</td>
<td>20</td>
</tr>
</tbody>
</table>
3. Seasonal Changes in Nutritional Condition .................................................................20
4. Effects of Previous Condition on Current Condition ...............................................21
5. Modeling Effects of Multiple Years of Lactation on Performance
   and Nutritional Condition ............................................................................................23
6. Effect of Long-Term Nutritional Status on Body Size ..............................................24
7. Pregnancy, Fetal Loss, and Lactational Infertility ...............................................24
8. Condition and Pregnancy of Sub-Adults .................................................................26
9. Causes of Year to Year Variation ..............................................................................26

RESULTS ...............................................................................................................................27

1. Preliminary Analyses: Confounding Influences of Age, Lactation,
   Year, and Body Size .....................................................................................................27
   a. Selecting age categories .......................................................................................27
   b. Influences of lactation status ..............................................................................28
   c. Annual variation within herd location .................................................................29
   d. Adjusting LOIN for body frame size ...................................................................30
2. Autumn and Spring Nutritional Condition .................................................................30
3. Seasonal Changes in Nutritional Condition .............................................................32
4. Effects of Previous Condition on Current Condition ..............................................34
5. Modeling Effects of Multiple Years of Lactation on Performance
   and Nutritional Condition ............................................................................................37
6. Effect of Long-Term Nutritional Status on Body Size ..............................................39
7. Pregnancy, Fetal Loss, and Lactational Infertility ...............................................39
8. Condition and Pregnancy of Sub-Adults .................................................................42
9. Causes of Year to Year Variation .................................................................43

DISCUSSION .............................................................................................................44

1. Nutritional Condition in Summer and Autumn ............................................46
   a. Body condition levels of lactating adult females .................................48

2. Nutritional Condition in Winter and Early Spring ..................................54
   a. Body condition levels of adult females ...............................................56

3. Annual Cycles in Nutritional Condition ....................................................60
   a. The equilibrium hypothesis ..............................................................61

   a. Pregnancy rates of prime-aged females ..........................................67
   b. Pregnancy rates of ‘old-age’ females ...............................................72
   c. Juvenile growth and development ...................................................72

5. Other Influencing Factors ............................................................................74

6. Sampling Nutritional Condition ...............................................................76

MANAGEMENT IMPLICATIONS ...........................................................................81

LITERATURE CITED ..............................................................................................91

FIGURE TITLES ...................................................................................................109

TABLES ................................................................................................................123

FIGURES .............................................................................................................136

APPENDIX
   A. Herd averages of LOIN depth in autumn and spring ..........................159
## LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Herd characteristics and description of capture efforts</td>
<td>123</td>
</tr>
<tr>
<td>2.</td>
<td>Herd by year body fat and change in body fat over winter relative to winter weather</td>
<td>126</td>
</tr>
<tr>
<td>3.</td>
<td>Pregnancy rates</td>
<td>130</td>
</tr>
<tr>
<td>4.</td>
<td>Levels of performance expected for elk</td>
<td>133</td>
</tr>
<tr>
<td>5.</td>
<td>Estimates of body fat loss from breeding to capture</td>
<td>135</td>
</tr>
</tbody>
</table>
# LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Location of elk herds sampled</td>
<td>136</td>
</tr>
<tr>
<td>2</td>
<td>Pregnancy rates relative to age</td>
<td>137</td>
</tr>
<tr>
<td>3</td>
<td>Body fat in autumn and spring</td>
<td>138</td>
</tr>
<tr>
<td>4</td>
<td>Body mass in autumn and spring</td>
<td>139</td>
</tr>
<tr>
<td>5</td>
<td>( \text{LOIN}_{\text{ADJ}} ) in autumn and spring</td>
<td>140</td>
</tr>
<tr>
<td>6</td>
<td>Seasonal depletion/accretion levels of body fat</td>
<td>141</td>
</tr>
<tr>
<td>7</td>
<td>Seasonal declines/increases of body mass</td>
<td>142</td>
</tr>
<tr>
<td>8</td>
<td>Seasonal depletion/accretion levels of ( \text{LOIN}_{\text{ADJ}} )</td>
<td>143</td>
</tr>
<tr>
<td>9</td>
<td>Relation of initial body fat with ending body fat over winter and summer</td>
<td>144</td>
</tr>
<tr>
<td>10</td>
<td>Relation of initial body mass with ending body mass over winter and summer</td>
<td>145</td>
</tr>
<tr>
<td>11</td>
<td>Relations of initial ( \text{LOIN}<em>{\text{ADJ}} ) with ending ( \text{LOIN}</em>{\text{ADJ}} ) over winter and summer</td>
<td>146</td>
</tr>
<tr>
<td>12</td>
<td>Modeling body fat across multiple years of lactation</td>
<td>147</td>
</tr>
<tr>
<td>13</td>
<td>Seasonal trends in body fat for wild elk lactating ( \geq 2 ) years in succession</td>
<td>148</td>
</tr>
<tr>
<td>14</td>
<td>Modeling body mass and ( \text{LOIN}_{\text{ADJ}} ) across multiple years of lactation</td>
<td>149</td>
</tr>
<tr>
<td>15</td>
<td>Relation of autumn ( \text{BM}_{\text{IFF}} ) and autumn body fat in lactating elk</td>
<td>150</td>
</tr>
<tr>
<td>16</td>
<td>Probability of pregnancy</td>
<td>151</td>
</tr>
<tr>
<td>17</td>
<td>Assessment of lactational infertility</td>
<td>152</td>
</tr>
<tr>
<td>18</td>
<td>Effects of body condition on pregnancy in older females</td>
<td>153</td>
</tr>
<tr>
<td>19</td>
<td>Distribution of body mass in yearlings</td>
<td>154</td>
</tr>
<tr>
<td>20</td>
<td>Probability of pregnancy in yearlings</td>
<td>155</td>
</tr>
<tr>
<td>21</td>
<td>Distribution of body mass of calves</td>
<td>156</td>
</tr>
<tr>
<td>22</td>
<td>Relation of body fat and ( \text{LOIN}_{\text{ADJ}} ) in autumn</td>
<td>157</td>
</tr>
</tbody>
</table>
23. Relation of cumulative precipitation and body fat in autumn for Sled Springs, OR ............158
INTRODUCTION

Understanding and managing mechanisms that affect population dynamics comprise perhaps the most fundamental aspect of wildlife management (Caughley 1977). However, identifying specific factors that influence population dynamics in large ungulate populations is challenging, largely because the complexity of interacting factors and compensatory feedback mechanisms vary greatly both 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). For large ungulates, abundance and nutritive value of forage are commonly thought to be the primary mediators of bottom-up regulation (Caughley 1979, McCullough 1984, Parker et al. 1999) because nutritional deficiencies can have important effects on reproduction, growth and development, and survival (Verme and Ullrey 1984, Cook 2002, Parker et al. 2009).

Bottom-up influences are classically thought to regulate large ungulate populations in a density-dependent manner because the imbalance between ungulate populations and forage supplies increases as ungulate populations increase (Caughley 1976, 1979, Fowler 1987). These concepts largely originated from early studies of spectacular density-dependent interactions between herbivore populations and their food supply (Leopold 1943, Klein 1968, Caughley 1970). In addition, many barren ground caribou and reindeer (Rangifer tarandus) populations oscillate widely at 50- to 100-year cycles evidently because of density dependent food limitation (Meldgaard 1986, Skogland 1986, 1990, Couturier et al. 1990, Crête & Huot 1993, Manseau et al. 1996). Large fluctuations in moose (Alces alces) populations on Isle Royale also point to important regulating effects of forage (Vucetich and Peterson 2004). These patterns imply that depressing effects of poor or inadequate nutrition on populations are important primarily when
populations approach carrying capacity (Skogland 1986, Fowler 1987). However, nutritional limitations may also be important at moderate or even low population density. Such limitations occur when forage conditions are marginally adequate 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, and plant succession (Merrill 1987, Crête and Courtois 1997, Peek et al. 2002).

Understanding the role of nutrition (i.e., bottom-up effects) on population productivity of elk (Cervus elaphus) has recently become more important given declining calf recruitment and population size in many herds ranging from Oregon to Montana over the last 2 decades (Irwin et al. 1994, Gratson and Zager 1999, Ferry et al. 2001, Johnson et al. 2005, WDFW 2006). Many hypotheses have been postulated, such as low bull:cow ratios, increasing predation, excessive illegal and legal harvest, and changing habitat conditions (Johnson et al. 2005), and these declines have spurred a reconsideration of a broad range of factors that may contribute to herd demographics for elk across much of the region. Because many elk herds in the western and northwestern United States increased during the last half of the 20th century (Christenson et al. 1999), nutrition was assumed to exert only minor influences on population productivity, and was deemed unimportant for management of western elk herds (e.g., Black et al. 1976, Thomas et al. 1979, Nelson and Leege 1982, Christensen et al. 1993). For example, most of the habitat evaluation models used for forest planning on behalf of elk at that time (e.g., Leege 1984, Thomas et al. 1986) deemphasized nutrition (Edge et al. 1990, Christensen et al. 1993). Moreover, the idea that any biological limitations to elk populations caused by nutrition occur only during winter, particularly during harsh winters, was pervasive (Marcum 1975, Lyon 1980, Hobbs et al. 1982, Houston 1982, Nelson and Leege 1982, Leege 1984, Christensen et al. 1993, Coughenour and Singer 1996, Unsworth et al. 1998). This
perception extended to other ungulate species throughout the northern hemisphere (e.g., Klein 1968, Wallmo et al. 1977, Adameczewski et al. 1987, Skogland 1990, Weladji and Holand 2003).


Because previous assessments of the effects of nutrition on population dynamics of free-ranging ungulate herds in North America have been few, and limited either temporally or spatially, little is known about the magnitude and seasonality of nutritional limitations, the mechanisms involved, how they interact with other influences such as predation (Wang et al. 2009), and how these vary over time and across ecological settings. Further, understanding influences of nutrition on demographics of wild ungulate herds across landscapes and regions has been hampered by a lack of practical, reliable, and cost-effective techniques for monitoring
elk condition and nutrition (Robbins 1983, Harder and Kirkpatrick 1994, Saltz et al. 1995, Cook 2002). Recent development of new approaches for measuring nutritional condition using ultrasonography of subcutaneous rump fat depth and longissimus dorsi muscle depth (Stephenson et al. 1998, Cook et al. 2001a, b) and body condition scoring (Gerhart et al. 1996, Cook et al. 2001a, b) have allowed accurate estimations of body condition on live animals. Collecting nutritional condition data on live animals, in turn, 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. 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 (i.e., cumulative energy balance; Parker et al. 2009).

Therefore, to provide a comprehensive evaluation of nutritional condition and productivity of elk across the western and northwestern United States and across the decade spanning 1998 through 2007, we surveyed nutritional condition and reproductive status of 21 wild elk herds across 5 western states using the new ultrasonography and body scoring techniques. Working with a variety of state, tribal, and federal agencies, we collected data on body fat and mass, a measure of protein status, lactation and pregnancy status, age of adults, and, where possible, body mass of calves, primarily in early spring and mid-autumn. We selected body fat of cow elk as our primary variable of interest because it (1) is a direct function of forage quality and quantity available to elk and energy expenditure (Parker et al. 2009), (2) directly and indirectly influences a host of reproductive/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) reflects the general fitness of the population. We used a repeated
measures design to track annual cycles in body fat dynamics and reproduction of individual animals when possible.

The specific objectives of our analyses were to:

(1) evaluate the occurrence, severity, and seasonality of nutritional deficiencies and limitations;

(2) evaluate the extent of variation in nutritional limitations among herds and regions of the western U.S.;

(3) improve understanding of how summer and winter nutrition influences, and interacts with, reproduction;

(4) identify the need for habitat management models, programs, and planning that explicitly account for nutritional limitations on behalf of elk; and

(5) provide a baseline data set as a reference or standard of comparison for future studies of nutritional condition and reproduction in North America.

We also tested 3 overarching hypotheses in terms of nutrition influences on wild herds, that:

(1) nutritional limitations are present and important in wild elk populations and have the potential to significantly influence demographic rates of elk herds;

(2) nutritional limitations in summer, in contrast to prevailing perceptions, are common and have important effects on demography and productivity of elk herds in many areas of the western U.S.; and,

(3) nutritional limitations, however they may be manifested, are not consistent in magnitude and seasonality among herds and regions of the western U.S.

Although many of the data were collected somewhat opportunistically and in deference to other objectives of the collaborating agencies, this is the largest multi-seasonal data set of nutritional condition and reproduction for a large ungulate species. With one exception (Dale et al. 2008), it is
also the only data set 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. To our knowledge, body fat of free-ranging female elk (Cervus elaphus), independent from data included herein, has only been reported in 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, Kohlmann 1999, Stussy 1993, Noyes et al. 2002), the Yellowstone area (Greer 1968, Houston 1978, Mech et al. 2001), and Canada (Flook 1970, Huggard 1993).

Our wild elk surveys largely extend research of nutritional influences on elk that began in the mid-1990s with controlled experiments of nutrition and reproduction using captive elk (Cook et al. 2001a, Cook et al. 2004a). The 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. Integrating research results from captive elk experiments with results of wild elk nutritional condition assessments with a multi-seasonal, multi-regional approach provides a unique and powerful approach to enhance understanding of nutrition’s effects in wild settings.

**STUDY AREA**

We collected body condition data from 21 elk herds in 5 states of the western U.S.: Washington, Oregon, Wyoming, Colorado, and South Dakota. Though herd location was included as a covariate in the majority of analyses, we also partitioned our study area into 4 regions based on broad climate, landform and vegetation differences: coastal plains and mountains (Coastal), west-slope Cascades range (Cascades), inland Northwest (Inland NW), and the Rocky Mountains.
region (Rocky Mtns) (Fig. 1).

**Coastal Plains and Mountains**

We collected data from 4 elk herds west of Interstate 5 in western Washington that we refer to as (1) Forks (10 km north of Forks on the Olympic Peninsula [48° 00’, 124° 22’]), (2) Wynoochee (50 km west of Olympia [47° 15’, 123° 38’]), (3) Chehalis Valley (30 km southwest of Olympia [46° 50’, 123° 20’]), and (4) Willapa Hills (75 km south of Olympia [46° 30’, 123° 10’]). In general, elk herds in this region are 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.

Topography at Forks (50 – 450 m), Wynoochee (100 – 500 m), and Chehalis Valley (20 – 200 m) ranged from flat to gently rolling with occasional ridge systems. Topography in the Willapa Hills was more rugged, with steep canyons and mountains in some portions, and with elevations ranging from 75 to 950 m. Climate was strongly maritime, with annual precipitation averaging 180 to 250 cm and greater at the higher elevations of these study areas. Average minimum January temperature ranged from 0 to 2.5°C and average maximum July temperature ranged 20 to 23°C at the lower elevations of each of these study areas. Snow was normally absent in winter except at higher elevations of Willapa Hills and hills surrounding the other study areas. At all 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, forest often contained substantial amounts of Pacific silver fir (*Abies amabilis*) and noble fir (*Abies procera*). Franklin and Dyrness (1988)
described in detail the plant communities of these study areas.

**West-slope Cascades Range**

We collected data from 8 elk herds along the west slope of the Cascades range, including 4 herds in Washington, (1) Nooksack (50 km east of Bellingham near Mount Baker [48° 35’, 122° 20’]), (2) Green River (50 km east of Tacoma [47° 15’, 121° 40’]), (3) White River (60 km east of Tacoma [47° 10’, 121° 30’]), and (4) Mt. Saint Helens (50 km north of Vancouver [46° 30’, 122° 30’]), and 3 herds in Oregon, (1) Springfield (immediately north of the Mackenzie River 40 km northeast of Springfield [122° 45’, 44° 13’]), (2) Steamboat (immediately north of the North Umpqua River 45 km east of Roseburg [43° 20’, 122° 40’]) and (3) Toketee (south of the North Umpqua River 80 km east of Roseburg [43° 13’, 122° 25’]). Elk along the west-slope of the Cascade Range in western Oregon and Washington are considered to be Rocky Mountain elk, although Roosevelt elk from near the coast have been trans-located in the Cascades at times in the past (Harper 1987); many of these herds were established from transplanted stock from Yellowstone National Park in the early 20th century. Although not all, many elk in these herds were migratory, particularly in the White River where elk moved to high elevations in Mount Rainier National Park during summer. Topography in all ranges of these herds was mountainous and rugged at least across portions of each landscape. Radio-marked elk occupied habitats at elevations from 100 to 1,400 m (Nooksack), 350 to 1200 m (Green River), 400 to 1,200 m (2,200) (White River), 350 to 400 m (1500) (Mt. Saint Helens), 350 to 900 m (Springfield), 500 to 1,800 m (Steamboat), and 900 to 3000 m (Toketee). In Washington, climate in the western Cascades also is strongly maritime, with annual precipitation of 150 cm at lower elevations and ≥ 250 cm at the higher elevations. Mean minimum January temperature ranged from 0 to −2.5°C and mean July maximum temperature was about 25°C at the lower elevations of these study
areas. Up to about 600 to 800 m in Washington, temperate rainforests supporting primarily Douglas fir and western hemlock with red cedar and red alder were common in this region. With increasing elevation, forest transitioned into the Pacific silver fir zone where western hemlock typically co-dominated with silver fir, to the mountain hemlock 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 to 160 cm at Springfield, 70 to 100 cm at Steamboat, and 80 to 120 cm at Toketee. Mean minimum January temperatures ranged from 0 to –2.5°C, and mean maximum July temperature from 27 to 29°C for these 3 herd locations. 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) tended to be rare in much of this study area except on wetter sites. The southern-most extension of the western hemlock zone occurred at our Steamboat and Toketee areas, and here forests were largely dominated by Douglas fir, occasionally with ponderosa pine \((\text{Pinus ponderosa})\) and incense-cedar \((\text{Libocedrus decurrens})\) with a variety of sclerophyllous shrubs often well represented in this area (Franklin and Dyrness 1988).

**Inland Northwest**

We collected data from 2 elk herds in central Washington (1) Yakima (spread along the east-slope of the Cascades just west of Yakima north to Ellensburg [46° 30’ to 47° 00’ and 120° 35’ to 121° 20’]), (2) Hanford (U.S. DOE, Fitzner/Eberhardt Arid Lands Ecology Reserve 20 km northwest of Richland [119° 35’, 46° 25’]) and 2 herds in northeast Oregon (1) Wenaha (70 km
north of La Grande [117° 50’ 45° 55’], and (2) Sled Springs (75 km northeast of La Grande [117° 40’, 45° 45’]). These elk were Rocky Mountain subspecies, with genetic stock trans-located from Yellowstone National Park (although indigenous elk were never completely_eliminated in extreme northeast Oregon ([Cliff 1939, Irwin et al. 1994]). Elk at Yakima, Wenaha, and Sled Springs were strongly migratory, although migration distances were variable depending on local elevation gradients; elk at Hanford were non-migratory.

Elevations ranged from 500 to 1,600 m (Yakima), 200 to 1,000 m (Hanford), 700 to 1,600 m (Wenaha), and 700 to 1,350 m (Sled Springs). Topography at Yakima ranged from gentle, long slopes as elevation gradually increased from the Yakima front 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 broke up an otherwise flat to gently rolling plateau at higher elevations of the Wenaha and Sled Springs areas.

Climate varied greatly across the Yakima study area, 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 to 250 cm, mean January minimum temperature from –5 to –9 °C, and mean July maximum temperature from 22 to 31°C along the elevational gradient of this area. At Hanford, annual precipitation averaged 20 cm, mean January minimum temperature was –3°C, and mean July maximum temperature was 33°C. At Wenaha and Sled Springs, annual precipitation was 75 cm, mean January minimum temperature was –7°C, and mean July maximum temperature was 28 to 29°C.

Vegetation was considerably more diverse across our inland northwest than our Pacific northwest study areas. At the lower elevations of each of our inland areas and throughout
Hanford, various xeric grassland or shrub-steppe rangeland plant communities predominated. These typically served as 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*), Engleman spruce (*Picea englemanii*), and lodgepole pine (*Pinus contorta*) at moderate to high elevations in the forest zone, and at the highest elevations of the Yakima herd, subalpine fir (*Abies lasiocarpa*) and mountain hemlock were common (Franklin and Dyrness 1988). At Hanford, a fire burned most native vegetation in June 2000, and no regrowth was evident until mid-autumn 2000. The fire burned over 113,000 ha (Fluor Hanford 2002) and markedly reduced forage available to these elk in early autumn 2000 across much of their core range.

**Rocky Mountain Region**

In the northern and central Rocky Mountains, we collected data from 4 herds, (1) Yellowstone (elk were captured from the winter range of the northern herd of Yellowstone National Park near Gardiner, Montana south into northwestern Wyoming [110° 35’, 44° 55’]), (2) 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 45’, 40 20’]), (3) 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° 45’, 37° 45’], and (4) Black Hills (south and east of Interstate 90 at Sturgis, South Dakota [103° 35’, 44° 25’]). All elk were Rocky Mountain subspecies, and herds varied from strongly migratory (Yellowstone, Rocky Mountain NP) to mixed or migratory (San Luis...
Valley, Black Hills).

Elevation ranged from 1,650 to 2,400 m (3200) (Yellowstone), 2,400 to 2,800 m (4,000) (Rocky Mountain NP), 2,400 to 3,000 m (4,000) (San Luis Valley), and 900 to 1600 m (Black Hills) (values in parentheses indicate approximate upper limits of elevation available to elk). Topography was flat to gently rolling in large wide valleys across the winter ranges where elk were captured. Annual precipitation averages were 43, 41, 24, and 65 cm; mean minimum January temperature was -14.3, -9.5, -16.5, and -10.4˚C; and mean maximum July temperature was 25.7, 25.5, 29.6, and 28.8˚C, respectively for each area. At Black Hills, elk occupied forest communities on a relatively flat to gently rolling plateau and surrounding plains at lower elevations, although occasional steep canyons added topographic diversity to this landscape.

The majority of the Yellowstone winter range supported xeric 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 NP included flat valley bottoms with wet meadows and mesic grasslands, while communities of ponderosa pine and big sagebrush dominated south-facing slopes and Douglas fir and lodgepole pine forests 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, ephemeral wetlands, and large areas of “sand sheet”, communities usually dominated by greasewood (*Sarcobatus vermiculatus*) and rabbitbrush (*Chrysothamnus viscidiflorus*) (Schoenecker et al. 2006). Woodland communities of pinyon pine (*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 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).

We captured female elk using 1 of 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 Saint 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 animals twice per year, usually in March to early April and November to early December. We fitted each female with a radiotelemetry collar at first capture, which provided for subsequent recaptures for $\geq 2$ years, in a repeated measures design. However, for 6 of the elk herds, individuals were captured only once (Mount Saint Helens, South Dakota, Chehalis Valley, South Rainier, Rocky Mountain National Park, and Yellowstone National Park).

Two experienced investigators (JGC, RCC) collected a rump body condition score (rump BCS) developed for elk (Cook et al. 2001$b, c$) and measured maximum subcutaneous rump fat
thickness (MAXFAT; Stephenson et al. 1998; Cook et al. 2001b, c) using a Sonovet ultrasound machine with a 5.0 MHz, 7.0 cm probe (Universal Medical Systems, Bedford Hills, New York, USA). Thickness of the longissimus dorsi muscle (LOIN) was measured between the 12th and 13th ribs near the backbone using ultrasonography (Herring et al. 1995; Cook et al. 2001b, c); this measurement was used as a general index of protein stores. We measured chest-girth circumference to estimate body mass (BM).

We estimated the percent of ingesta-free body fat (IFBF) using the scaledLIVINDEX for elk, which is 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 animals (x) to a sternally-recumbent basis (y), using the equation $y = 0.88x + 15.39$ (Cook et al. 2003), before calculating body mass (BM) because the position of the front legs when hobbled inflates the circumference measurement. We calculated body mass 3 ways depending on the objectives of the analysis. For all females > 1 year-old when using BM 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 animals, 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-olds, 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 ($BM_{IFT}$) 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. (2001b), and we removed fat mass by multiplying percent ingesta-free body fat (IFBF) by BM 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, Montana). Pregnancy status was determined through ultrasonography via rectal entry or Pregnancy Specific Protein B (PSPB) analysis (Noyes et al. 1997) of blood serum samples taken at each capture (Biotracking, Moscow, Idaho). We classified females with an udder from which milk could be extracted as lactating (milk indicated either a cow is still nursing a calf, or had been nursing a calf within 3 to 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 of capture. We classified each female as a true non-lactator (or ‘spring non-pregnant’) if sequential capture events were available indicating it was not pregnant the previous spring.

STATISTICAL ANALYSIS

Our evaluation of nutritional condition was based on 4 condition variables. Our primary variable was IFBF, but we also evaluated BM_{NP}, BM_{FF}, and LOIN. Although body mass has frequently served as a surrogate for nutritional condition (Hudson et al. 1991, Harder and Kirkpatrick 1994), it is often poorly correlated with nutritional condition (Torbit et al. 1985, Cook et al. 2001b) because it varies not only with body fat and lean mass, but also frame size, gut fill, hydration, or pregnancy, confounding estimates of nutrient storage with unrelated variables. In addition, because elk are too large to easily weigh in the field, BM estimates calculated from girth circumference are not precise, particularly for adult elk (Cook et al. 2003; \( r^2 < 0.83 \) for adults and yearlings). Thus, caution is
warranted when using BM solely as a measure of nutritional condition particularly when it is calculated from an index. In addition, because it is a marginal predictor of IFBF ($r^2 = 0.44$, Cook et al. 2001b) and its relation to total lean mass not well-established, LOIN mostly has been used as a threshold index to identify animals that may be relatively near death in the spring. Thus, our analysis of both BM and LOIN were supplemental.

Our analysis centered on point estimates of these 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. For seasonal change, we included only individuals with sequential pairs of data (i.e., spring and subsequent autumn, autumn and subsequent spring).

To avoid inflating degrees of freedom and potential autocorrelation associated with collecting multiple samples over time from the same elk, we analyzed the data with repeated measures analysis of variance (ANOVA) or analysis of covariance (ANCOVA) in PROC MIXED (SAS Institute 1993). 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). The error structures considered were simple or variance component, compound symmetry, spatial power, spatial Gaussian, and spatial exponential; in all cases except where noted, compound symmetry was used. However, regression techniques provide no basis to analyze via repeated measures, and for some analyses, unequal sample sizes within the herd location variable created complexity that could not be accounted for in standard statistical packages (i.e. multiple comparison tests). In these cases, as noted, we either averaged data values per individual to eliminate potential autocorrelation and inflation of degrees of freedom, or stated that we were unable to analyze the data as per repeated measures (e.g., logistic regression).
Preliminary Analyses: Confounding Influences of Age, Lactation Status, Year, and Body Size

Before the main analyses of the condition variables, we addressed possible confounding effects of age on pregnancy status and IFBF, lactation status and year on IFBF, and the influence of body size or region on LOIN depth. Our primary goal with these analyses was to reduce the number of covariates and simplify subsequent analyses.

Selecting age categories.—Our first preliminary analysis was intended to identify “prime-aged” and “old aged” categories. We used logistic regression (PROC LOGISTIC, SAS Institute 1993) of pregnancy status in relation to IFBF and age for different age ranges to define these age categories. We conducted the analysis with all females ≥ 9-years old, to ensure that older cows and prime-aged cows were approximately equally represented in the data set (thereby making the test of an age effect more liberal). We ran the logistic regression iteratively, first including females 9- to 12-years old, then 9- to 13-years old, and so on until all older animals were included. We selected our prime age category at 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 re-ran the iterative analysis with animals from each subspecies separately to identify the age range for each age classification.

We also made sure that within our prime-age category, nutritional condition was uninfluenced by age. As a check, for those elk included in the prime-age category, we conducted repeated measures ANCOVA for autumn condition (IFBF, LOIN, BMNP; lactating females only)
and spring condition (IFBF, LOIN, BM_{NP} using only females which were lactating the previous autumn) with 3 covariates: age at capture, herd location, and their interaction.

Influences of lactation status.—Our second preliminary analysis was to determine if lactation status masks relations between IFBF and other variables, such as herd location or season. Substantial evidence indicates data for each elk would need to be stratified by lactation status during summer-autumn because fat accretion of lactating cows and non-lactating cows varies substantially despite identical levels of nutrition (i.e., IFBF of non-lactating females might be insensitive to their nutritional environment; Clutton- Brock et al. 1982, Landete-Castillejos et al 2003, Cook et al. 2004a). We checked to ensure this pattern held in wild elk and throughout all the herds we sampled. 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 analysis. Though some analyses required using only elk that lactated the previous autumn, we did not want to group animals into a physiological category unless biologically necessary for other analyses, especially those involving influences of previous condition on current condition.

For this preliminary analysis of lactation influences, we focused only on the seasonal change variables in case starting IFBF influenced changes in IFBF later in the season. Females were classified as lactating or non-lactating at the time of autumn capture. We used individual repeated measures ANCOVAs for each dependent variable (change in IFBF over summer, change in IFBF over winter) with previous season IFBF, herd location, lactation status, and the interactions as dependent variables. Only prime-age animals were included in this analysis.

For change in IFBF over winter, we also took a slightly different approach in a separate analysis. 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. To address effect of lactation on condition changes 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 were still lactating the subsequent spring. We used repeated measures ANCOVA with change in IFBF over winter with herd location, lactation status, and the interaction as dependent variables. Only prime-age animals were included in this analysis.

Annual variation within herd location.—We evaluated the effect of year within herd location on IFBF to determine if pooling across years was justified or whether herd year needed to be included as a covariate 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 location, and the interaction of the 2. Only the interaction term was relevant for this analysis because we were interested only in annual variation within locations. We used least squares means (LSMEANS, SAS Institute 1993) to identify which herds had significant year effects.

Adjusting LOIN for body frame size.—We evaluated the effect of body size (as measured by the girth circumference), body fat, and region on LOIN thickness. If body size influenced LOIN, an adjustment to the measurement would be necessary if using LOIN as an index of protein stores when comparing across populations or across animals varying greatly in size. Using all data from animals where body fat and girth measurements were collected, we conducted repeated measures ANCOVA for LOIN muscle thickness with girth (cm), region, IFBF and all possible interactions as independent variables. If the relation between girth and LOIN was significant with these other variables included in the ANCOVA, we used linear regression (PROC REG, SAS Institute 1988) of
LOIN and girth circumference to produce residuals of LOIN with effects of body size (i.e., girth circumference) removed. We added these residuals to the overall mean LOIN depth such that the adjusted LOIN data would be presented in the same range of values as originally collected. All subsequent analyses would use the new LOIN variable adjusted for body size (LOIN$_{adj}$).

**Autumn and Spring Nutritional Condition**

Using results from the preliminary analyses described above and using prime-age females only, we evaluated herd-level differences in nutritional condition between spring and autumn and tested for differences among herd locations. As an initial screening to identify differences in nutritional condition among herd locations, we used a 1-way, fixed effects ANOVA (with Duncan’s multiple range test) for each of our condition indices (IFBF, BM$_{NP}$, LOIN$_{adj}$ as dependent variables) with herd location as the independent variable. We ran separate ANOVAs for autumn and spring. We averaged condition estimates for individual animals across years such that no individual was included more than once in the data set. Because lactating females are substantially more sensitive to their nutritional environment over summer and early autumn than are non-lactating females (Clutton- Brock et al. 1982, 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.

**Seasonal Changes in Nutritional Condition**

To examine the extent to which different elk herds across the region were able to regain body condition lost over winter, we evaluated population level trends in changes of nutritional condition across summer and winter with respect to herd location. Only animals for which we had paired samples (autumn and subsequent spring or spring and subsequent autumn) were included in this...
analysis. Because the number of days between sequential captures among herds was not always the same, we compared differences in analysis results using change-in-condition expressed as daily change (which would account for differences in number of days between sequential samples) with total change over the season. We performed the analyses both ways, with the intention of presenting only the latter if results were significantly and biologically equivalent.

Using ANCOVA, we performed separate analyses for each condition index (change in IFBF [percentage points], change in BM$_{NP}$ [percent], and change in LOIN$_{ADJ}$ [cm] as dependent variables) with herd location, season (winter, summer) and their interaction as independent variables. For this analysis, the dependent variable was seasonal change either in winter or summer because, by including season (winter, summer) as an independent variable, we tested for a difference in change as a function of season (no difference would mean that winter losses equaled summer gains). We averaged the change estimates for individual animals across years such that no 1 animal was represented more than once in the data set. Pending a significant season effect, we partitioned the data by season and used Duncan’s multiple range tests to determine which herd locations gained different levels of condition over summer and which lost different levels of condition in winter. We then used LSMEANS to determine which, if any, individual herds were unable to replenish winter losses over summer (i.e., summer change in condition was significantly less than winter change in condition). We restricted the sample for statistical analysis to prime-age, autumn-lactating females only. This was true for winter change analysis (i.e., only females that were lactating at the beginning of winter were included) and for summer change analysis (i.e., only females that were lactating at the end of summer were included) so that comparisons were made on like individuals.

**Effects of Previous Condition on Current Condition**

Expecting that winter weather (temperature and precipitation) may influence IFBF dynamics over
winter, we first evaluated the 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 through February \((n = 10\) herds) or we asked biologists associated with each herd to delineate winter range boundaries \((n = 4\) herds). We obtained weather data for December, January, and February for the winter range of each herd for each year that nutritional condition data were collected 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 generate gridded estimates of annual, monthly and event-based climatic parameters (Daly et al. 1994). Weather data from PRISM were spatially explicit and presented for 4 km\(^2\) pixels across North America. We randomly selected 6 to 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 included average December through February precipitation (mm), the sum of December through February precipitation (mm), and average December through February minimum temperature (°C).

Using each herd x year as an independent sample \((n = 32)\), we evaluated the relationship between spring IFBF with each individual weather variable (average December through February precipitation, or the sum of December through February precipitation, or average December through February minimum temperature) plus previous autumn IFBF using multiple regression (PROC REG, SAS Institute 1988). We ran the same regressions using change in IFBF over winter as the dependent variable. We plotted relations between each of our independent variables and used CurveExpert 1.37 (Copyright© 1995-2001; Daniel Hyams) to help identify significant nonlinear relations between these variables and spring IFBF or change in IFBF over winter. If winter weather
was not significant, it was dropped from subsequent analyses.

To evaluate the direct effect of previous condition on current condition, we used repeated measures ANCOVA to evaluate the relation of autumn condition (IFBF, BM\textsubscript{NP}, and LOIN\textsubscript{ADJ} analyzed separately), herd location, and the interaction on subsequent spring condition and change in condition over winter. We repeated the analysis using region instead of herd location. 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, BM\textsubscript{NP}, and LOIN\textsubscript{ADJ} analyzed separately), herd location, and the interaction on both autumn condition and the change in condition across the summer.

**Modeling Effects of Multiple Years of Lactation on Performance and Nutritional Condition**

We then modeled the effect of multiple years of successfully producing a calf on individual females. We used the results from individual regressions (PROC REG) to calculate spring condition (IFBF, BM\textsubscript{NP}, LOIN\textsubscript{ADJ}) from previous autumn condition and autumn condition (IFBF, BM\textsubscript{NP}, LOIN\textsubscript{ADJ}) from previous spring condition. We developed these regressions for each region of our study, and thus modeled annual cycles of nutritional condition separately for each region. We assigned 4 levels of starting autumn condition representing the range of data found in our entire data set (IFBF: 2, 6, 10, 14\%, BM\textsubscript{NP}: 200, 220, 240, 260 kg, LOIN\textsubscript{ADJ}: 4.5, 5.0, 5.5, 6.0 cm) and modeled loss over winter and gain over summer for 5 consecutive years assuming the female successfully raised her calf each year. We plotted these values and included data from wild elk that managed to raise a calf at least 2 years in succession, as a qualitative comparison between predicted and observed multi-year nutritional condition cycles.
Effect of Long-Term Nutritional Status on Body Size

To examine whether summer nutrition levels have long-term effects on adult animal size (Skogland 1983), we evaluated the relation between autumn fat level of adult, lactating females, a measure of summer nutritional adequacy, and body size of adult females. We hypothesized that summer ranges that provided relatively high quality summer forage should support larger elk. Using a herd-level approach, we used linear regression to examine the relationship between BM_{IFF} and autumn IFBF, including lactating females because they are more indicative of summer forage conditions. We repeated this analysis using the same set of females and examined the relationship between girth circumference (cm) and autumn IFBF. Because Roosevelt elk tend to be larger than Rocky Mountain elk and we had data from only 3 herds of Roosevelt elk, we performed the analysis on Rocky Mountain elk only.

Pregnancy, Fetal Loss, and Lactational Infertility

To compare how pregnancy rates differed among herds and to evaluate whether pregnancy was related to autumn body condition, we calculated herd-level pregnancy rates (number of pregnant females/total number females captures) across years based on both spring and autumn samples. We calculated rates separately by lactation status and included prime-age females only. We removed 5 adult females from Wynoochee, WA, that appeared to be permanent non-breeders because we found no evidence of pregnancy for 3 consecutive years. 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 individual herds and regions, and to examine the relationship between IFBF and probability of pregnancy for each region. 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.

Using the same data sets (with spring and autumn evaluated separately), we explored the possibility of lactational infertility by including autumn lactation status (yes or no) and herd location along with autumn IFBF with all 3-way and 2-way interactions in the logistic regression model. If the interactions were not significant, we removed them from the model and simple effects were evaluated.

We also evaluated probability of breeding relative to spring IFBF in order to assess whether nutritional condition data collected during that time period could be related to either current reproductive success (breeding the previous autumn) or future reproductive success (breeding the subsequent autumn). We examined the relationship between spring IFBF and probability of current pregnancy and between spring IFBF and the following autumn pregnancy status for those animals for which we had successive data. We used logistic regression for both analyses and including herd location and its interaction with IFBF as covariates.

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 (>15-years old). Because so few animals were included in the old age category, we did not include region or location as a covariate. We ran separate analyses for spring pregnancy and autumn pregnancy status. Our focus was on the
interaction term which, if significant, would suggest that the best predictor of the probability of pregnancy for younger animals may be different than for older animals. Given our small samples of older animals and the effect this may have on logistic regression results (see Cook et al. 2011), we also used ANCOVA to evaluate the effect of pregnancy status (pregnant or not; autumn only) and age category on autumn body fat. Again, the interaction term (age x pregnancy status) was of interest. If significant, we used LSMEANS by region to find which age categories had significantly different autumn IFBF relative to pregnancy status.

**Condition and Pregnancy of Sub-Adults**

To examine the effects of nutrition on sub-adult elk, we compared body mass of calves and body mass and body fat of yearlings in spring and autumn among herds. 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**

Although we performed an initial global preliminary analysis on year effects to determine whether pooling across years was justified, we nevertheless scrutinized our data with a more liberal analysis to identify which factors might induce annual variation in body fat levels for those herds in which differences among years were found. Using only autumn lactating females, we performed individual ANOVA’s for each herd location to first identify significant year effects on autumn IFBF, spring IFBF, change in IFBF over summer, and change in IFBF over winter.

For any herd location for which the year effect was significant, we then added previous-season IFBF and its interaction with year as covariates in an ANCOVA. If year remained significant, this indicated that previous-season IFBF was not the cause of the year effect and that something else (e.g., differences in weather among years) caused the year effect. So, if year was
still significant, we replaced year with weather (precipitation and temperature in winter, precipitation in summer) and reran the ANCOVA. These analyses were conducted 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 herd locations.

For all analysis of statistical hypotheses, we used a significance level of $\alpha = 0.05$.

**RESULTS**

We captured and estimated nutritional condition and pregnancy of elk at least once in each of 21 herds in the Northwest and Rocky Mountain region (Table 1). We captured 861 individual elk over 2114 captures during late autumn (from early November to mid-December) and early to late spring (mid-February through early April). Data collected outside these 2 periods were censored from the analysis ($n = 106$ capture events from 2 herds).

**Preliminary Analyses: Confounding Influences of Age, Lactation Status, Year, and Body Size**

*Selecting age categories.*—Pregnancy rates tended to decline about 15 years of age for all Rocky Mountain regions (Fig. 2). Although pregnancy rates seemed to decline at age 13 – 14 years in the Coastal herds, sample sizes for these older age classes were $\leq 4$ (Fig. 2). We found an age effect on the relationship between autumn IFBF and probability of pregnancy for all females $>1$ year-old ($\chi^2 = 12.59, n = 729, P < 0.001$) and for all females $\geq 9$-years-old ($\chi^2 = 4.59, n = 389, P = 0.03$). Using the latter subset iteratively, age was not significant with all animals $\geq 12$ years removed ($\chi^2 = 0.07, n = 239, P = 0.80$), $\geq 13$ years removed ($\chi^2 = 0.12, n = 286, P = 0.12$), $\geq 14$ years removed ($\chi^2 = 1.39, n = 349, P = 0.24$), but approached significance when females $\geq 15$ years were removed ($\chi^2 = 3.6, n = 324, P = 0.059$). Therefore, we classified females $\geq 2$ but $<15$ 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 x herd location on IFBF of lactating females in autumn (age: $F_{(1,85)} = 1.53, P = 0.22$; age x herd location: $F_{(16,85)} = 1.33, P = 0.20$), LOIN (age: $F_{(1,84)} = 3.63, P = 0.06$; age x herd location: $F_{(16,84)} = 0.70, P = 0.79$), or BM$_{NP}$ (age: $F_{(1,77)} = 1.21, P = 0.27$; age x herd location: $F_{(16,77)} = 1.47, P = 0.13$). We also found no effect of age or age by herd location on spring IFBF (age: $F_{(1,51)} = 0.08, P = 0.77$; age x herd location: $F_{(16,51)} = 1.87, P = 0.06$), LOIN (age: $F_{(1,48)} = 0.84, P = 0.36$; age x herd location: $F_{(16,48)} = 0.71, P = 0.77$), or BM$_{NP}$ (age: $F_{(1,46)} = 0.06, P = 0.81$; age x herd location: $F_{(16,46)} = 0.91, P = 0.56$). Consequently, we only used prime-aged animals and did not include age as an independent variable for subsequent analyses unless otherwise noted.

*Influences of lactation status.*—We found that change in IFBF over winter was not affected by lactation status ($F_{(1,44)} = 0.71, P = 0.40$), herd location ($F_{(12,232)} = 1.66, P = 0.08$) or the 2-way or 3-way interactions of herd location, 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 lactation status in spring had no effect 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. Further, this effect did not change among herd locations (location x lactation interaction; $F_{(9,29)} = 0.00, P = 0.978$). Based on these results, we conducted subsequent analyses of changes in condition over winter without respect to over-winter 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 location \((F_{(12,295)} = 20.91, \ P < 0.001)\) influenced the change in IFBF over summer, but all 2-way and 3-way interactions were insignificant \((P > 0.08)\), 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, animals were classified according to lactation status at the time of autumn capture and all subsequent analyses for autumn condition levels and change in nutritional condition over summer were limited to lactating females only. We restricted analyses in this manner because those females not lactating in autumn are a heterogeneous group of elk that were either not pregnant or lost their calf sometime between parturition and autumn capture making analysis of this group difficult and mostly meaningless.

*Annual variation within herd location.*—Including only lactating females in our analyses such that we were comparing like individuals, we found no year x location 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 \((F_{(11,38)} = 0.90, \ P = 0.59)\). We did, however, find a year x location effect on change in IFBF over winter \((F_{(11,23)} = 2.62, \ P = 0.02)\). Significant yearly variation existed for Green and White River herds located in the WA Cascades and the Yakima herd located in central WA. However, if autumn IFBF was included 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 location x year was not \((F_{(11,22)} = 1.67, \ P = 0.15)\). Given these results and sample sizes that were too small to support valid within-location analyses for each year data were collected, we chose to
pool data across years within location.

Adjusting LOIN for body frame size.—The LOIN measurement was affected by girth ($F_{(1,991)} = 56.94, P < 0.001$), IFBF ($F_{(1,991)} = 13.62, P < 0.001$), and their interaction ($F_{(1,991)} = 8.77, P = 0.003$). Neither the remaining 3-way or 2-way interactions, nor the main effect of region were significant ($P > 0.51$). Given these results, we generated residuals from the regression of LOIN on girth circumference and added these values to overall mean LOIN depth (5.4 cm). This new variable adjusts LOIN for body size (LOINADJ) and was used in all subsequent analyses. We suggest that for future comparisons with these data or comparisons across populations, the original LOIN measurement should be adjusted for body size (i.e., girth circumference) with the following equation:

$$\text{LOIN}_{\text{ADJ}} \text{ (cm)} = 5.398 + [\text{LOIN} \text{ (cm)} – (0.036 \times \text{girth circumference (cm)} – 0.08360)]$$

Autumn and Spring Nutritional Condition

Although our sample sizes were small for many herds (10 to 40 elk per sampling period; Table 1), IFBF estimates for most herds were relatively precise within our lactating category, with SEs of ±0.5 to 1.5 percentage points of IFBF (Fig. 3). In every herd evaluated, lactating females in both autumn and spring were in poorer condition than their non-lactating counterparts.

For prime-age, lactating females in autumn and spring, our data indicated substantial variation in nutritional condition among regions and among herds within regions (Fig. 3A, 4, 5A). We found an effect of herd location on autumn IFBF ($F_{(16, 300)} = 15.59, P < 0.001$), BMNP ($F_{(16, 276)} = 11.73, P < 0.001$), and LOIN$_{\text{ADJ}}$ ($F_{(16, 286)} = 5.51, P < 0.001$). We also found an effect of herd location on spring IFBF ($F_{(16, 206)} = 7.99, P < 0.001$), BMNP ($F_{(16, 201)} = 14.15, P < 0.001$), and LOIN$_{\text{ADJ}}$ ($F_{(16, 216)} = 4.5, P < 0.001$).

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. The magnitude of variation among herd locations and regions tended to be less in spring than autumn, although IFBF still significantly varied among areas. Herd averages of spring IFBF levels of females that lactated through the previous growing season ranged from 2.2 to 3.2% in the Coastal plains and foothills, 0.6 to 5.6% in the Cascades, 2.8 to 9.3% in the inland Northwest, and 2.3 to 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, two herds showed a marked exception: 1) Chehalis Valley (Herd 3, Fig. 3B) where elk were captured from agricultural pastures in early March and 2) spring fat levels at Hanford (Herd 13, Fig. 3B) were markedly higher the second year of data collection that occurred after the fire.

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

On the other hand, LOINADJ across herds and regions showed a different pattern.
Evidently because LOIN is asymptotic at higher levels of condition (Cook 2000), we found fewer differences among herd locations in autumn. Our LOIN\textsubscript{ADJ} averaged ~5.4 cm in autumn with only a handful of exceptions (i.e., Mount Saint Helens, WA [Herd #9], Toketee, OR [Herd #12] and Rocky Mountain National Park, CO [Herd #18]) (Fig. 5A). Herd averages of autumn LOIN\textsubscript{ADJ} of lactating females ranged from 5.3 to 5.5 cm in the Coastal plains and foothills, 4.8 to 5.9 cm in the Cascades, 5.1 to 5.5 cm in the inland Northwest, and 5.0 to 5.4 cm in the Rocky Mountains (Fig. 5A). In spring, however, because animals were in poorer condition, their LOIN\textsubscript{ADJ} varied more among herd locations and within lactation status. Herd averages of spring LOIN\textsubscript{ADJ} levels of females that lactated through the previous growing season ranged from 4.9 to 5.9 cm in the Coastal plains and foothills, 4.8 to 5.7 cm in the Cascades, 4.9 to 5.3 cm in the inland Northwest, and 5.0 to 5.3 cm in the Rocky Mountains (Fig. 5B). Though we recommend using LOIN\textsubscript{ADJ} for any future, especially when comparing across populations, we also present the original LOIN data as a reference (Appendix A).

**Seasonal Changes in Nutritional Condition**

Gains in nutritional condition over summer and losses over winter varied among herds and among summer lactation categories (Fig. 6, 7, 8). In general, non-lactating females improved in condition during summer and declined in condition during winter to a greater extent than their lactating counterparts. In addition, females that lactated over summer typically failed, in most herds, to replenish fat lost the previous winter (Fig. 6A, 7A, 8A) whereas non-lactating females typically fully recovered fat lost the previous winter, particularly those that did not lactate at all (Fig. 6B, C; 7B, C; 8B, C).

The interaction between herd location and season (winter or summer) was unrelated to over-season changes in IFBF of lactating females ($F_{(12, 431)} = 0.89, P = 0.56$), but season ($F_{(1, 431)}$)
= 30.15, \( P < 0.001 \)) and herd location \( F_{(12, 431)} = 15.33, \ P < 0.001 \) were significantly related to changes in IFBF (Fig. 6A). These results indicated that losses in winter were unequal to (i.e., greater than) gains in summer, and that seasonal changes in IFBF differed among herds (Fig. 6).

For changes in BM\(_{NP}\) and LOIN\(_{ADJ}\) thickness, the interaction between herd location and season was not significant (BM\(_{NP}\): \( F_{(12, 389)} = 1.14, P = 0.33 \); LOIN\(_{ADJ}\): \( F_{(12, 358)} = 1.11, P = 0.35 \)), nor was the main effect of season (BM\(_{NP}\): \( F_{(1, 389)} = 1.64, P = 0.19 \); LOIN\(_{ADJ}\): \( F_{(1, 358)} = 2.03, P = 0.16 \)). We found that over-season change in BM\(_{NP}\) varied among herd locations (\( F_{(12, 389)} = 5.44, P < 0.001 \)), but changes in LOIN\(_{ADJ}\) (\( F_{(12, 358)} = 1.2, P = 0.28 \)) did not. Thus, for these alternative measures of nutritional condition, only seasonal changes in BM\(_{NP}\) differed among herds.

In all herds except 3 (Hanford, WA [Herd #13], San Luis Valley, CO [Herd #19], and Forks, WA [Herd #1]), females gained condition in summer and lost condition in winter. Herd averages of nutritional condition accretion during summer of lactating females ranged from 1.4 to 1.9 percentage points IFBF (6.9 – 11.5% BM\(_{NP}\), -0.06 – 0.31 cm LOIN\(_{ADJ}\) depth) in the Coastal plains and foothills, 2.9 to 6.5 points IFBF (9.9 – 16.7% BM\(_{NP}\), -0.03 – 0.51 cm LOIN\(_{ADJ}\) depth) gained in the Cascades, 2.0 to 3.3 points IFBF (11.1 – 12.5% BM\(_{NP}\), 0.07 – 0.14 cm LOIN\(_{ADJ}\) depth) gained in the inland Northwest, and -0.18 points IFBF (5.7% BM\(_{NP}\), -0.1 cm LOIN\(_{ADJ}\) depth) gained in San Luis Valley, CO (Fig. 6A, 7A, 8A).

Herd averages of nutritional condition lost during winter by females that were lactating the previous autumn ranged from 2.4 to 3.5 percentage points IFBF (9.1 – 10.7% BM\(_{NP}\), 0.06 – 0.25 cm LOIN\(_{ADJ}\) depth) lost in the Coastal plains and foothills, 4.6 to 6.5 points IFBF (12.5 – 17.1% BM\(_{NP}\), -0.13 – 0.54 cm LOIN\(_{ADJ}\) depth) in the Cascades, 3.8 to 5.3 points IFBF (13.5 – 15.3% BM\(_{NP}\), 0.29 – 0.42 cm LOIN\(_{ADJ}\) depth) in the inland Northwest, and 2.2 points IFBF (7.5% BM\(_{NP}\), 0.1 cm LOIN\(_{ADJ}\) depth) lost in San Luis Valley, CO (Fig. 6A, 7A, 8A).
Overall, these data indicate that winter loss exceeded summer gain and that magnitude of these effects was about equal among herds (based on the insignificant herd location by season interaction). However, within herd samples of lactating females were quite small in many cases, probably masking differences among herd locations. For example, our data suggest the 3 northern Cascades herds (Nooksack, WA, White River, WA, and Green River, WA) and Hanford, WA, were able to recover most of the condition lost over winter while the remaining herds were not, including Sled Springs, Wenaha, Yakima, Steamboat, and Toketee.

**Effects of Previous Condition on Current Condition**

Although winter conditions varied dramatically among herd locations and among years within herds (Table 2), we found no significant influence of winter weather on either spring IFBF ($F_{1,1} > 0.13; P > 0.36$) or change in IFBF over winter ($F_{1,1} > 0.12; P > 0.35$) when previous-autumn IFBF was also included as a covariate. We therefore did not include 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 0.37; $P < 0.04$) (Fig. 9A). This positive relation with slope significantly $> 0$ indicates that though fatter females lose IFBF more rapidly than thinner females, they still exit winter in better condition (i.e., a horizontal line would indicate complete convergence of body condition). Thinner females compensated over winter, but they nevertheless ended winter in poorer condition than their fatter counterparts (Fig. 9A).

There was no evidence of a herd location, herd location x autumn IFBF interaction effect ($F_{(12, 201)} \leq 1.39, P \geq 0.17$), region, or region x autumn IFBF interaction effect ($F_{(12, 201)} \leq 1.64, P \geq 0.180$) on the relationship between spring IFBF and previous-autumn IFBF. The insignificant region x autumn IFBF interaction on spring IFBF suggests that the rate of IFBF loss was
relatively consistent across regions, indicating that winter fat loss, for any given levels of previous-autumn body fat, was invariant among region, despite considerably different winter climatic regimes among them.

We obtained a similar result using over-winter change in IFBF as the dependent variable (Fig. 9A). Change in IFBF over winter was positively related to previous-autumn IFBF ($F_{(1,131)} = 26.24, P < 0.001$), herd location, ($F_{(12,232)} = 4.35, P < 0.001$), and to the interaction of herd location and previous-autumn IFBF ($F_{(12,131)} = 1.84, P = 0.049$). Using region in place of herd location produced similar results. As suggested by the significant interaction effect of spring IFBF with location or region, the relationship between change in IFBF across winter and previous autumn IFBF varied across herd locations was most likely due to a difference in starting autumn body fat across herds. Herds starting winter in better condition would lose more IFBF across winter than herds starting winter in poorer condition.

Similar patterns existed for changes in $\text{LOIN}_{\text{ADJ}}$ and $\text{BM}_{\text{NP}}$ over winter (Fig. 10A, 11A). For both, we found no evidence of an interaction between autumn $\text{LOIN}_{\text{ADJ}}$ or $\text{BM}_{\text{NP}}$ with herd location or region ($P > 0.14$) or a main effect of herd location ($P \geq 0.27$) or region ($P \geq 0.23$). However, spring $\text{LOIN}_{\text{ADJ}}$ and $\text{BM}_{\text{NP}}$ were significantly related to previous-autumn levels ($P < 0.001$) whether using herd location or region as a covariate. A regression of autumn condition ($\text{BM}_{\text{NP}}$ or $\text{LOIN}_{\text{ADJ}}$) on spring condition also produced positive slopes (range from 0.53 to 0.79 for $\text{BM}_{\text{NP}}$; range from 0.32 to 0.77 for $\text{LOIN}_{\text{ADJ}}$) indicating heavier/bigger cows in autumn, though losing BM more rapidly, were still heavier/bigger in the spring for each region (Fig. 10A) and females with larger $\text{LOIN}_{\text{ADJ}}$ depths in autumn had larger $\text{LOIN}_{\text{ADJ}}$ depths in the spring (Fig. 11A).

Ingesta-free body fat of lactating females in autumn, however, was unrelated to IFBF the
previous spring \( (F_{(1, 216)} = 3.02, P = 0.084) \), because thinner females in spring effectively compensated over summer (Fig. 9B). Autumn IFBF also was unrelated to the interaction of herd location and spring IFBF \( (F_{(12, 216)} = 0.79, P = 0.659) \), but was related to herd location \( (F_{(12, 216)} = 4.53, P < 0.001) \). As a check, we evaluated spring and autumn IFBF relations within regions, and found a very weak \( (r^2 = 0.03) \) but positive relationship between autumn IFBF and previous spring IFBF only in the Cascade region \( (P < 0.027) \) (Fig. 9B). Separating this analysis for North and South Cascades indicated a similar pattern (parallel regression lines) in the two sub-regions. Thus, our results indicate very little advantage of having higher IFBF levels in spring in terms of IFBF levels in autumn.

Using change in IFBF over summer in a similar analysis illustrates the considerable ability of thin elk in spring to compensate over summer while raising a calf (Fig. 9B). Change in IFBF over summer was negatively related to previous spring IFBF condition \( (F_{(1, 216)} = 146.94, P < 0.001) \), herd location, \( (F_{(12, 216)} = 2.72, P = 0.002) \), but was unrelated to the interaction of herd location and spring IFBF \( (F_{(12, 216)} = 0.89, P = 0.559) \). Using region in place of herd location produced similar results. The relation between spring and autumn IFBF of lactating elk varied across regions (Coastal: \( y = 4.85 – 0.779x, S_{yx} = 1.65, P < 0.001, r^2 = 0.49 \); North Cascades: \( y = 10.07 – 0.800x, S_{yx} = 2.52, P < 0.001, r^2 = 0.34 \); South Cascades: \( y = 7.95 – 0.814x, S_{yx} = 2.26, P < 0.001, r^2 = 0.37 \); Inland Northwest: \( y = 6.75 – 0.842x, S_{yx} = 2.79, P < 0.001, r^2 = 0.48 \); San Luis Valley, CO: \( y = 4.11 – 0.711x, S_{yx} = 2.19, P < 0.001, r^2 = 0.52 \) (Fig. 9B1). 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. 9B).

In contrast, our analysis indicated that across all herds and habitat conditions, lactating
females were unable to completely compensate for lower spring lean mass; females that had lower BMNP or LOINADJ measurements in the spring also had lower values in the autumn (Fig. 10B, 11B). Autumn BMNP or LOINADJ were significantly related to previous spring levels for both \(F(1, 192) = 50.72, P < 0.001; F(1, 190) = 18.59, P < 0.001\). For both dependent variables, neither herd location (BMNP = \(F_{(12, 192)} = 0.83, P = 0.62; \) LOINADJ = \(F_{(12, 190)} = 1.22, P = 0.27\)) nor the interaction of herd location and spring IFBF (BMNP: \(F_{(12, 192)} = 0.84, P = 0.61; \) LOINADJ: \(F_{(12, 190)} = 1.18, P = 0.30\) ) was related to autumn levels of BMNP or LOINADJ.

**Modeling Effects of Multiple Years of Lactation on Performance and Nutritional Condition**

Using the regression equations generated above on a regional basis to predict spring IFBF from previous autumn IFBF, and autumn IFBF from previous spring IFBF, we modeled the effect of multiple years of lactation on autumn and spring IFBF. Elk that were relatively fat at the beginning of the series quickly lost fat each year they raised a calf and achieved autumn IFBF equilibrium by the second year of raising a calf (Fig. 12). Elk that started the time series with relatively low IFBF levels gained fat until they reached the same equilibrium. Thus, no matter the starting fat levels, within a year or 2, all females would arrive at about the same autumn IFBF equilibrium level (Fig. 12). Evidently, the equilibrium levels are caused by increasing compensatory responses as nutritional condition declines.

Comparisons among regions illustrate other patterns. First, the autumn equilibrium IFBF level for lactating females varied almost 2-fold among regions, corresponding to the y-intercept of summer fat gain shown in Fig. 12, at: 6, 10, 7, and 5% IFBF for Coastal, Cascade, Inland Northwest, and for Rocky Mountain females. This suggests that the maximum amount of body fat lactating females can achieve over summer (or the height of the equilibrium in summer) was dependent on nutritional adequacy of summer habitat and its ability to support the population,
which varies among regions. Second, the level of the equilibrium IFBF during late winter/early spring is relatively constant from region to region, about 3 to 4% IFBF, indicating that winter weather and nutrition have less influence on annual cycles of IFBF than do summer weather and summer nutrition. Finally, although our \( n \) of elk that successfully raised a calf and lactated more than 2 successive years was very low, the data illustrate a tendency to mimic our modeled equilibrium (Fig. 13). At least, these data support (1) the model’s prediction of substantial differences in autumn maxima of IFBF at equilibrium among regions, (2) the ability for thinner animals to compensate over summer, and (3) the results showing equilibrium of autumn and spring fat levels will be reached within 2 years of raising a calf successfully. Finally, both our modeled and empirical estimates of autumn maxima indicate that the autumn equilibrium may fall below important thresholds that can affect reproduction and survival.

However, modeling the same multi-season pattern with respect to \( \text{LOIN}_{\text{ADJ}} \) and \( \text{BM}_{\text{NP}} \) suggests potential differences (Fig. 14). Most notably, as expected given previous results and the inability of a lactating female to regain lean mass over summer in a nutritionally inadequate environment, these models predict a longer time period before equilibrium is reached (Fig. 14). When the model approaches equilibrium evidently reflected nutritional adequacy of the summer range. Modeled \( \text{BM}_{\text{NP}} \) of North Cascades elk, the fattest and most productive in our sample, hardly decline at all from year to year and approached equilibrium at only 2 years of successive lactation. Modeled \( \text{BM}_{\text{NP}} \) of elk in the coastal foothills and the southern Cascades, some of the thinnest animals with the lowest pregnancy rates, lost more mass and required 4 years or more to achieve equilibrium. In addition, as with the regional difference in maxima IFBF levels in autumn, \( \text{BM}_{\text{NP}} \) maxima varied from a low of 202 kg in the San Luis Valley, CO, herd to 232 kg in the North Cascade herds.
The most apparent difference with the modeled LOIN\textsubscript{ADJ} is that animals with small LOIN\textsubscript{ADJ} measurements actually appeared to gain muscle depth over winter until equilibrium was reached (Fig. 14). Like BM\textsubscript{NP} and IFBF models, maxima equilibrium of LOIN\textsubscript{ADJ} varied across regions.

**Effect of Long-term Nutritional Status on Body Size**

We found a significant decline in herd level fat-free, ingesta-free body mass (BM\textsubscript{IFF}) as autumn condition of lactating females declined for Rocky Mountain females ($t_{(1,1)} = 2.65$, $P = 0.021$).

We found the same significant decline in herd level girth circumference as autumn condition of lactating females declines for both Rocky Mountain females ($t_{(1,1)} = 4.05$, $P = 0.002$, $r^2 = 0.58$).

Each 1 percentage point change in autumn IFBF corresponded to a 1.13 kg change in BM\textsubscript{IFF} (Fig. 15) or 1.35 cm change in girth circumference, and our data indicate that elk ranges that support fatter elk in autumn also support larger elk.

**Pregnancy, Fetal Loss, and Lactational Infertility**

Spring pregnancy rates of all prime-age cows regardless of lactation status ranged from a low of 68% to a high of 100% across herds (Table 3). Lowest pregnancy rates were found in the coastal herds of Forks, WA (65.9% in autumn, 70.0% in spring), Wynoochee, WA (58.2% in autumn, 64.1% in spring), the Cascades herds of Toketee near Roseburg, OR (68.4% in autumn, 76.9% in spring), and Mt. St. Helens, WA (72.1% in spring), and the Rocky Mountains herd of Rocky Mountain National Park (77.8% in autumn). The spring Toketee estimate was slightly overestimated because we avoided catching known non-pregnant females in spring. Other herds exhibiting depressed pregnancy rates (75-85%) included Springfield, OR, Yakima, WA, Wenaha, OR, and Willapa Hills, WA.

We found evidence of delayed breeding (not pregnant in late autumn, but pregnant in
spring indicating some females were not breeding until late October at the earliest) from Willapa Hills, WA (n = 1 of 27 capture events), Wynoochee, WA (n = 10 of 61 capture events), San Luis Valley, CO (n = 1 of 54 capture events), Hanford, WA (n = 1 of 35 capture events), Wenaha, OR (n = 4 of 60 capture events), Green River, WA (n = 12 of 128 capture events), and Sled Springs, OR (n = 4 of 137 capture events). Delayed breeding probably was more common, however, because our techniques were not designed to identify delayed breeding unless it was markedly delayed. Based on 417 samples for which we identified autumn and spring pregnancy, we found evidence of termination in 5 (1.2%) elk (a 6-year-old from Forks, WA, a 4-year-old who lost her fetus 2 years in a row in Wynoochee, WA, a 7-year-old from Sled Springs, OR, a 17-year-old from Wenaha, OR, and a 5-year-old from Green River, WA).

Based on data for those herds for which we had estimates of pregnancy and autumn fat, there was a significant effect of autumn IFBF on probability of pregnancy in prime-age cows (n = 390; P = 0.003; Fig. 16). This pattern held within each region for autumn pregnancy determination (Coastal: n = 114, P = 0.006; Cascades: n = 229, P = 0.011; Inland NW: n = 267, P = 0.007; Rocky Mtns: n = 70, P = 0.035) but reduced sample sizes produced variable results using spring pregnancy determination (Coastal: n = 71, P = 0.015; Cascades: n = 125, P = 0.476; Inland NW: n = 178, P = 0.010; Rocky Mtns: n = 160, P = 0.556) (Fig. 15). Lack of significance in the Cascades probably is due to autumn IFBF levels that were in excess of thresholds where body fat should be limiting to pregnancy (i.e., very few unbred elk with low body fat levels are represented in the logistic analysis; Fig. 16).

Within individual herds, sample sizes were too small to develop a logistic regression model (< 30 animals), thus we generally failed to find a significant effect of autumn condition within herds (P > 0.100 except Forks, WA, where P = 0.035).
We found no evidence of lactational infertility on spring pregnancy status (Fig. 17).

Neither the 3-way interaction between autumn IFBF, herd location, and autumn lactation status \((n = 390; \chi^2 = 3.42; P = 0.99)\), nor any 2-way interaction \((n = 390; \chi^2 \leq 3.62; P \geq 0.318)\) were related to pregnancy status. Removing all interactions to evaluate simple effects, autumn IFBF remained significantly related to pregnancy status \((n = 390; \chi^2 = 11.18; P \leq 0.001)\), but neither herd location \((n = 390; \chi^2 = 18.03; P = 0.16)\) nor autumn lactation status \((n = 390; \chi^2 = 0.42; P = 0.52)\) were related to spring pregnancy status. Using autumn pregnancy status nearly doubled the sample size \((n = 679)\) and yet produced the same results. 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.

We found no indication that spring IFBF overall \((n = 967; \chi^2 = 0.01; P = 0.91)\) or its interaction with herd location \((n = 967; \chi^2 = 25.28; P = 0.09)\) was related to current year pregnancy status. We also found no indication that spring IFBF overall \((n = 480; \chi^2 = 1.75; P = 0.19)\) or its interaction with herd location \((n = 480; \chi^2 = 9.11; P = 0.69)\) was related to future (subsequent autumn) pregnancy status.

We found that 68% of females \(\geq 15\)-years old were pregnant \((n = 116)\). Average age of non-pregnant females was not different than that of pregnant females (16-years old for both) in our ‘old-age’ category. We observed pregnancy in animals up to 19-years old, although 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 did not find a strong significant age category x autumn IFBF interaction to predict probability of pregnancy (autumn pregnancy: \(n = 749; \chi^2 = 3.49; P = 0.06\); spring pregnancy: \(n = 422; \chi^2 = 1.67; P = 0.20\)). In addition, we found no age category x autumn pregnancy status effect \((F_{(1,745)} = 1.98, P = 0.16)\) or age.
category effect \((F_{(1,745)} = 2.34, P = 0.13)\) 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. 18).

**Condition and Pregnancy of Sub-Adults**

We captured 46 yearlings but only estimated BMI_NP on 39 and pregnancy on 23 (capture efforts on 13 yearlings at Mt. Saint Helens were too early in the autumn for pregnancy determination; Table 1). Body mass of 11 yearlings in autumn averaged 161.9 kg (range: 146.2 – 177.4 kg) and 27% of these were pregnant (Fig. 19). Ingesta-free body fat averaged 6.1% in autumn (range: 1.5% – 9.2%). Body mass (BMI_NP) of 28 yearlings in the spring averaged 163.1 kg (range: 148.4 – 182.5 kg; Fig. 19), 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%) vs. 170.5 kg and 6.9% IFBF (range: range: 169 – 201 kg; 2.7 – 9.8%) for pregnant yearlings.

We found an effect of spring BMI_NP on probability of pregnancy in yearling females \((n = 28; P = 0.009)\) (Fig. 20). When compared to the curve generated by Cook et al. (2004a) in autumn using yearling females in captivity, the wild elk data were shifted substantially to the left indicating that the wild yearlings were able to become pregnant at much lower body mass than was predicted from the captive animal data. Because the captive animal data were based on autumn mass, we adjusted our spring BMI_NP estimates to reflect previous autumn BMI_NP by adding a conservative 10% to spring BMI_NP (Fig. 20). This adjustment produced predictions similar to Cook et al. (2004a). Probability of pregnancy began to decline when BMI_NP of yearlings in autumn was lower than 200 kg, and approached zero when BMI_NP of yearlings in autumn was lower than 160 kg (Fig. 20).
We were able to obtain weights on calves from 3 herd locations (Fig. 21A). Average mass of calves weighed during winter on winter feed grounds near Yakima, WA, was 97 kg ($n = 208$ [unknown mix of males and females]; S. McCorquodale, Washington Department of Fish and Wildlife, unpubl. data); average mass of calves weighed during October at Mt. St. Helens, WA, was 75 kg ($n = 9$; 2 males and 7 females); average mass of calves weighed during November at San Luis Valley, CO, was 81 kg ($n = 25$; 15 males and 10 females). In general, calf weights were as predicted by Cook et al. (2004a) based on body condition of female elk in the same herds (Fig. 21B). Calves at the Yakima, WA, feed ground were the exception with a higher proportion of calves occurring in the marginal and good categories than would have been predicted (Fig. 21B).

**Causes of Year to Year Variation**

Using a more liberal test for evaluating annual variation within herds (analyzing herds individually rather than globally), we found significant differences in IFBF of lactating elk among years during autumn only at Hanford, WA (Herd #13). There, autumn IFBF was depressed following a very large, early summer rangeland wildfire that removed vegetation from much of the summer range of this herd (appreciable vegetation growth failed to occur until autumn rains in October). 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 significant year effects at Yakima, WA (Herd #14; $F_{(1,17)} = 4.67$; $P = 0.045$), Wynoochee, WA (Herd #4; $F_{(1,22)} = 5.79$; $P = 0.025$), and Green River, WA (Herd #7; $F_{(5,30)} = 3.62$; $P = 0.011$). Including autumn IFBF as a covariate removed the year effect at all 3 herd locations ($P > 0.29$). With respect to change in IFBF
over summer, we found White River, WA (Herd #6; $F_{(2,18)} = 8.29; P = 0.003$) and Sled Springs, OR (Herd #16; $F_{(5, 31)} = 4.50; P = 0.034$) to have a significant year effect. Including spring IFBF as a covariate removed the year effects for both herds ($P > 0.13$). These data indicate that what first appears to be significant year-to-year variation on 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 body condition and reproduction in 21 elk herds over nearly 10 years, clearly demonstrated that summer and early autumn forage conditions across the areas in western U.S. we sampled, were typically inadequate and substantially reduced growth of juveniles and yearlings, fat accretion in adults during summer and autumn, pregnancy rates, and may have reduced probability of over-winter survival via carry-over effects of summer-autumn nutrition. These data also refute the common perception 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, it was the nutritional adequacy of summer ranges that influenced vital rates, herd productivity, and consequently, would be expected to influence population size. Evidently due to a variety of physiological adaptations, adult elk were able to reduce or even halt the decline in fat and lean tissue over winter as their body condition declined, despite relatively harsh winters in some areas, and those elk that exited winter in unusually poor body condition effectively compensated and caught-up with their fatter counterparts by autumn. Therefore, our data support the conclusion of Torbit et al. (1985) that the primary value of winter ranges to elk is as a holding area of relatively moderate weather and snow conditions to slow the loss of body condition until nutritious forage on summer ranges becomes
available again. In contrast, elk in most herds we studied were unable to overcome limits of inadequate summer nutrition on body fat accretion, pregnancy rates, and growth and development of calves and sub-adults.


Our data also indicate effects of nutrition are rarely catastrophic and obvious; instead, the influence of nutrition on elk populations largely occurred through subtle, but cumulative, effects on
a suite of animal performance attributes. Our data included estimates of nutritional condition, pregnancy rates, adult body size, yearling body size and pregnancy rates, and calf body size. All point to the same conclusion: summer nutrition was moderately to substantially inadequate in most herds sampled and operated via multiple pathways simultaneously. Thus, we found that annual cycles of nutritional condition and performance result from complex interactions between winter nutritional deficiencies, summer nutritional deficiencies, and mechanisms by which elk respond to these deficiencies. 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 nutritional condition estimates collected in autumn as indicators of the adequacy of summer range can be masked by several influences. First, whether females produce a calf and how long it survives during summer greatly affects over-summer energy balance and autumn nutritional condition (Clutton-Brock et al. 1982, Gerhart et al. 1997, Landete-Castillejos et al. 2003, Cook et al. 2004). Lactating elk that are replacing mass lost the previous winter, assuming 10% mass loss, require about 18,500 kcal/day of metabolizable energy (ME), about 50% more than an equivalent non-lactating female (Oftedal 1985, Cook 2002, Cook et al. 2004). When summer nutrition is inadequate, accretion of body fat by lactating females is substantially lower than that of non-lactating females; however, 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. 2004). Equally important, non-lactating females maintained on nutrition levels that are inadequate for lactating females (to the point of terminating reproduction) nevertheless are able to exit summer with body fat levels exceeding 15% (Cook et al.
2004a). Hence, females escaping the energetic costs of lactation are insensitive to the nutritional adequacy of their environment, and data collected from them provides little information regarding nutritional adequacy of summer range in most situations (Gerhart et al. 1997).

Estimates of nutritional condition of non-lactating females also are confounded because no validated approach exists to identify lactation history over the previous 5 to 6 months before autumn capture. A non-lactating elk may not have given birth that year or, if she did, there is generally no way to know how long she supported a calf (unless her calf was marked and monitored over summer and autumn). Using a tame elk herd with additional observations from wild elk whose calves had been marked, we have been unable to identify reliable, objective characteristics of the udder or fluid, if any, to identify time since weaning and capture (J. and R. Cook, National Council of Air and Stream Improvement, unpubl. data). Thus, females deemed non-lactating at the time of capture include a very heterogeneous group of animals in terms of their nutritional demand and expenditure over the previous several months, and analyses of their condition data would be ambiguous and potentially misleading (e.g., Piasecke et al. 2009).

Point estimates of nutritional condition may be confounded by condition in previous seasons. If spring IFBF greatly influences subsequent autumn IFBF, then change in IFBF over summer may be more indicative of summer range conditions than point estimates of ending autumn IFBF. Surprisingly, our analysis indicated that spring IFBF, no matter the herd location or region, had no significant influence on subsequent autumn IFBF (Fig. 9B), and thus estimates of autumn IFBF provided a more relevant indication of summer nutritional adequacy than change in IFBF over summer. Renecker and Samuel (1991) and Dale et al. (2008) reported similar patterns relative to juvenile growth. Spring levels of BMNP and LOINADJ in adults, however, did show a significant relationship with subsequent autumn levels (Fig. 10B and 11B),
and thus having sequential spring and autumn data for those variables may be more important to evaluate summer range effects on lean mass recovery.

Body condition levels of lactating adult females.— We found a substantial ability of adult females to compensate for relatively low levels of nutritional condition in spring despite the nutritional demands of pregnancy and subsequent lactation. Compensatory growth probably is an adaption that can improve reproductive success and winter survival in variable, stochastic environments (Renecker and Samuel 1991, Dale et al. 2008). Though often assumed to occur via hyperphagia (Wairimu and Hudson 1993, Dale et al. 2008), Cook et al. (1998) demonstrated winter compensatory responses in elk calves held on constant, sub-maintenance food during winter.

Compensatory responses during summer of small animals, particularly those still growing, is reasonably 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). Though it has also been reported for body mass in adult elk (Watkins et al. 1991) and red deer (Cervus elaphus; Suttie et al. 1983, Suttie et al. 1984, Adam and Moir 1985), ours is 1 of the first comprehensive data sets illustrating strong spring-summer compensation of nutritional condition in adult ungulates in a wild setting. Although we do not discount hyperphagia as a key method of compensation, compensatory responses also probably included physiological and anatomical pathways. A key way that large mammals adapt to energy restriction is by reducing organ size and thus energy expenditure and by reducing skeletal muscle size. Organs account for 70% of resting whole-body energy expenditure—size, and energy use, particularly of the liver, viscera, kidneys, and heart is highly dynamic in response to energy intake levels (Ramsey and Hagopian 2006). Substantial reductions in organ size and
skeletal muscle mass greatly reduce maintenance energy requirements (Ramsey and Hagopian 2006, Dale et al. 2008). Those animals that exit winter at the lowest levels of condition therefore are “primed” to outperform when nutrition improves, because a greater portion of energy they consume can be shunted to anabolic processes.

Our data cannot rule out the possibility that compensation in spring-summer may occur at the expense of perinatal viability and post-natal growth and development. While numerous studies have shown the effect of nutritional plane of females on milk composition, nursing bouts, and thus juvenile performance (Landete-Castillejos 2003, Cook et al. 2004a, Tollefson 2007), few have been able to evaluate how female body condition may influence calf performance independent of nutritional plane (i.e., given the same nutritional plane, will calves from fatter females perform better than calves from skinnier females?). In wild ungulate populations, results are inconsistent. Keech et al. (2000) found a positive relation between both calf birth mass and calf birth date relative to nutritional condition of female moose in March while Adams (2005) found female condition in autumn rather than spring to be related to calf birth mass in caribou. In Sled Springs, OR, a herd in our sample where up to 50% of females in a given year exited winter with IFBF <2%, Rearden (2005) found no relation of female condition in early spring with birth date or birth mass of calves. Whatever means animals use to compensate at this time of year, we found that this compensatory capability was a powerful attribute that greatly enhances recovery over summer of unusually thin elk in spring.

The upper limit of IFBF lactating females could achieve in autumn, however, varied among herds and regions and these levels were dependent on the nutritional resources available to them. Several important thresholds of autumn body fat for adults are relevant to survival and reproduction (Cook et al. 2004a). Good to excellent nutrition during summer should result in
body fat >13% to 20% by autumn for females that raise a calf over this time. Probability of breeding declines markedly and timing of breeding is delayed as autumn body fat declines below about 9% with breeding probability significantly reduced below 6% body fat (Cook et al. 2004a; see also Testa and Adams 1998). Over harsh and long winters, survival probability is significantly greater if elk leave the summer range with >13 to 15% body fat, and survival probability declines significantly at pre-winter fat levels <8 to 10% (Cook et al. 2004a).

Overall, our data revealed low to moderate autumn fat levels among elk herds and regions throughout much of the area in which elk were sampled (Fig. 3A). Fat levels of lactating females in autumn of most herds averaged 30 to 75% of levels that elk are capable of achieving if digestible energy levels in summer-autumn forage are not deficient. Only 1 herd in our sample (Nooksack in the Northern Cascades) averaged body fat levels indicating no substantial nutritional limitations (12 to 13%). In contrast, 11 of 17 herds for which we had autumn data averaged ≤8% body fat, levels suggesting important depressions in pregnancy probability and elevated winter mortality probability, assuming long and harsh winters. Our data indicated substantial differences in autumn body fat among regions, the highest in the Northern Cascade herds, and lowest in the coastal Roosevelt herds. However, body fat varied nearly as much within regions as it did among regions, probably because of substantial differences in vegetation, weather, and topography. This pattern was most evident in the Cascade region where a general trend of declining condition was evident along a north-to-south gradient (Figs. 1 and 3A).

We found similar trends for BM estimates. In general, autumn BM_{NP} ranged substantially below that of which female elk are capable achieving regardless of lactation state (Fig. 4). Female Rocky Mountain elk offered good nutrition during most of their early adult life are capable of reaching 275 to 325 kg (Hudson et al. 1991, Hudson et al. 1994). No elk in our sample exceeded
275 kg and only 2% of females were > 250 kg; these animals were primarily from the North Cascades of Washington and several coastal herds of Roosevelt elk. In contrast, 15% of the females in our sample, primarily from the inland NW herds and the San Luis Valley herd had autumn $BM_{NP} < 210$ kg, levels equivalent to yearlings under conditions without summer nutritional limitations. Our fat-free, ingesta-free analysis on $BM_{IFF}$ of lactating elk in autumn followed the same pattern and offered an explanation for these abnormally small-framed animals: areas with fatter lactating females in autumn also had larger-framed females within the Rocky Mountain subspecies. That is, better summer nutrition available while calves are growing increases growth rates, resulting in larger juveniles, sub-adults and ultimately adult body size (Fig. 15) (see also Clutton-Brock et al. 1982, Festa-Bianchet et al. 1996, Bigersson and Ekvall 1997).

We also found, regardless of region, a positive relation between spring $BM_{NP}$ and subsequent autumn $BM_{NP}$ for lactating females. These results suggest that nutrition during summer was inadequate for BM recovery except possibly in the Northern Cascades herds of Nooksack, White River, and Green River (Fig. 7). Because BM is a function of both lean mass and IFBF, these results alone cannot be used to evaluate lean mass recovery. However, we also found a positive relation between $LOIN_{ADJ}$ in spring and $LOIN_{ADJ}$ the subsequent autumn (Fig 11B) in lactating females. These results combined suggest an advantage of having more lean mass in the spring (which was a function of lean mass the previous autumn; Fig. 11A) and indicate an inability of lactating females in summer to fully recover $LOIN_{ADJ}$ lost the previous winter. Evidently, lactating females are more likely to recover IFBF over summer than $LOIN_{ADJ}$. However, $LOIN_{ADJ}$ actually declined in ¼ to ½ of lactating elk over summer (Fig. 11B), a considerably greater number of females than those that lost IFBF and BM over summer (except perhaps at San Luis Valley, CO) (Fig. 9B, 10B). In general, elk with larger $LOIN_{ADJ}$ were more likely to experience declines than
those with relatively small LOIN\textsubscript{adj} in spring, which may be the result of the aforementioned compensatory mechanisms. In other words, thin animals in spring were able to gain lean mass over summer because of reduced energy requirements when summer nutrition is limiting, whereas non-compensating elk in relatively good condition in early summer may actually lose lean mass over summer.

The inability for females to regain lean mass during summer if nursing a calf might indicate that dietary protein is more limiting on summer range than is dietary metabolizable energy. However, reviews of protein and energy deficiencies of large ungulates in western North America suggest that overall, dietary protein levels typically are adequate whereas dietary energy levels often are not (Cook 2002, Cook and Sleep, in review). Further, accretion of protein stores requires not only adequate dietary protein, but adequate dietary energy. Considerably more energy per gram of tissue is required for protein than for fat accretion (Robbins 1993). Our data show body fat levels of lactating elk far below what would be expected given adequate metabolizable energy levels in diets, suggesting significant deficiencies in dietary energy levels. Thus, we hypothesize that dietary energy is more limiting to lean mass recovery rather than dietary protein; when female elk are faced with deficiencies in metabolizable energy during summer, they sacrifice rebuilding lean tissues in lieu of rebuilding fat stores. In winter, fat provides far greater energy for survival than protein (Robbins 1993) during periods of energy shortage, making it more essential for winter survival than lean mass. The tendency for cervids to switch to obligatory fat storage at the expense of protein accrual in late summer when consuming diets deficient in dietary energy but with adequate protein has been reported for white-tailed deer (Verme and Ozoga 1980\textit{a, b}).

How this pattern of obligatory fat storage at the expense of protein accrual may affect productivity is unclear, but possibilities of how this might work arise from 2 anomalous herds in our
data: Toketee, OR, and Rocky Mountain National Park, CO. Both had substantially lower pregnancy rates than would be expected based on their autumn IFBF, and both had substantially lower LOIN\textsubscript{ADJ} than would be expected also based on their IFBF (Fig. 22). Lactating females in both areas had autumn fat levels of ~9.5% and LOIN\textsubscript{ADJ} of 5.0 cm vs. 5.4 to 5.5 cm for herds with similar levels of autumn IFBF (as IFBF declines, so does LOIN at an accelerating rate [Mitchell et al. 1976, Torbit et al. 1985, Watkins et al. 1992, Parker et al. 1993, Cook 2000]). Pregnancy rates of lactating females were 73% and 33% in Toketee and Rocky Mountain National Park (Fig. 16). Pregnancy rates at 9.5% IFBF corresponds to >90% for lactating elk (Cook et al. 2004\textsuperscript{a}), much higher than we observed in either of these herds or in the other herds in our sample with equivalent IFBF. Both of these herds spent winter at high elevations for their region (~1,500 m in Toketee and ~2,800 m in Rocky Mountain National Park). One possible explanation for their low pregnancy rates in relation to IFBF is that relatively late initiation of vegetation growth in spring may hinder recovery of lean tissue to a greater degree than fat by late summer, perhaps a strategy that favors winter survival over breeding/reproduction for that year. If this is the case, then elk in these settings may be in poorer overall condition in autumn than their body fat levels would suggest, and thus their pregnancy levels would be lower than expected.

**Nutritional Condition in Winter and Early Spring**

The value of nutritional condition estimates collected in spring as indicators of nutritional adequacy of winter range potentially might be masked by several influences including lactation status, previous autumn condition, and winter weather. Lactation during summer produces large energetic demands on females during the first few months after parturition, but Robbins et al. (1981) suggested that the value of nursing after late summer primarily is to maintain mother-calf bonds because amount of milk produced at this time imposes minor energy costs. Similarly, our analyses
indicated that stratifying animals by lactation status for analysis of nutritional condition dynamics in winter is unnecessary because lactation status over winter had no detectable effect on nutritional condition in winter.

However, IFBF in spring was a highly significant function of IFBF the previous autumn, and autumn IFBF was significantly affected by both nutritional adequacy of summer range and lactation status in late summer and early autumn (these same patterns held for our other measures of animal condition as well, BMNP and LOINADJ). Thus, very thin elk in spring indicated only that they entered winter in relatively poor condition, and elk in relative good condition in spring indicated only that they entered winter in relatively good condition. For elk across the regions of our study, nutritional condition in late winter or early spring, without concurrent data of autumn nutritional condition, was an unreliable and potentially misleading indicator of nutritional adequacy of summer or winter ranges.

We were surprised to find virtually no evidence indicating that nutritional condition in spring was influenced by winter weather and, more generally, by herd location or region, as long as nutritional condition the previous autumn was included as a covariate in our analyses. The relationships between autumn and spring nutritional condition were remarkably similar between regions varying widely in winter weather including mild dry winters, mild, wet winters, cold, dry winters, and cold, wet winters (Fig. 9A). For example, the fattest elk we sampled in late winter were from Yellowstone National Park, the area with the harshest winter weather in our study and, often, the coldest region in the U.S.

Holand 2003). We acknowledge that our results may be less applicable in areas further north where
the effects of winter weather are probably greater or during unusually harsh winters in our region.
Also, our analysis of winter precipitation and temperature may be inadequate to detect the
intricacies of winter weather effects (Knape and Valpine 2010). However, we submit that by using
a multi-regional approach and including autumn condition as a significant covariate, the lack of any
year, region, or winter weather effect on spring nutritional condition indicates that winter plays a far
less dominant role in female nutritional condition patterns, and thus productivity and probability of
survival, than previously believed. Our data indicate that coupling estimates of nutritional condition
taken in autumn with those taken in spring is very useful for identifying winter effects on nutrition
and reproduction, and for separating winter from summer effects. However, to date such coupling
using a repeated measures approach is very rare in the ungulate literature. To our knowledge, such
a repeated measures design has only been published by Dale et al. (2008) and Adams (2005) in
linked studies of mountain caribou in central Alaska, and their results strongly support our findings.
Adams (2005) reported, as we did, no effect of winter severity on body mass of adult caribou in
spring, and Dale et al. (2008) reported minor effects of winter but significant effects of summer on
body mass of sub-adult caribou in this region. Using multiple sampling periods around the annual
cycle (albeit without repeated measures), Hout (1989) documented the considerably greater
influences of summer nutrition than winter nutrition on caribou body fat and pregnancy based on
monthly lethal collections of caribou in northern Quebec, as did Gerhart et al. (1997), based on
lethal sampling in March through October in northern Alaska (see also Cameron et al. 2005). Using
the same techniques, however, Adamczewski et al. (1987) clearly illustrated that winter nutrition
was considerably more limiting to caribou than summer nutrition on Coats Island in northern
Hudson Bay. Whatever the case, studies that relied solely on late-winter or early-spring sampling
bouts had limited ability to identify adequacy of winter nutrition or separate relative influences of summer vs. winter nutrition.

*Body condition levels of adult females.*— Although spring fat of female elk was largely a function of autumn fat, our data also showed that elk entering winter in lower nutritional condition declined in condition significantly less than did elk that were fatter in autumn. The ability of some of the thinnest elk to tolerate winter with virtually no loss in condition, or even an increase in condition, attests to the adaptability of adult elk to poor food and harsh weather in winter. This adaptability evidently results from a variety of physiological responses to declining energy intake and increasing severity of weather. For example, whole-body metabolic rate of temperate and arctic ungulates evidently fluctuate with seasonal changes in forage availability (Nordan et al. 1968, Silver et al. 1969, Bandy et al. 1970, McEwan and Whitehead 1970, Lieb 1981, Argo and Smith 1983, Hudson et al. 1994). One of the first responses to declining energy intake is a decline in organ size. Organs account for about 70% of resting energy expenditure despite comprising only 10% of BM, so changes in organ size can have very large effects on energy needs with little changes in BM (Ramsey and Hagopian 2006). Energy expenditure of liver and viscera declines 30 to 65% soon after energy restriction begins, the first major response to energy restriction that can occur even before catabolism of adipose tissue begins. Declines in kidneys and heart soon follow. Overall, the body dynamically adjusts the amount of metabolically active tissue, mainly organs and skeletal tissue, to match energy intake levels (Kleiber 1947, Burrin et al. 1990, Robbins 1993, Fluharty and McClure 1997, Ramsey and Hagopian 2006). Although less well understood, energy expenditure at the cellular level also probably declines, mainly via declines in substrate oxidation, mitochondrial proton, and sodium-potassium ATPase activity (Ramsey and Hagopian 2006). Together, these changes greatly reduce maintenance energy requirements even during early stages of body mass
loss. Elk also may compensate for lower body condition in winter by increasing forage intake rates (Wairimu and Hudson 1993) or by reducing activity levels (Verme and Ozoga 1980b). Whatever the strategy may be, our data indicate that winter compensatory responses play an important role in the nutritional ecology of elk.

Despite our finding that spring body fat is primarily a function of body fat the previous autumn and that dynamics of nutritional condition over summer is little affected by body fat that spring, our data indicate many elk exit winter in very poor condition. In fact, substantial levels of mortality from winter starvation have been reported for 2 herds in our analysis, the Mount St. Helens, WA herd (Washington Department of Fish and Wildlife 2006) and, during harsh winters, Yellowstone National Park (Houston 1982). Probability of late winter starvation mortality will vary with winter weather and duration of harsh winter conditions, and Cook et al. (2004a) identified mortality thresholds in a captive setting by inducing nutritional deficiencies that simulated very harsh winter weather. In combination with highly deficient nutrition, adults below 2% IFBF and calves losing >17 to 18% BM in late winter were susceptible to mortality. Others reported that survival was reduced in female elk with >2% IFBF, suggesting elk may be predisposed to mortality even at moderate nutritional limitations (Bender et al. 2008). This may occur because elk at moderately low levels of condition may be less vigilant, less likely to flee perceived dangers, and may be more susceptible to parasites or disease (Davidson and Doster 1997, Fortin et al. 2004, 2005).

Herd averages in our sample exceeded 3% IFBF in all years, suggesting that elk herds were exiting winter, even in the worse cases, in sufficient condition to avoid starving (Fig. 3B). But herd averages may be misleading. Pooling all spring captures across years within a herd, between 14 and 33% of prime-age females in 10 herds sampled had ≤2% body fat at spring captures. Within a
single year, many herds had up to 50% of females exiting winter with ≤2% body fat. In addition, LOIN\textsubscript{ADJ} during winter or spring may also provide a threshold for the probability of winter survival; LOIN\textsubscript{ADJ} <4.4 cm in late winter suggests starvation may be imminent (Cook et al. 2004a). Five percent of prime-aged females in the Coastal, Cascades, and inland Northwest regions and 2% in the Rocky Mountain region had LOIN\textsubscript{ADJ} <4.4 cm. Associated average IFBF values for these animals were 1.7% for the Coastal and Cascades region, 1.9% for the Inland Northwest, and 1.0% for the Rocky Mountains. Whether animals in this range of body condition can survive winter depends on a number of factors, particularly weather severity and forage phonology at the time and soon after the measurements were taken. Regardless, females in our study that successfully raised a calf the previous summer-autumn were typically those in the poorest body condition (i.e., <2% IFBF or LOIN\textsubscript{ADJ} <4.4 cm) in late winter (Fig. 3B, 4B), and these elk were clearly at elevated risk of dying during late winter. Because of these tradeoffs between reproduction (i.e., successfully raising a calf) and winter mortality (i.e., dangerously poor winter body condition) in areas with inadequate summer ranges, predation on juveniles in summer may improve overwinter survival of adult females, a compensatory mechanism between predation and nutrition.

As with IFBF, we found that BM\textsubscript{NP} loss over winter was a function of previous autumn condition; elk starting the winter heavier lost more mass but ended winter heavier than their lighter counterparts (see also Parker et al. 1993, Allaye Chan-McLeod et al. 1999, Hudson and Haigh 2002, Festa-Bianchet and Côté 2008). Among individual elk, the range in BM change was −25% of their BM (up to 63 kg lost) to +2% BM. Herd averages ranged from −7% (San Luis Valley, CO) to −17% (Toketee, OR) of their body mass over winter. More than 50% of the females in our sample ended winter at BM\textsubscript{NP} <200 kg and only 8% ended winter with BM\textsubscript{NP} >220 kg. We saw the same regional trends in spring as in autumn, herds from the southern Cascades and inland Northwest
exited winter with the lowest BM_{NP} and herds from the northern Cascades and Coastal areas had the highest BM_{NP}.

We found a substantially greater tendency of elk to increase LOIN_{ADJ} over winter and reduce LOIN_{ADJ} over summer compared to changes in IFBF during the same time periods (compare Fig. 11A, B to 9A, B). Over winter, about \frac{1}{3} of elk sampled in autumn and the subsequent spring increased LOIN_{ADJ}, whereas IFBF and BM increased in <4 elk. On average, those elk that entered winter with small LOIN_{ADJ} were most likely to increase LOIN_{ADJ} by spring. Several explanations may exist for these winter patterns. First, unlike summer when elk seem to preferentially accrue fat over lean mass, in winter, elk may preferentially spare lean mass, particularly that of skeletal muscle, to a greater degree than fat. Muscle function and strength decline as a result of protein loss (Harlow et al. 2001), thus retaining skeletal muscle mass to the extent possible confers survival advantages as winter progresses (Lohuis et al. 2007). Though little work on this topic has been conducted on large ungulates to our knowledge, substantial work in hibernating bears and other organisms that deal with long periods of little or no food may provide insight. During periods of winter anorexia, animals rely on fat rather than protein as an energy source to the extent possible. Bears are extraordinarily effective at sparing protein in skeletal muscle, or even synthesizing skeletal muscle (as our data suggest may occur in some elk), by using protein from other endogenous sources (such as organs), greatly reducing protein synthesis and breakdown rates, and by recycling virtually all urea and thus nitrogen arising from protein catabolism. Ruminant ungulates do not hibernate, but they are highly effective at recycling urea and nitrogen, and the relatively high rates of fat catabolism coupled with very low rates of protein catabolism or even synthesis are similar to that reported for bears (Lohuis et al. 2007). Thus our observations that elk may switch from an obligate fat storage
mode in summer and autumn to a state in winter where protein is spared and fat is catabolized relatively rapidly has empirical support.

Second, the rate of catabolism of lean tissue during negative energy balance increases compared to the rate of fat catabolism at very low levels of condition and recovery of these endogenous tissues tends to work in the opposite direction (Robbins 1993, Cook 2002). Thus, if forage conditions were beginning to improve in late winter before we captured the elk in spring, then elk may have increased lean mass to a greater extent than fat at the time of capture. Finally, assuming that elk with small $\text{LOIN}_{\text{ADJ}}$ in autumn also have less metabolically active tissue (organs and skeletal muscle) in autumn, then their daily metabolic requirements in winter would be lower (Ramsey and Hagopian 2006). Hence, they would less frequently experience a negative energy balance over winter, lose less $\text{LOIN}_{\text{ADJ}}$, and, particularly if the above statements are true, these animals might have increased $\text{LOIN}_{\text{ADJ}}$ by the time they were captured in early spring. Reverse patterns have been reported in caribou, where animals gain fat over winter but lose lean mass, probably because lichens, very high in energy and deficient in protein, dominate in the diet (Adamczewski et al. 1987, Huot 1989). These examples in caribou may not explain the tendency to increase lean mass as fat declines that we observed in many elk but do demonstrate that relative levels of protein and energy in diets may affect changes in overwinter body composition.

**Annual Cycles in Nutritional Condition**

One of the fundamental debates regarding nutritional influences on populations, and 1 of the most important to resolve if managing nutritional resources is to be a practical goal, involves the seasonality of nutritional limitations on ungulate populations (Skoglund 1983, Post and Klein 1999, Cook 2002). Though our data indicate greater effects of summer nutrition, it is probably most
realistic that summer and winter nutrition interact to some degree to influence population dynamics. Others have attempted to integrate influences of winter and summer nutrition to predict their combined effects on vital rates (Cameron 1994), and our equilibrium model represents another step to conceptually, at least, understand how such integration might work.

*The Equilibrium Hypothesis.*—Nutrition in winter, spring, and summer most likely interact in complex ways such that their relative effects vary among ecological settings and herbivore densities. Much of this complexity arises due to several attributes of the animal, the interplay among pregnancy, lactation, and nutrition on nutritional condition, the ability of animals to compensate in a variety of ways to their nutritional environment, and the relation of animal performance in 1 season to its productive stage and nutritional condition in previous seasons, a carry-over effect (Cameron 1994, Cook 2002, Parker et al. 2009).

In temperate ecosystems with seasons of nutritional deficiency, animals must at least balance their total endogenous energy levels over time, or they will eventually die (Albon et al. 1983, Moyes et al. 2006). In settings where nutrition is inadequate to balance the annual energy budget of females that successfully raise a calf, endogenous energy levels will decline. Depending on starting nutritional condition and how severe the nutritional inadequacy, assumptions are that at some point over time females that successfully raise a calf each year eventually will have to cease reproduction (Festa-Bianchet and Côté 2008) and recover her condition, or die. This has been described as a ‘step-down’ process and was demonstrated with caribou where females lost 10-13% of body fat each year she successfully raised a calf (Reimers 1983), until reproduction failed (Cameron 1994). At least with elk, reproductive pauses are unnecessary on herd ranges where nutrition is adequate. Cook et al. (2004a) demonstrated that when summer nutrition is adequate, female elk have no difficulty providing milk and completely replenishing endogenous reserves lost
the previous winter in time to breed successfully and early in the breeding season.

Depending on how nutrition on winter and summer ranges interact, however, several possible seasonal patterns of nutritional condition might be expected for females that succeed in raising a calf across multiple sequential years: (1) adequate nutrition in summer and winter (i.e., adequate winter nutrition refers to winter ranges and weather conditions in which loss of nutritional condition is not excessive), (2) inadequate summer nutrition and adequate winter nutrition such that animals are unable to recover tissue lost the previous winter, (3) adequate summer nutrition and inadequate winter nutrition (very harsh winters causing severe loss of nutritional condition such that animals cannot recover the following summer despite “adequate” summer nutrition), and (4) inadequate summer and inadequate winter nutrition. How ruminant herbivores respond to these scenarios physiologically and behaviorally may greatly affect viability of populations and their resilience to predation and competition from other organisms.

Based on the literature, if nutrition on an annual basis is inadequate, we would predict 3 possible scenarios reflecting differential influences of summer range, winter range, or both on productivity of females. First is the hypothesis that there exists complete convergence of nutritional condition over winter such that spring IFBF is unrelated to previous autumn IFBF, even if autumn IFBF varies widely among animals. Though this scenario is not reported often in the literature, Clutton-Brock et al. (1983) found that rump fat (g) and kidney fat (g) of lactating and nonlactating red deer hinds on Rhum, Scotland, converged over winter so that the 2 groups were in equivalent condition by late spring. Thus, differences in autumn nutritional condition would fail to carry-through to the subsequent spring. This scenario still allows for reproductive pauses given inadequate nutrition on the summer range. However, because all animals would exit winter at the same level of condition regardless of autumn body fat, being fatter in autumn because of a
reproductive pause the previous autumn would fail to enhance late winter survival probability and would fail to enhance fetal development during the third trimester. This scenario seems particularly unrealistic in arctic ungulates that depend on fat and protein stores to support fetal growth in late spring (Parker et al. 2005) before vegetation growth begins. Whatever the implications, based on large sample sizes collected in a wide variety of ecological settings and using sequential repeated measures of individuals rather than herd- and season-level group means, our data unambiguously refute the hypothesis that nutritional condition of elk completely converges over winter. Findings of convergence in other studies may be an artifact of inaccurate body fat estimations (e.g., collecting body condition scores without adequate training), use of condition indices with limited range of usefulness (e.g., subcutaneous fat indices), or analysis conducted on herd averages rather than paired sampling of individual animals (Piasecke 2006).

The second scenario in which nutrition is inadequate, the step down hypothesis (Cameron 1994, Parker et al. 2009), assumes little or no congruence of nutritional condition between autumn and subsequent spring (or spring and autumn). This hypothesis generally assumes that change in nutritional condition of fat and thin animals is equal over winter and, similarly, gain in nutritional condition over summer varies little between fat and thin animals. Thus, it predicts nutritional condition will decline approximately equal amounts each year the female raises a calf until her level of condition fails to support successful breeding or over-winter survival (Cameron 1994). This scenario should occur whenever nutrition in summer is inadequate to support lactation and simultaneously support recovery of all tissue catabolized the previous winter (e.g., where winters are mild and summer nutrition is poor, or even where summer nutrition is quite good but nevertheless unable to compensate for very harsh winters).
Our data suggest this step-down scenario is incomplete in that it fails to include the compensatory capabilities of elk in winter and summer. These compensatory capabilities introduce 2 defining attributes crucial for understanding nutritional ecology of these animals. First, compensation reduces the rate of decline in nutritional condition as forage conditions decline and accelerates the rate of improvement in relatively thin animals when nutrition improves, such that very thin animals greatly outperform fatter animals in winter or summer. It is primarily this attribute that terminates the step-down procession of the model and enables females to achieve nutritional condition levels in equilibrium with their nutritional environment after a year or 2 of seasonal oscillation (Fig. 12).

Second, compensation strategies also greatly ameliorate influences of winter weather and nutrition such that winter has little influence on annual cycles of nutritional condition and reproduction. This is because adult elk are able to (1) greatly reduce or even halt the decline in condition, despite even relatively harsh winters, such that late winter starvation mortality generally is quite rare, and (2) for those elk that exit winter in unusually poor shape, compensation allows these animals to recover more quickly than their fatter counterparts. In fact, elk in our regions of study were largely able to survive in winter equally well (i.e., remained above starvation thresholds in late winter) over a remarkably wide range of winter conditions and do so in a way that greatly reduced the winter’s negative influences on subsequent reproductive performance. In the herd we sampled that experiences substantial late-winter starvation of adult elk (Mount St. Helens, WA [WDFW 2006]), our autumn fat data suggests these mortalities occur due to unusually low levels of autumn body fat in lactating females (<5% IFBF), not because winters are unusually harsh.

During summer, the compensatory recovery of elk exiting spring eliminated most
lingering effects of previous winter weather and nutrition and previous summer lactation and nutrition. However, we were able to show that the intercept of the relation between spring IFBF (x-axis) and autumn IFBF (y-axis) significantly varied across herds and region (Fig. 9B). This intercept is approximately synonymous with the maximum level of IFBF that could be achieved by lactating elk by autumn and represent the upper limit of nutritional condition elk can achieve given the nutritional resources available to them. In fact, the intercept for each region closely matches the average autumn body fat of lactating elk in each herd. These maximum levels ranged from a low of 5.9% in the Coastal region and San Luis Valley, CO to 10.8% in the north Cascades region.

Also unlike the complete convergence or step-down models, our equilibrium model does not necessarily predict that females periodically must forego breeding in nutritionally inadequate environments. Instead, the female experiences a decline in condition each year she succeeds in raising a calf but only for a year or 2, because compensatory responses reduce or preclude further loss in condition. The key is whether this “equilibrium” level of condition in autumn is high enough to avoid reproductive pauses and if the equilibrium level in spring is adequately high to avoid elevated susceptibility to overwinter starvation.

The autumn equilibrium level of nutritional condition provides substantial information regarding nutrition’s likely influence on vital rates and other performance attributes of ungulate populations, as long as there is a frame of reference for interpreting the biological implications of the equilibrium levels. Integrating captive and wild elk studies helps provide this reference. For example, autumn body fat levels of about 12% are indicative of herds that are little influenced by nutritional limitations, levels ≥9 to 10% are indicative of herds where lactating females rarely need to avoid breeding, and levels ≤6-7% are indicative of herds where lactating females often
resort to reproductive pauses (Cook et al. 2004a). Captive elk experiments indicate a very strong relation between summer nutrition and autumn body fat, and thus autumn estimates of body fat becomes a useful surrogate of summer nutrition to predict not only pregnancy rates, but size of calves and yearlings in autumn, yearling breeding probability, delays in breeding dates, and other attributes (Table 4; Cook et al. 2004a: 55). Our data from Mount St. Helens, where autumn body fat of lactating elk was about 5% and the lowest level we documented, possibly suggest a threshold linking autumn body fat to incidence of late-winter starvation, the 1 herd for which winter starvation was often documented (WDFW 2006).

In striking contrast, spring lows of nutritional condition predicted by our equilibrium model were largely unaffected by winter weather and winter nutrition and thus spring nutritional condition was nearly constant among regions (approximately 3-4% IFBF; Fig. 12), precluding any predictions of thresholds. That spring nutritional condition was unaffected by winter weather, location, or year corroborates the model’s predictions of constant spring lows among regions.

Evidently, annual cycles of LOINADJ and BMNP (i.e., lean mass) operate similarly to body fat in respect to summer and winter nutrition. The difference is the time required to reach equilibrium. By the second year a female supported a calf, regardless of region, her IFBF equilibrated mostly because of the complete convergence over summer of IFBF regardless of spring condition. Our indices of lean mass, however, showed that lactating elk in some herd locations failed to recover during summer the lean mass catabolized the previous winter. At some point, however, the amount of metabolically active tissue and maintenance energy requirements of the animal will decline year-over-year until it equilibrates with summer nutrition levels, as does IFBF, but more slowly. Thus, time to reach equilibrium varied relative to the
nutritional adequacy of the summer range. Herds in the North Cascades demonstrated
equilibrium at 2 years of lactation, whereas herds subsisting on summer ranges with lower
nutritional adequacy required up to 4 to 5 years to reach equilibrium. In other words, we suspect
that the obligate fat storage in late summer/early autumn favors accretion of fat rather than
accretion of lean tissue on nutritionally inadequate summer ranges, and thus it takes more years
for lean mass to equilibrate in females that successfully raise a calf year after year.

We caution that our regional equilibrium models are intended to offer insight into the
relative roles of summer and winter influences on productivity patterns in elk herds. These
should not be used to calculate spring and autumn fat patterns in individual herds because each
summer range will have its own summer maxima. Herbivore density, micro-habitat use by
individual animals, and stochastic summer weather events particularly in dry ecosystems
probably also influence the summer equilibrium levels. A bottom up approach to calculate these
equilibrium levels, particularly if it accounted for herbivore density, would be useful for
management. However, to our knowledge, no such protocols exist.

**Summer Limitations – Evidence in Performance Estimates?**

*Pregnancy rates of prime-aged females.*— Perhaps one of the most frequently
documented effects of inadequate nutrition is its effect on pregnancy rates. Significant relations
between body fat levels and pregnancy rates are well-documented across a variety of ungulate
species (e.g., Trainer 1971, Dauphiné 1976, Reimers 1983, White 1983, Cameron et al. 1993,
2001a, Cook et al. 2004a). In addition, inadequate nutrition in the months before the breeding
season may delay the timing of conception and desynchronize the birth pulse the following
spring, making late-born calves more susceptible to predation (Adams et al. 1995, Singer et al.

For prime-aged elk, Cook et al. (2001, 2004) 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 a high probability of breeding. Thus, pregnancy rates much below 90 to 95% of prime-aged elk most likely indicate substantially inadequate summer nutrition. Our data indicated at least two-thirds of the herds 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 region confirming what our nutritional condition data suggest, important 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. 2004), we observed pregnancy rates higher and lower than predicted based on body fat in many of our free-ranging elk herds (Fig. 16). 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. 1997, National Council for Air and Stream Improvement 2007). Because of this complexity, the use of herd-level pregnancy data alone as an indicator of habitat’s nutritional adequacy potentially 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 4 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 (e.g., a pulse of high quality forage available at or near the time of breeding may increase the chance of pregnancy [Gerhart et al. 1997]). For example, many of the herds we sampled in drier communities of the inland northwest and Rocky Mountains in particular have higher pregnancy rates than may be predicted by their late autumn body fat levels. These areas, given adequate precipitation, frequently experience vegetative regrowth events in autumn (Westenskow-Wall 1994) that may provide a caloric boost enabling thinner females to breed.

Second, lactation before or during the breeding season may confound the relation between nutrition and pregnancy in 2 ways: (1) the strongly elevated nutritional demands required to support lactation greatly hinder fat accretion prior to 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. 1997). We found no evidence that lactating females had a lower probability of breeding over any level of condition than their non-lactating counterparts (Fig. 18) and although not statistically significant, our data suggested the opposite (Fig. 18). This latter finding is most likely an artifact of both sample size and timing of capture. Very few non-lactating females exited summer with IFBF values <10% unless something was physically wrong with them or they had lactated at least some portion of summer. More than likely they had been lactating at the time of breeding, but ceased before we captured them and thus were classified as ‘non-lactating’. However, in herds where calf mortality was 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 (Verme and Ullrey 1984). Thus, relatively high predation, particularly in summer, effectively masks the effects of nutrition on reproductive performance (i.e., overall herd fat levels may be higher in herds hard-hit with predation than those experiencing little predation, a compensatory effect) (Verme 1962, Verme and Ullrey 1984, Gerhart et al. 1997).

Third, 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 1990), though recent research on leptin, a hormone primarily produced in fat tissue, demonstrated its role in signaling nutritional status to the central reproductive axis of mammals (Zieba et al. 2005). Instead, plasma levels of metabolic substrates such as glucose, triglycerides, and/or certain amino acids play a direct causal role (Bronson and Manning 1990, Molle et al. 1995, 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. 1997). We add that the oft-cited relation between pregnancy and body weight in adult females is probably spurious and occurs primarily because weight and body fat are inter-correlated, not because weight per se controls ovulation in adults (Cook 2002: 296).

In addition, breeding occurred as much as 3 months before our autumn nutritional condition data were collected and thus it is possible that females lost IFBF between the breeding season and when captured in our study. Reviewing as many data sets as were available, Cook et al. (2011) found that animals did indeed lose IFBF over the course of autumn (Table 5). These results indicate that variable sampling dates over autumn may greatly confound IFBF-pregnancy relations because IFBF evidently declines in many herds over autumn and because the rate of change in IFBF over
autumn evidently can be quite variable (Table 5).

Fourth, nutrition levels just adequate to maintain high pregnancy rates are 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 nutritional limitations that in all probability have a suite of detrimental effects on animal performance. Depressed pregnancy rates also likely indicate 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, and in fact is less sensitive to nutritional deficiencies than many of these other performance attributes (Cook et al. 2001a, Cook et al. 2004a). Thus, for the purpose of evaluating nutritional adequacy of the habitat, comparisons of pregnancy rates among herds may be misleading, especially in those herds with high predation rates on juveniles in summer. Barring disease or other such effects, low pregnancy rates clearly indicate nutritional deficiencies, especially in summer. High pregnancy rates, without corroborating data, provide little reliable inference of nutritional adequacy in summer or any other season (Cook et al. 2001a).

Finally, fetal loss either from resorption early in the pregnancy or abortion later in the term was virtually nonexistent in our data, as was reported in captive elk studies where pregnant cows were fed highly deficient winter rations (Cook et al. 2001a, Cook et al. 2004a). Fetal loss only accounted for 1% of our sample and most notably, in those cases where vaginal implants were inserted for other study objectives (n = ~220 females from Toketee, Steamboat, Sled Springs, Wenaha, and White River herds), no evidence of fetal loss was found between the time of capture in March or early April and calving (B. Johnson and D. Immell, Oregon Department
of Fish and Wildlife, and D. Vales, Muckleshoot Indian Tribe, unpublished data.). Despite growing literature alleging that factors such as nutritional condition, predation risk (Creel et al. 2007, 2009, Cunningham et al. 2009), and capture drugs may cause fetal loss, 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 very poor condition by late winter.

**Pregnancy rates of ‘old-age’ females.**—Our data suggest that IFBF more than chronological age was most likely related to pregnancy status in elk ≥15-years old (Fig. 18). 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 on years they lactated compared to younger animals resulting in more frequent reproductive pauses. Combined, these results suggest an interaction between age and nutritional condition (in that older animals have a harder time recovering nutritional condition while supporting a calf) may be more responsible for declining pregnancy rates in animals ≥15-years old, rather than any physiological changes related to chronological age.

**Juvenile growth and development.**—Body mass for yearlings in autumn captured 1 to 3 months after the breeding season ranged from 146 to 177 kg (\(\bar{x} = 161\) kg); 65 – 80% of levels they are capable of attaining if summer-autumn nutrition is not limiting (Cook et al. 2004a). Our data was 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, 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 substantially lower than the 220 kg reported by Blood and Lovaas (1966) for a yearling female in Manitoba.

The largest yearlings in our sample occurred in the regions with the largest adult
females, in the North Cascades of Washington. Simulating winter nutritional regimes in which calves were forced to lose 15-25% of their BM, 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 the severe winter nutritional limitations, good to excellent nutrition during their first 2 summers of life resulted in autumn BM of yearling females typically >185 kg (up to 225 kg) and pregnancy rates at nearly 100% (Cook et al. 2004a; Table 4). Dale et al. (2008) found similar patterns with young caribou and concluded that status at the end of winter had relatively little influence on subsequent body size and no influence on growth during the subsequent summer. They suggested that growth rates during summer were not at physiological maximums during summer but rather a function of the foraging environment.

Pregnancy rates of yearlings, pooled by region, ranged from 17 to 50% (average 30%), higher than would have been predicted from their BM based on experiments in captive trials (Fig. 20; Cook et al. 2004a). Our body mass estimates and pregnancy rates fell within the ranges reported for yearlings in other herds (Greer 1968, Piasecke et al. 2009). However, like adults, yearling pregnancy probably is affected as much or more by energy balance than BM or body fat per se. Thus, comparing differences among herds using logistic regression based body mass or IFBF can be misleading or flawed depending on sample sizes, influential data points, and patterns of BM or IFBF change between the breeding season and time of capture later in autumn or early winter (Table 5; Cook et al. 2011). Regardless, low BM of yearlings relative to their potential and reduced pregnancy rates provide evidence of summer nutritional limitations.

Juvenile growth is highly sensitive to nutrition (Price and White 1985, Jiang and Hudson 1994, Cook et al. 1996, 2004a). Although we had BM estimates of calves for only 3 herds, these data provided some of the most striking evidence of strong summer nutritional limitations that
we collected. In every herd for which we had calf data, 30 to 90% of calves weighed less than 90 kg, and nearly all calves were < 110 kg (Fig. 21; Table 4; Cook et al. 2004a). Captive studies demonstrated that elk calves obtain mid-autumn mass of 120-140 kg in the absence of summer nutritional limitations (Jiang and Hudson 1994, Hudson et al. 1994, Cook et al. 2004a). Blood and Lovaas (1966) reported mean BM of 2 wild calves (1 male and 1 female) of 133 kg in Manitoba. However, in Northwest Wyoming, Dean et al. (1976) reported elk calf BM of 101 kg and 110 kg in females and males during December and January on winter feed grounds, somewhat larger than we found but still substantially below their potential.

Experiments to identify relationships between BM 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 < 85 kg in autumn were highly susceptible to overwinter starvation mortality when in environments simulating 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).

Other Influencing Factors
We acknowledge 3 additional factors with the potential to influence aspects of our analyses and conclusions, or future interpretations of body condition collected from free-ranging elk. First, low autumn IFBF levels and depressed pregnancy rates in the elk herds we sampled may have been caused by the interaction between herd density and the nutritional adequacy of summer range. The estimates of density we could obtain for the herds in our study in most cases were rough estimates or even guesses, far too general in our opinion to justify including in our analysis. However, most of the herds in our sample were subjected to typical hunting levels and
substantial predation pressure, thus most herds likely occurred at densities below carrying capacity and herd management objectives (Table 1). Traditionally, populations of K-selected species such as elk are thought to be controlled by density dependent mechanisms such that reproduction and survival decline only when populations approach carrying capacity (Skoglund 1986, Fowler 1987). Hence, we assume that density had relatively little influence on nutritional condition and reproduction in this study. This may not be true for every herd at the time we sampled them, however, such as for herds at Rocky Mountain National Park (Lubow et al. 2002), Yellowstone National Park (Coughenour and Singer 1996), and Mount St. Helens (WDFW 2006).

Second, especially in drier ecosystems, summer and autumn precipitation may have a large effect on vegetation among years and thus lactating female performance and condition (Coe et al. 1976, Vavra and Phillips 1980, Douglas and Leslie 1986). We found no effect of year on autumn IFBF levels, which should reflect differences in summer weather if they occurred. However, this study was not designed to detect effects of summer weather on nutritional condition, and because our sample contained areas ranging from rangelands to rainforests, it is probably unrealistic to expect an overall year effect that might reflect summer precipitation. Also, our data for herds in drier settings tended to be limited in terms of sample size of lactating females in autumn and number of years of data and thus annual variation in summer weather. At Sled Springs, OR, the herd with the largest number of years of data (7 years) in this type of climate, we found a positive trend (albeit insignificant with \( n = 7 \)) between autumn IFBF and April through October cumulative precipitation (Fig. 23).

Finally, we pooled our data across years (within seasons) largely because we typically had insufficient years of data for a conclusive analysis of year effects. We note that especially
without repeated measures data, results that indicate a significant effect of year (e.g., where year is related to spring fat) may reflect a variety of influences. Traditionally, a significant year effect might occur due to differences in weather among years, perhaps changes in range use patterns, or other effects. Change in range use patterns occurred in our Hanford, WA study herd, when an early summer wildfire blackened a large portion of the herd’s summer range, and nutritional condition patterns evidently were greatly altered by this event (Fig. 3). The literature is replete with examples of studies showing effects of weather on large ungulates, and we do not intend to discount the importance of weather. In our data set, however, every analysis of winter nutritional condition dynamics where year was significant, more detailed analysis showed that this occurred because of differences in autumn nutritional condition, which in turn was mostly explained by proportion of females in our sample that were lactating. The fact that the significant year effect of winter condition data was merely an artifact of the proportion of lactating females illustrates that 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 insights into the influence of nutrition on herd productivity. However, these data are expensive and time-consuming to obtain, require extensive training to collect accurately, and require appropriate 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, avoid stress to fetuses in spring, and to document winter’s effect on nutritional condition because of the presumption of winter’s over-
riding effect on nutritional condition.

Our data suggest important limitations of single sampling operations conducted in mid- to late winter. This approach does not allow: 1) differentiation between winter and summer nutrition effects on nutritional condition and reproductive performance, 2) identification and focus on lactating females, the class of animals that are most sensitive to their nutritional environment, and 3) establishment of reproductive and condition “histories” of each animal that are essential for testing several important hypotheses. With only mid- to late-winter sampling, key findings of this study would never have surfaced, particularly that: 1) neither spring IFBF, nor the change in IFBF over winter were influenced by winter weather for the herds we sampled, 2) spring IFBF was only a function of previous autumn IFBF which in turn was a function of lactation status and previous summer nutrition, 3) spring IFBF was unrelated to subsequent autumn IFBF, and 4) spring IFBF, unlike autumn IFBF, was not related to current reproductive status nor to future reproductive status (see also Boertje et al. [2007]). Thus if 2 groups of animals (or even 2 different years within a herd) have different late winter levels of body fat, this could be a result of different resource levels available to the animals (either winter or summer), it could be a result of different levels of winter severity, or it could be a result of different proportions of females in the sample that nursed a calf through the previous growing season compared to those that did not.

Equally important, documenting lactation status of females is critical to understand not only limitations occurring in the summer, but also those carry-over effects throughout winter. Classifying animals by lactation status past late autumn has the potential to introduce bias into the data set. Although elk in our study could nurse 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 to identify elk that raised a calf the previous summer. Pregnancy data from Toketee, OR and Mount St. Helens, WA clearly illustrate this point (Table 2). In our spring capture at Mount St. Helens, we caught new females in late February and thus had no prior history for them. None of the females ($n = 6$) that were still lactating at the time of capture were pregnant, which resulted in a calculated, but improbable, pregnancy rate of 0\% for lactating females. More likely, females that lactated the previous autumn and successfully bred had ceased lactation by the spring capture date, whereas those females that lactated the previous autumn but failed to breed continued to nurse their calves through winter. Similarly, at Toketee, pregnancy rate in autumn was 73\% for lactating females but was only 22\% by March. Repeated measures data were difficult to collect on this herd so the spring sample was primarily comprised of elk captured for the first time.

Our repeated measures approach also revealed that 6 females continued to nurse their yearling offspring through autumn, further complicating the role of lactation on IFBF and pregnancy because these elk had autumn IFBF levels equivalent to non-lactating elk despite the presence of milk in the udder. Without reproductive histories, these animals would have been incorrectly categorized as lactators. This has never before been reported for elk in the wild to our knowledge and likely only occurs in herds with depressed pregnancy rates.

Even with our repeated measures approach, we may have missed important relationships because of the frequency and timing of sampling in our study. For example, monthly lethal sampling of barren-ground caribou revealed remarkable declines in body fat between March and the end of spring during the third trimester (Adamczewski et al. 1987, Huot 1989). We assume that such declines did not occur in our data because initiation of vegetative growth was apparent for most herds during our spring captures, but we cannot prove our assumption is valid in part,
because sampling during spring introduces the possibility of stress-caused termination of pregnancy. The state wildlife agencies we worked with had varying policies regarding capture in spring. Several permitted capture of elk until 15 April, others considered capture past 1 March to be unacceptable. However, in 3 of the herds included herein, we inserted vaginal implant radiotransmitters during March and April captures to capture and monitor calves shortly after birth. These studies did not detect a reduction in survival of calves (B. Johnson and D. Immell, Oregon Department of Fish and Wildlife, and D. Vales, Muckleshoot Indian Tribe, unpublished data.).

In addition, scheduling capture operations for elk in autumn to avoid hunting seasons is difficult. If chemical restraint is used, 30-day clearance typically is required if meat is to be consumed. Some states were liberal in their policies, allowing captures to occur if special ear tags were used to mark animals and alert hunters to contact the agency to see if consuming the meat was safe. The policy of other states was more conservative. Thus, scheduling of our captures often reflected policies to minimize complications with hunting at the expense of collecting data less useful than it might have been. Hence, there remain unanswered questions in our data sets regarding changes in nutritional condition over autumn and the best time to sample animals in light of research objectives.

Based on our experiences and our results, we offer some guidelines regarding sampling protocol for nutritional condition and pregnancy in elk. Evaluating nutritional condition and associated vital rates in a way that provides insightful data that is useful for management purposes requires an explicit sampling design well-considered in light of project objectives. Collecting condition data as a supplement to operations with other primary goals, such as deploying radiotransmitters in winter, typically will provide data of marginal value. Our data suggest the most valuable data will be obtained using repeated measures designs with at least
twice per year captures, late March and mid-autumn (mid- to late November). Useful data still can be gathered if repeated measures is not an option, but sampling should be conducted in both spring and autumn. If only a single capture operation can be conducted, the most valuable data will be gained from a mid- to late autumn operation mainly because lactation status can be incorporated into data analysis and because of this season’s overriding importance to 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 nutrition 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 signals a serious nutritional limitation probably 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. 2001b, c) that can permit evaluation of lactation status, but (1) precludes repeated measures designs, and (2) probably will preclude 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 IFBF, for example, can greatly alter conclusions regarding nutrition’s influences. Many of the techniques are not user-friendly, and such levels of error as a minimum can be expected as the rule rather than the exception when used by inadequately trained and inexperienced personnel particularly with, but not limited to, ultrasound and body scoring techniques (Cook et al. 2001b, Cook et al. 2007). Use of the ultrasound and body scoring techniques is proliferating widely across the continent (Cook et al. 2010) with no means in place to enforce, certify, or evaluate quality and accuracy of data collection. In some cases, new users strive to obtain necessary training and experience, but others do not. Our data
combined with research world-wide increasingly identifies the importance of nutrition in linking habitat to population dynamics of herbivores. Continuing advances in the realm of nutrition ecology requires that methods to measure nutritional are accurate and repeatable. Clearly, the proliferation of data sets collected without adequate quality control in terms of methods greatly risks doing more to harm rather than enhance future advances.

**MANAGEMENT IMPLICATIONS**

The results of our research have direct implications to land management planning strategies and evaluation protocols that were developed 30 years ago and are still in use today across much of the western U.S. Beginning in 1969, new federal legislation, including the National Environmental Policy Act of 1969, National Forest Management Act of 1976, and others required ecological- and habitat-based approaches to wildlife management. One result was the designation of featured species as a means of implementing the new laws (Thomas 1982), and elk were granted this status on federal lands in many areas (Christensen et al. 1993). Thus, management of habitat for elk became federally mandated, ushering in a new era of elk management in the West (Thomas 1982).

Concurrently, logging was escalating and changing habitat dramatically especially in terms of road construction in unroaded or lightly roaded areas (Peek et al. 1982, Thomas et al. 1988b). By the mid-1970s, impacts of logging on habitat quality for elk were of considerable concern among wildlife biologists (Heib 1976, Thomas et al. 1979) and controversy increased even more over the next decade (Christensen et al. 1991). Aided by advances in radio–telemetry, habitat-use research increased, soon followed by new management protocol that were formalized largely in habitat suitability or “effectiveness” models (e.g., Black et al. 1976, Thomas et al. 1979, Lyon 1980, 1983, Leege 1984, Lyon et al. 1985, Wisdom et al. 1986, Thomas et al. 1988b).
These models provided the primary means to incorporate habitat needs of elk into the planning process, particularly the federal forest plans (Thomas et al. 1988a, Edge et al. 1990, Christensen et al. 1993). The enormous geographic scope of the effort, which included most federal wildlands that supported elk, remains unmatched to this day, to our knowledge.

Although there were exceptions (e.g., Wisdom et al. 1986), the guidelines and the application of the guidelines largely ignored nutrition (Edge et al. 1990, Cook et al. 1998) probably because biologists were focused on potentially negative impacts of logging, elk herds were increasing throughout much of the West (Christensen et al. 1999), and thus nutrition’s effects were deemed to be relatively unimportant. Despite a general lack of nutrition research, the perceptions arose that (1) nutritional limitations in summer were unimportant, (2) habitat alterations that improved forage quality or quantity were unnecessary, and (3) nutritional limitations even in winter were largely unimportant or at least secondary to other habitat needs (Marcum 1975, Lyon 1980, Nelson and Leege 1982, Leege 1984, Christensen et al. 1993, Coughenour and Singer 1996, Unsworth et al. 1998). These perceptions were firmly integrated by 1990 in the preponderance of our scientific literature of habitat management for elk, although alternative perceptions of nutrition’s influences existed (e.g., Trainer 1971, Hobbs et al. 1982, Collins and Urness 1983, Hobbs and Swift 1985, Wisdom et al. 1986, Harper 1987, Merrill and Boyce 1991).

The mid-1990s marked a considerable change in the biopolitics regarding elk and their habitat: (1) calf recruitment in particular and population size of many herds began declining particularly in the Pacific and Inland Northwest (Schommer 1991, Irwin et al. 1994, Gratson and Zager 1999, Ferry et al. 2001), and (2) logging was greatly curtailed on federal forests throughout most of the West. Thus, the considerable concern in the past regarding the removal
of cover and construction of new roads probably is less warranted today, and inadequate nutrition, largely due to long-term forest succession, is now highlighted as a possible cause of declining recruitment and population size (Irwin et al. 1994, Bomar 2000, Peek et al. 2001, 2002, Johnson et al. 2005). Moreover, over the last 30 years, research has accumulated that has repeatedly rejected the hypothesis that nutritional value of habitats in summer exceeds or at least satisfies requirements for reproduction and survival in the northern hemisphere for most large ungulate species, including elk (Trainer 1971, Harper 1987, Merrill and Boyce 1991, Kohlmann 1999, Cook 2002, Cook et al. 2004a, Hutchins 2006) and other species (Julander et al. 1961, Peek et al. 2002, Crête and Huot 1993, Sæther and Heim 1993, Cameron et al. 2005).

Our data for elk illustrate the ubiquity of nutritional limitations both in winter and summer/early autumn, and illustrate that summer nutritional limitations have considerably greater influence than do winter nutritional limitations for the biomes of the West that we sampled. This is true despite the fact that most of our data were from elk herds that were hunted and thus should be well below “carrying capacity”. Of the various potential influences of habitat on elk populations, our data clearly indicate that nutritional effects are among the most important in many settings across western North America. Now, the debate should shift beyond whether nutritional limitations are important and instead answer questions about how severe the nutritional limitations might be, what factors are responsible for inadequate nutrition, and what managers can do about it. Certainly, managing continuity of cover and security areas, managing access roads and trails, judicious management of livestock grazing, and other such standard practices (Thomas et al. 1988b, Christensen 1993) remain important. However, we think the data are now clear—management paradigms and strategies, including habitat models and standards and guidelines used to support management, can be significantly improved by integrating
Declining recruitment rate and population size evidently beginning in the early 1990s also generated new concerns regarding predation effects (Gratson and Zager 1999, Johnson et al. 2005), particularly in light of increasing cougar (Keister and Van Dyke 2002) and, more recently, wolf populations (White et al. 2011). Research of nutritional condition for 5 or 6 herds in our sample were part of larger efforts to compare nutrition and predation on elk. Details from this work should appear elsewhere, but we mention several general points regarding nutrition vs. predation. First, our findings herein do not necessarily prove that recent declines in recruitment and population size in elk herds are due to acute nutritional limitations. In the ecological settings of this study, our data indicate that nutritional limitations alone normally will not cause strikingly low recruitment rates, such as the <10 calves:100 cows in 3 herds we studied. Nevertheless, nutritional limitations were operative in these 3 herds and probably contributed as predisposing agents to predation. In 1 of these herds, experimental control of the cougar population greatly increased calf recruitment (from 8 to 40 calves:100 cows) but the very high pregnancy rates (≥93% over the 4 years prior to predator control) declined to 80% within 2 years after reducing the predator population. These changes in pregnancy rates pre- and post-predator control corroborate what Gerhart et al. (1997) noted for caribou, that predation effects can mask nutrition effects and that removal of 1 limiting effect (predation) merely increases the influence of some other limiting effect (nutrition). Such confounding greatly complicates mensurative studies of predation vs. nutrition, because such interactions are difficult to identify without controlling predators and, simultaneously, rigorously monitoring responses in nutritional condition, reproduction, and survival of the prey population.

Second, Gustine et al. (2006) noted that the long-standing debate regarding predation vs.
nutrition is largely pointless. Numerous studies clearly have documented the importance of each, and the relative contribution of each likely varies spatially and temporally. In contrast to predation’s effects, nutritional influences are subtle, hard 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, susceptibility of juveniles to predation, overwinter susceptibility to starvation mortality, and delays in age at first breeding). The magnitude of effects on any 1 attribute may be quite small, but the cumulative effects may be quite large. Predation was important in some of the herds we sampled but had minor influences in others. Nutritional limitations were important in most herds but had minor influences at least in a few. Consequently, regardless of predation’s influences, our data unambiguously establish the importance of nutritional influences across much of the West, and thus we conclude that effectiveness of habitat planning and management will be enhanced if nutritional needs of elk are explicitly incorporated. This is true where predation is unimportant and just as true where predation is important.

Based on the White House Conference on North American Wildlife Policy, the Sporting Conservation Council (2008) identified as 1 of the main threats facing large ungulates in the western U.S. was declining “abundance and productivity of early-successional habitats that regulate the reproductive potential of many wildlife species”. The conference noted that the large-scale disturbances from fire maintained early–seral habitats but neither the periodicity nor the magnitude of historical disturbance regimes have been replicated on federal lands. Losses of these habitats were implicated in issues of growing concern to states, including loss of hunter opportunity, license revenue, reduced economic contributions from hunters to rural economies, and increased damage on private lands as large ungulates shift to private lands (Sporting
The conference called for better understanding of the roll of active management of disturbance-dependent habitats and associated wildlife. It noted a need for land management planning tools and processes that can better identify the long-term implications to wildlife of potential land management decisions. Several specific recommendations of relevance to large ungulate nutrition were quoted below (Sporting Conservation Council 2008: 38-39):

1. Establish protocols to promote regular and routine coordination between federal and state agencies so that state wildlife habitat and population objectives can be used to aid in…land management activities on federal lands.

2. Use projects designed to reduce wildfire fuel loads; provide woody biomass for nontraditional products, including biofuels; or to control invasive species to coordinate the spatial and temporal distribution of early-successional wildlife habitats consistent with the needs of game wildlife populations.

3. Review existing habitat evaluation and population modeling processes in light of changing landscape conditions to verify or enhance their usefulness in game population management.

How to develop land management planning tools that can factor in nutritional needs of elk and other ungulates for land management purposes is unclear. Parker et al. (1999) noted that nutrient requirements, foraging and digestive efficiencies, and forage characteristics provide functional cause-and-effect relations that influence nutritional condition and body mass dynamics, and ultimately, reproduction and survival, and that most interrelations among them are quantitatively predictable. Thus, nutritional ecology offers the prospect of a quantitative, predictive, and general theory of key relations between large ungulates and their habitat (Parker et al. 1999). Carrying capacity algorithms are one approach to quantify nutritional resources.
(Hett et al. 1978, Hobbs and Swift 1985, Hanley and Rogers 1989), and detailed simulation models (Hobbs 1989, Coughenour and Singer 1996) have been used to link nutritional resources with population dynamics.

Despite these models, however, our profession has largely failed to develop practical, proven methods to bolster nutritional resources and enhance nutritional status of populations. Thus, a considerable challenge facing planners and managers is how to manage habitat to improve and maintain nutritional resources in a way that benefits large ungulate populations, and how to effectively integrate nutrition-explicit habitat management with management of other habitat attributes for elk and satisfy other natural resource objectives. Our data of nutritional condition helps to establish the importance of nutrition, but it provides few specific insights of what managers can do to address the topic.

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 must first identify if nutritional limitations are important and, if so, on which seasonal ranges the limitations are important. Our data indicate the importance of summer/early autumn nutritional limitations, but our data also indicate considerable variation across regions and even within regions. 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 (e.g., Harder and Kirkpatrick 1994, Kohlmann 1999), although sampling to augment hunter-harvest samples may be needed in many situations (Cook et al. 2001b, c). Further, careful consideration of what types of data may best provide insights of nutritional limitations are important as we outlined above. Poorly designed monitoring programs may provide little useful information and, frankly, 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 (plant parts); developing protocol that effectively integrates animal interactions with vegetative attributes at such scales and yet are relevant for planning and management across large landscapes is a considerable challenge (Hobbs 2003, Hobbs et al. 2003). Until these protocols are developed and validated, biologists, managers, and planners will be hard-pressed to design useful nutrition-explicit habitat improvements even where nutritional limitations are known to occur.

Our findings of the considerable importance of summer nutrition have important implications for habitat improvement. Our profession has a long history of creating small areas of high quality food (food plots) usually on winter range for large ungulates (e.g., Lopez 2006). Although typically small, these food plots nevertheless potentially can influence a large number of animals because they often concentrate in winter. Animals usually occur at much lower density on summer ranges. Thus, the kinds of forage improvements typically conducted for winter ranges probably have little value on summer ranges. To affect a high proportion of animals in summer, habitat manipulations will have to be large-scale in scope, and thus manipulations of elk habitat to benefit elk via nutritional pathways normally 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, to a greater degree than in the past, knowing how to improve habitat in a manner that effectively improves the nutritional status of large ungulate herds is
increasingly important. Our profession has much to learn in this regard.

We contend that the importance of summer nutrition also probably has important implications in the context of climate change. Nutrition is a primary mechanism through which changing climate might affect dynamics of large ungulate populations, because growth and nutrient levels of forage are controlled by light, moisture, and temperature regimes (Van Soest 1982). Milder winters may become more common in the future, an effect that may have little direct negative influence on large ungulates, but warming temperature particularly in combination with reduced soil moisture may increase summer nutritional limitations by (1) causing earlier vegetative growth in spring and earlier vegetative senescence in summer, and (2) increasing drought during summer, at least in some areas. These effects, particularly in combination, would decouple seasonal peaks in nutritional requirements for late third trimester of gestation and over-summer lactation and peaks in forage quality and quantity. During late spring and summer, declines in caribou calf survival in Greenland (Post and Forchhammer 2008) and low pregnancy rate of elk in northwestern Wyoming (Middleton et al., in review) were attributed to warming temperature that increasingly decoupled peaks in nutritional requirements and forage quality and quantity. At least, our data suggest that forecasting climate change effects on large ungulate populations will be enhanced if nutrition on summer range is included as a key component of the effort.

Finally, our findings highlight the value of summer range, but we do not imply that protection and management of winter ranges are unimportant. Substantial losses in nutritional condition occur on winter ranges, and minimizing disturbance and harassment on these ranges is important (Christensen et al. 1993). For herds that enter winter in unusually poor condition, maintaining relatively good food might make the difference between life and death in late winter
for many animals, especially those that raised a calf the previous summer. In several herds in our sample, 20 to 40% of female elk exited winter at <2% IFBF, and these animals need all the help they can get. Additionally, some areas of the U.S. and Canada experience longer winters and deeper snows than for most areas we sampled, and our findings in no way imply that overwinter mortality, particularly during unusually harsh winters for these areas, will not substantially impact survival and reproduction (Houston 1982, Hobbs 1989). What managers can do in these situations is unclear, however. Management to improve forage resources on winter ranges may do little to alleviate declines in survival and reproduction during periods of unusually deep snow and cold temperatures and may be less effective than management to improve nutritional condition of animals as they migrate from their summer range as winter begins.
LITERATURE CITED


Fluor Hanford. 2002. Radiological review of conditions created during and after a fire on the Hanford site in the BC Crib controlled area and areas of radiological concern in the 600 area. Report #HNF-15850, Richland, Washington, USA.


Harrisburg, Pennsylvania, USA.


Mysterud, A., R. Langvatn, N.G. Yoccoz, and N.C. Stenseth. 2001. Plant phenology, migration,


Piasecke, J.R. 2006. Relationships among condition, health, and reproduction in free-ranging elk (Cervus elaphus) populations throughout the United States. Thesis. New Mexico State University, Las Cruces, New Mexico, USA.


York, USA.


Stussy, R. J. 1993. The effects of forage improvement practices on Roosevelt elk in the Oregon Coast range. Thesis, Oregon State University, Corvallis, OR, USA.


Management 70:1445–1454.


Figure 1. Locations of 21 elk herds in Washington, Oregon, Wyoming, Colorado, and South Dakota, USA, from which nutritional condition and reproduction data were collected during 1998 through 2007. Herd numbers presented on this map correspond to the herd numbers presented in all figures and tables. We also partitioned our study area into 4 regions based on broad climate, landform and vegetation differences: coastal plains and mountains (Coastal; Herds 1 – 4), west-slope Cascades range (North Cascades, Herds 5 – 7; South Cascades, Herds 8 – 12), inland Northwest (Inland NW; Herds 13 – 17), and the Rocky Mountains region (Rocky Mtns; Herds 18 – 21).

Figure 2. Percent pregnant and sample size (frequency) by age class of elk in 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 from the crest of the Cascades east across Washington and Oregon (*C. e. nelsoni*); and 4) the northern and central Rocky Mountains of Wyoming, Colorado, and South Dakota (*C. e. nelsoni*). We determined age to the nearest year by examination of annuli of a vestigial upper canine collected during the initial capture. Data were collected during 1998-2007.

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 1 and Fig. 1 for herd numbers) 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 from the crest of the Cascades.
east across Washington and Oregon (C. e. nelsoni); and 4) the northern and central Rocky Mountains of Wyoming, Colorado, and South Dakota (C. e. nelsoni). Data are grouped according to lactation status: lactating indicates milk present at time of capture, previously lactating applies to spring data only and indicates females that were lactating the previous fall but had ceased by spring capture, non-lactating indicates no evidence of milk at capture but were pregnant the previous spring so did experience the demands of lactation for an unknown amount of time during the growing season, spring non-pregnant indicates females that were not pregnant the previous spring so never experienced the demands of lactation. Data were collected during 1998-2007, and typically included 2 years of sampling (range 1 to 7) and 40 sampled elk (range 11 to 160) per herd. Error bars represent the standard error of the average. Different letters among herds denote significant differences in IFBF.

Figure 4. Average body mass (BMNP; estimated via girth circumference without products of conception included) in late autumn and early spring for female elk in 21 herds (see Table 1 and Fig. 1 for herd numbers) 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 from the crest of the Cascades east across Washington and Oregon (C. e. nelsoni); and 4) the northern and central Rocky Mountains of Wyoming, Colorado, and South Dakota (C. e. nelsoni). Data are grouped 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 thus may or may not have experienced the
demands of lactation for an unknown amount of time during the growing season, spring (NL) indicates no evidence of milk at capture, spring (fall L) indicates either evidence of milk at capture or repeated measures were available showing evidence of milk the previous fall, and spring (UNK) indicates lactation status is unknown. Data were collected during 1998-2007, and typically included 2 years of sampling (range 1 to 7) and 40 sampled elk (range 11 to 160) per herd. Error bars represent the standard error of the average. Different letters among herds denote significant differences in BMNP within a season.

Figure 5. Average longissimus dorsi muscle depth scaled for body size (LOINADJ) in late autumn (A) and early spring (B) for female elk in 21 herds (see Table 1 and Fig. 1 for herd numbers) 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 from the crest of the Cascades east across Washington and Oregon (C. e. nelsoni); and 4) the northern and central Rocky Mountains of Wyoming, Colorado, and South Dakota (C. e. nelsoni). Data are grouped according to lactation status: lactating indicates milk present at time of capture, previously lactating applies to spring data only and indicates females that were lactating the previous fall but had ceased by spring capture, non-lactating indicates no evidence of milk at capture but were pregnant the previous spring so did experience the demands of lactation for an unknown amount of time during the growing season, spring non-pregnant indicates females that were not pregnant the previous spring so never experienced the demands of lactation. Data were
collected during 1998-2007, and typically included 2 years of sampling (range 1 to 7) and 40 sampled elk (range 11 to 160) per herd. Error bars represent the standard error of the average. Different letters among herds denote significant differences in LOIN<sub>ADJ</sub>.

Figure 6. Average depletion (loss) of ingesta-free body fat (IFBF) over winter paired with average accretion (gain) of IFBF over summer for female elk in 21 herds (see Table 1 and Fig. 1 for herd numbers) across 4 regions of the western United States: 1) the coastal plains and mountains west of Interstate 5 in western Oregon and Washington (<i>Cervus elaphus roosevelti</i>) (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 (<i>C. e. nelsoni</i>) (herds 5 – 12); 3) the inland Northwest from the crest of the Cascades east across Washington and Oregon (<i>C. e. nelsoni</i>) (herds 13 – 17); and 4) the northern and central Rocky Mountains of Wyoming, Colorado, and South Dakota (<i>C. e. nelsoni</i>) (herds 18 – 21). Data are grouped according to lactation status: (A) fall lactating are females with milk present at time of fall capture or spring capture, (B) fall non-lactating are females with no evidence at time of fall capture or spring capture, and (C) spring non-pregnant are females known to be non-pregnant the previous spring. Data were collected during 1998-2007, and typically included 2 years of sampling (range 1 to 7) and 40 sampled elk (range 11 to 160) per herd. Error bars represent the standard error of the average and sample sizes are reported for each herd and season. Different letters among herds denote significant differences in IFBF gains or losses within that season. Stars indicate herds in which winter IFBF depletion was significantly higher than summer accretion (<i>P</i> < 0.05).

Figure 7. Average decline of body mass (BM<sub>NP</sub>; estimated via girth circumference without products of conception included) over winter paired with average increase of BM<sub>NP</sub> over
summer for female elk in 21 herds (see Table 1 and Fig. 1 for herd numbers) 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*) (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 (*C. e. nelsoni*) (herds 5 – 12); 3) the inland Northwest from the crest of the Cascades east across Washington and Oregon (*C. e. nelsoni*) (herds 13 – 17); and 4) the northern and central Rocky Mountains of Wyoming, Colorado, and South Dakota (*C. e. nelsoni*) (herds 18 – 21). Data are grouped according to lactation status: (A) fall lactating are females with milk present at time of fall capture or spring capture, (B) fall non-lactating are females with no evidence at time of fall capture or spring capture, and (C) spring non-pregnant are females known to be non-pregnant the previous spring. Data were collected during 1998-2007, and typically included 2 years of sampling (range 1 to 7) and 40 sampled elk (range 11 to 160) per herd. Error bars represent the standard error of the average and sample sizes are reported for each herd and season. Different letters among herds denote significant differences in BMNP gains or losses within that season.

Figure 8. Average decline in longissimus dorsi muscle depth scaled for body size (LOINADJ) over winter paired with average increase in LOINADJ over summer for female elk in 21 herds (see Table 1 and Fig. 1 for herd numbers) 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*) (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 (*C. e. nelsoni*) (herds 5 – 12); 3) the inland Northwest from the crest of
the Cascades east across Washington and Oregon (C. e. nelsoni) (herds 13 – 17); and 4) the northern and central Rocky Mountains of Wyoming, Colorado, and South Dakota (C. e. nelsoni) (herds 18 – 21). Data are grouped according to lactation status: (A) fall lactating are females with milk present at time of fall capture or spring capture, (B) fall non-lactating are females with no evidence at time of fall capture or spring capture, and (C) spring non-pregnant are females known to be non-pregnant the previous spring. Data were collected during 1998-2007, and typically included 2 years of sampling (range 1 to 7) and 40 sampled elk (range 11 to 160) per herd. Error bars represent the standard error of the average and sample sizes are reported for each herd and season. Different letters among herds denote significant differences in LOINADJ gains or losses within that season. Stars indicate herds in which winter LOINADJ depletion was significantly higher than summer accretion (P < 0.05).

Figure 9. Relations of ending ingesta-free body fat (IFBF) and either starting ingesta-free body fat (closed squares) or the change in IFBF (on a percentage point basis; open circles) over the season for winter (graph A) and for summer (graph B). Data represent 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 while South Cascades herds are shown with a dotted line); 3) the inland Northwest 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). Data were collected during 1998-2007, and include only those females that were handled during both the fall capture and the subsequent spring capture (A) or both the spring capture and subsequent fall capture (B). Winter graphs (A) include all females regardless of lactation status while summer graphs (B) include only those females with milk at capture in the autumn. Regression statistics are presented on the graphs; all relations significant at the $P = 0.05$ level are marked (*) in the upper right corner of each graph.

Figure 10. Relations of ending body mass (BM$_{NP}$; estimated via girth circumference without products of conception included) and either starting ingesta-free body fat (closed squares) or the change in BM$_{NP}$ (on a percentage point basis; open circles) over the season for winter (graph A) and for summer (graph B). Data represent 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 rooseveltii); 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 while South Cascades herds are shown with a dotted line; 3) the inland Northwest 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). Data were collected during 1998-2007, and include only those females that were handled during both the fall capture and the subsequent spring capture (A) or both the spring capture and subsequent fall capture (B). Winter graphs (A) include all females regardless of lactation status while summer graphs (B) include only those females with...
milk at capture in the autumn. Regression statistics are presented on the graphs; all relations significant at the $P = 0.05$ level are marked (*) in the upper right corner of each graph.

Figure 11. Relations of ending longissimus dorsi muscle depth scaled for body size (LOIN$_{ADJ}$) and either starting LOIN$_{ADJ}$ (closed squares) or the change in LOIN$_{ADJ}$ (on a percentage point basis; open circles) over the season for winter (graph A) and for summer (graph B). Data represent 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 while South Cascades herds are shown with a dotted line); 3) the inland Northwest 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*). Data were collected during 1998-2007, and include only those females that were handled during both the fall capture and the subsequent spring capture (A) or both the spring capture and subsequent fall capture (B). Winter graphs (A) include all females regardless of lactation status while summer graphs (B) include only those females with milk at capture in the autumn. Regression statistics are presented on the graphs; all relations significant at the $P = 0.05$ level are marked (*) in the upper right corner of each graph.

Figure 12. Using individual regression results generated to calculate spring ingesta-free body fat (IFBF) relative to previous autumn IFBF and autumn IFBF relative to previous spring.
IFBF on a regional basis (Fig. 9), we modeled the effect of multiple years of successfully producing a calf on individual females relative to 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) and South Cascades herds are represented with different graphs; 3) the inland Northwest from the crest of the Cascades east across Washington and Oregon (*C. e. nelsoni*); and 4) San Luis Valley, CO, the only herd from the Rocky Mountain region with repeated sampling (*C. e. nelsoni*). We randomly chose 4 levels of starting autumn IFBF (2, 6, 10, 14%) and modeled loss over winter and gain over summer for 5 consecutive years (F1 represents the first fall, S1 the subsequent spring, and so forth). Equilibrium ‘maxima’ are reported for each region.

Figure 13. Seasonal ingesta-free body fat (IFBF) data from individual females lactating ≥2 years in succession. Data are presented by herd and multiple females within each herd are represented by different lines and symbols. The initial spring IFBF value is graphed at S0, F1 the subsequent fall, and so forth.

Figure 14. Using individual regression results generated to calculate spring body mass (BM<sub>NP</sub>; estimated via girth circumference without products of conception included) relative to previous autumn BM<sub>NP</sub> and autumn BM<sub>NP</sub> relative to previous spring BM<sub>NP</sub> on a regional basis (Fig. 9) as well as using corresponding relations for longissimus dorsi muscle depth scaled for body size (LOIN<sub>ADJ</sub>; Fig. 10), we modeled the effect of multiple years of successfully producing a calf on individual females relative to 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) and South Cascades herds are represented with different graphs; 3) the inland Northwest from the crest of the Cascades east across Washington and Oregon (*C. e. nelsoni*); and 4) San Luis Valley, CO, the only herd from the Rocky Mountain region with repeated sampling (*C. e. nelsoni*). We randomly chose 4 levels of starting autumn BMNP (200, 220, 240, 260 kg) and and LOINADJ (4.5, 5.0, 5.5, 6.0 cm) and modeled loss over winter and gain over summer for 5 consecutive years (F1 represents the first fall, S1 the subsequent spring, and so forth). A LOINADJ graph is not shown for San Luis Valley, CO due to non-significant regression relations. Equilibrium ‘maxima’ are reported for each region.

Figure 15. Relationship between the average fat-free, ingesta-free body mass (BMFF) and average autumn 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. We present 95% confidence intervals around the regression line for Rocky Mountain elk (*Cervus elaphus roosevelti*).

Figure 16. Probability of pregnancy (y) based on ingesta-free body fat (IFBF) in the autumn (x) plus 95% confidence intervals for prime-age female elk in 15 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 from the crest of the Cascades
east across Washington and Oregon \((C. \textit{e. nelsoni})\); and 4) the northern and central Rocky Mountains of Wyoming, Colorado, and South Dakota \((C. \textit{e. nelsoni})\). Individual herd pregnancy rates (number of prime-aged females pregnant/total number of prime-aged females) are represented by open circles for each region. Two herds with abnormally low pregnancy rates relative to autumn IFBF are labeled. Matched with each regional probability graph is a frequency histogram (% of 100) of pregnant females and non-pregnant females relative autumn IFBF. Vertical bars delineate the nutritional categories depicted by Cook et al. (2004\textsuperscript{a}) in Table 3; IFBF < 6% would predict greatly depressed pregnancy rates, IFBF >6% but < 12.5% would predict some depression in pregnancy rates or evidence of delayed breeding, IFBF > 12.5% would predict very little limitations on pregnancy rates. Percent pregnant in each of these categories are included.

Figure 17. Probability of pregnancy \((y)\) plus 95% confidence intervals based on ingesta-free body fat in autumn \((x)\) for lactating (solid lines) versus non-lactating (dotted lines) prime-age female elk (Graph A). Matched with the probability graph are breakdowns for percent of females pregnant relative to lactation status (Graph B) and autumn ingesta-free body fat (%), and along with frequencies (% of 100) of pregnant females and non-pregnant females relative to lactation status and autumn ingesta-free body fat (%) (Graphs C, D). Data are from 15 herds from Oregon, Washington, and Colorado collected during 1998—2007.

Figure 18. Average ingesta-free body fat (IFBF) in autumn (%) for pregnant and non-pregnant females grouped according to prime-age (2-14 years-old) and reproductively senescent \((\geq 15\text{ years old})\) for female elk in 15 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 from the crest of the Cascades east across Washington and Oregon (*C. e. nelsoni*); and 4) the northern and central Rocky Mountains of Wyoming, Colorado, and South Dakota (*C. e. nelsoni*). Error bars represent the standard error of the average and stars indicate significant differences in IFBF between pregnant and non-pregnant females within age category.

Figure 19. Distribution of body mass (BMNP; estimated via girth circumference without products of conception included) of 39 yearlings collected in late autumn (A) or early spring (B) relative to nutritional categories depicted by Cook et al. (2004a) and presented in Table 3. Categories reflect adequacy of the summer range; “excellent” refers to settings with virtually no nutritional limitations in summer and autumn (dietary digestible energy levels >2.9 kcal/g of forage required), “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 (2.75 to 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, and limit growth; 2.45 to 2.75 kcal/g), and “poor” pertains to nutrition levels that markedly affect reproduction, reduce survival probability, and limit growth of sub-adults (<2.45 kcal/g).

Figure 20. Probability of pregnancy (y) relative to body mass (BMNP; estimated via girth circumference without products of conception included) (x) for (1) 29 yearlings captured during spring 1998 – 2007 and (2) captive Rocky Mountain yearlings during the 1997 breeding season (captive data are from Cook et al. [2004a]). When compared to the
curve generated by Cook et al. (2004a) in autumn using yearling females in captivity, the wild data is shifted substantially to the left indicating the ability to become pregnant at much lower body mass than was predicted. We estimated an autumn BM_{NP} by adding back 10% body mass to spring BM_{NP} (a conservative estimate of mass loss over winter based on Fig. 4). The resulting curve produced probability of pregnancy based on body mass quite similar to Cook et al. (2004a).

Figure 21. Distribution of body mass (kg) of 242 calves collected in late autumn or through the winter relative to nutritional categories depicted by Cook et al. (2004a) and presented in Table 3) (A). Categories reflect adequacy of the summer range; “excellent” refers to settings with virtually no nutritional limitations in summer and autumn (dietary digestible energy levels >2.9 kcal/g of forage required), “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 (2.75 to 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, and limit growth; 2.45 to 2.75 kcal/g), and “poor” pertains to nutrition levels that markedly affect reproduction, reduce survival probability, and limit growth of sub-adults (<2.45 kcal/g). For comparison, we include the distribution of prime-age female autumn ingesta-free body fat (%) for the same herds relative to the same nutritional categories.

Figure 22. Relationship between ingesta-free body fat in autumn (%) and herd-level longissimus dorsi depth adjusted for body size (LOIN_{ADJ}) for 17 herds collected during 1998-2007 in Washington, Oregon, and Colorado. Two herds with LOIN_{ADJ} depths substantially below what would be predicted by their fat levels are labeled.
Figure 23. Relationship between cumulative precipitation from April through October (mm) and ingesta-free body fat in autumn (%) for Sled Spring, OR during 2001-2007. One year is depicted as outlier (open circle) but no statistics were run on this relationship; it is presented for discussion purposes only.

Appendix A. Average longissimus dorsi muscle depth (LOIN; original measurement without adjusting for body size) in late autumn and early spring for female elk in 21 herds (see Table 1 and Fig. 1 for herd numbers) 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 from the crest of the Cascades east across Washington and Oregon (C. e. nelsoni); and 4) the northern and central Rocky Mountains of Wyoming, Colorado, and South Dakota (C. e. nelsoni). Data are grouped according to lactation status: lactating indicates milk present at time of capture, previously lactating applies to spring data only and indicates females that were lactating the previous fall but had ceased by spring capture, non-lactating indicates no evidence of milk at capture but were pregnant the previous spring so did experience the demands of lactation for an unknown amount of time during the growing season, spring non-pregnant indicates females that were not pregnant the previous spring so never experienced the demands of lactation. Data were collected during 1998-2007, and typically included 2 years of sampling (range 1 to 7) and 40 sampled elk (range 11 to 160) per herd. Error bars represent the standard error of the average. Different letters among herds denote significant differences in LOIN.
Table 1. Herd characteristics and description of capture efforts for 21 elk herds in Washington, Oregon, Wyoming, Colorado, and South Dakota, USA, from which nutritional condition and reproduction data were collected during 1998 through 2007. Herd numbers presented correspond to Figure 1.

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<th>Year</th>
<th>Seasons</th>
<th>Females</th>
<th>Captures&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Age&lt;sup&gt;b&lt;/sup&gt;</th>
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<td>38</td>
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<td>2</td>
<td>4</td>
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<td>18</td>
<td>6</td>
<td>1</td>
<td>0</td>
<td>D/H/ P, Pr.</td>
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<sup>a</sup> Total number of capture events. If the capture events are greater than the number of females, this indicates a repeated measures approach at some level.

<sup>b</sup> Average age of all females at first capture estimated by canine tooth rings except where indicated.

<sup>c</sup> Number of capture events where the female was ≥15 years old.

<sup>d</sup> Age estimated to the nearest year via counts of cementum annuli in the canine (Hamlin et al. 2000; Matson’s Laboratory, Milltown, Montana).

<sup>e</sup> 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 recovering), hunting (H = hunted, U = un-hunted, M = mix of hunted and un-hunted; refers to National Park animals where a portion of animals leave Park Service land and are exposed to hunting), and land ownership (P = public lands, Pr. = private lands [commercial timber, agriculture etc.]).
Table 2. Herd by year specific spring body fat (%) and change in body fat over winter (on a percentage point basis) paired with winter weather statistics. Data were collected during 1999 through 2007 from herds in Washington, Oregon, and Colorado and include 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 1 and Figure 1.

<table>
<thead>
<tr>
<th>Herd</th>
<th>Region</th>
<th>Winter</th>
<th>Spring Body Fat (%)</th>
<th>Winter Change Body Fat</th>
<th>Precipitation (mm)</th>
<th>Precipitation (mm)</th>
<th>Temperature (˚C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Green River</td>
<td>Cascades</td>
<td>1999</td>
<td>4.96</td>
<td>-6.91</td>
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<td>-8.54</td>
<td>253.91</td>
<td>761.72</td>
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<tr>
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<td>Cascades</td>
<td>2001</td>
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<td>-7.40</td>
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<td>2004</td>
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<td>587.14</td>
<td>-1.39</td>
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<td>Cascades</td>
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<td>Cascades</td>
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<td>794.96</td>
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Table 2 continued.

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<th>Spring Body Fat (%)&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Winter Change Body Fat&lt;sup&gt;bc&lt;/sup&gt;</th>
<th>Precipitation (mm)&lt;sup&gt;d&lt;/sup&gt;</th>
<th>Precipitation (mm)&lt;sup&gt;e&lt;/sup&gt;</th>
<th>Temperature (&lt;sup&gt;°C&lt;/sup&gt;)&lt;sup&gt;f&lt;/sup&gt;</th>
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<tr>
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<td>Cascades</td>
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<td>-5.41</td>
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<td>911.88</td>
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</tr>
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<td>Region</td>
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<td>Spring Body Fat (%)&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Winter Change Body Fat&lt;sup&gt;b,c&lt;/sup&gt;</td>
<td>Precipitation (mm)&lt;sup&gt;d&lt;/sup&gt;</td>
<td>Precipitation (mm)&lt;sup&gt;e&lt;/sup&gt;</td>
<td>Temperature (°C)&lt;sup&gt;f&lt;/sup&gt;</td>
</tr>
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Table 2 continued.

<table>
<thead>
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<th>Herd</th>
<th>Region</th>
<th>Winter</th>
<th>Spring Body Fat (%)&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Winter Change Body Fat&lt;sup&gt;b,c&lt;/sup&gt;</th>
<th>Precipitation (mm)&lt;sup&gt;d&lt;/sup&gt;</th>
<th>Precipitation (mm)&lt;sup&gt;e&lt;/sup&gt;</th>
<th>Temperature (˚C)&lt;sup&gt;f&lt;/sup&gt;</th>
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<sup>a</sup> Winter refers to that associated with January (e.g., December 2000 would be part of winter 2001).
<sup>b</sup> Females that were lactating in autumn only.
<sup>c</sup> Currency is percentage points of ingesta-free body fat.
<sup>d</sup> Average December through February precipitation.
<sup>e</sup> Sum of December through February precipitation.
<sup>f</sup> Average minimum temperature December through February.
Table 3. Pregnancy rates (%; number of pregnant females/total number of females) for each elk herd evaluated (n). Data are from 21 elk herds in Washington, Oregon, Wyoming, Colorado, and South Dakota, USA, from which nutritional condition and reproduction data were collected during 1998 through 2007. Herd numbers presented correspond to Figure 1.

<table>
<thead>
<tr>
<th>Herd</th>
<th>Herd #</th>
<th>Region</th>
<th>Spring</th>
<th></th>
<th></th>
<th>Autumn</th>
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<th></th>
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<tbody>
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<td>Lactating</td>
<td>Non-lactating</td>
<td>All</td>
<td>Lactating</td>
<td>Non-lactating</td>
</tr>
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<td>58.8 (17)</td>
<td>73.5 (34)</td>
<td>63.6 (44)</td>
<td>66.7 (21)</td>
<td>60.9 (23)</td>
</tr>
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<td>81.8 (11)</td>
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<td>73.7 (19)</td>
<td>100.0 (6)</td>
</tr>
<tr>
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<td>100.0 (7)</td>
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<td></td>
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</tr>
<tr>
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<td>Non-lactating</td>
<td>All</td>
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<td>Non-lactating</td>
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<td>Spring</td>
<td>Autumn</td>
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<td>Non-lactating</td>
<td>All</td>
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<td>50.0 (2)</td>
<td>86.7 (15)</td>
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</table>

*a* 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 fall sampling) or females whose pregnancy status was unknown. During the spring capture, autumn non-pregnant females were avoided.

*b* Females that were still lactating at the time of the spring capture or capture data from the previous autumn showed her to be lactating.

*c* Females that were not lactating at the time of the spring capture. This category could include fall lactators that had ceased lactating by spring capture if previous data had not been collected.
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 cows, we assume lactating and prime-age (3 to 10 years of age). This table was developed from captive elk under controlled experimental conditions in a penned setting (Cook et al. 2004\(^a\)).

<table>
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<tr>
<th>Summer-autumn Nutritional status</th>
<th>Calf Body mass (kg)</th>
<th>Yearling female Body mass (kg)</th>
<th>Adult Female Body fat (%)</th>
<th>Yearling Pregnancy (%)</th>
<th>Adult Pregnancy (%)</th>
<th>Adult Female Breeding date</th>
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<tr>
<td>Excellent</td>
<td>125 to 145</td>
<td>195 to 230</td>
<td>17 to 25(^c)</td>
<td>≥90</td>
<td>≥90</td>
<td>≤30 Sep</td>
</tr>
<tr>
<td>Good</td>
<td>105 to 125</td>
<td>180 to 195</td>
<td>13 to 17</td>
<td>30 to 90</td>
<td>≥90</td>
<td>≤5 Oct</td>
</tr>
<tr>
<td>Marginal</td>
<td>90 to 105</td>
<td>160 to 180</td>
<td>8 to 13</td>
<td>0 to 30</td>
<td>70 to 90</td>
<td>≤10 Oct</td>
</tr>
<tr>
<td>Poor</td>
<td>&lt;90</td>
<td>&lt;160</td>
<td>&lt;8</td>
<td>&lt;5</td>
<td>40 to 70</td>
<td>&gt;10 Oct</td>
</tr>
</tbody>
</table>

\(^a\) These levels of performance should be robust across a reasonable range of winter conditions. However, winter conditions that are appreciably milder than mimicked in this study may compensate for and mask the effects of summer-autumn nutritional limitations. This effect probably would most apply to the values presented for yearling cows.
"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 to 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 to 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.

The higher levels (>22%) were observed in non-lactating cows.
Table 5. Estimates of body fat (BF) loss (percentage points; PP) based on this and different studies.

Table originally developed in Cook et al. (2011).

<table>
<thead>
<tr>
<th>Beginning BF (%)</th>
<th>End BF (%)</th>
<th>No. of days</th>
<th>Daily PP change</th>
<th>Aut PP change</th>
<th>n</th>
<th>Season</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>13.30</td>
<td>12.00</td>
<td>na</td>
<td>0.040</td>
<td>2.60</td>
<td>500b</td>
<td>Nov – Jan</td>
<td>Kohlmann</td>
</tr>
<tr>
<td>8.69</td>
<td>6.70</td>
<td>33</td>
<td>0.061</td>
<td>3.93</td>
<td>1</td>
<td>Mid-Nov – mid-Dec</td>
<td>Cook et al.</td>
</tr>
<tr>
<td>7.16</td>
<td>4.97</td>
<td>33</td>
<td>0.067</td>
<td>4.32</td>
<td>1</td>
<td>Mid-Nov – mid-Dec</td>
<td>Cook et al.</td>
</tr>
<tr>
<td>9.18</td>
<td>7.05</td>
<td>33</td>
<td>0.065</td>
<td>4.20</td>
<td>1</td>
<td>Mid-Nov – mid-Dec</td>
<td>Cook et al.</td>
</tr>
<tr>
<td>15.1</td>
<td>7.80</td>
<td>~45</td>
<td>0.162</td>
<td>10.50</td>
<td>329c</td>
<td>Late Oct – mid-Dec</td>
<td>McCorquodale</td>
</tr>
</tbody>
</table>

\( ^a \) Autumn IFBF change in PP units assuming that elk lose IFBF from the end of the breeding season (15 Oct) through Autumn (20 Dec), a period of 65 days.

\( ^b \) Data from hunter-killed elk in Oregon. Kohlman (1999) presented a linear regression equation \((KFI = 283 – 1.367\text{(day)})\) to describe the decline in body fat of cow elk during hunting season mainly Nov and Dec.

\( ^c \) Sample size was 127 hunter-killed elk in late October and early November and 202 captured live elk sampled in mid-December, 2004-08 (S. McCorquodale; Washington Department of Fish and Wildlife, unpubl. data).
FIGURE 1
FIGURE 2

Coastal

Cascades

Inland Northwest

Rocky Mountains

Age (years)

Pregnant (%)

Sample size
FIGURE 3

Coastal

Cascades

Inland NW

Rocky Mtns.

A

Herd number

Autumn ingesta-free body fat (%)

B

Herd number

Spring ingesta-free body fat (%)

Lactators

Previously Lactating

Not Lactating at capture

Non-Lactators

Unknown
FIGURE 5

A

Coastal Cascades Inland NW Rocky Mtns.

Autumn LIOMD thickness (cm)

Herd number

B

Spring LIOMD thickness (cm)

Herd number

Lactators Previously Lactating Not Lactating at capture Non-Lactators Unknown

- • - □ - ○ - ★ - ◆
FIGURE 6

A

Winter depletion ■ Summer accretion □

Fall Lactating

Herd number

B

Winter depletion ■ Summer accretion □

Fall non-lactating

Herd number

C

Winter depletion ■ Summer accretion □

Spring non-pregnant

Herd number
FIGURE 7

A

- Winter loss
- Summer gain

Fall Lactating

B

- Winter loss
- Summer gain

Fall non-lactating

C

- Winter loss
- Summer gain

Spring non-pregnant
FIGURE 9

A  Coastal  Cascades  Inland NW  San Luis Valley, CO

\[ y = 0.255 + 0.450x \]
\[ r^2 = 0.36 \]

\[ y = 1.56 + 0.241x \]
\[ r^2 = 0.27 \]

\[ y = 0.95 + 0.471x \]
\[ r^2 = 0.24 \]

B  Coastal  Cascades  Inland NW  San Luis Valley, CO

\[ y = 4.85 + 0.22x, r^2 = 0.07 \]

\[ y = 7.95 + 0.19x^2 \]
\[ r^2 = 0.032 \]

\[ y = 4.11 + 0.29x, r^2 = 0.152 \]

\[ y = 10.07 + 0.20x^2, r^2 = 0.07 \]

\[ y = 6.75 + 0.16x, r^2 = 0.03 \]
FIGURE 10

A

Coastal  
\[ y = 22.64 + 0.791x \]  
\[ r^2 = 0.64 \]

Cascades  
\[ y = 77.48 + 0.529x \]  
\[ r^2 = 0.33 \]

Inland NW  
\[ y = 51.771 + 0.626x \]  
\[ r^2 = 0.42 \]

San Luis Valley, CO  
\[ y = 44.76 + 0.703x \]  
\[ r^2 = 0.39 \]

B

Coastal  
\[ y = 139.13 + 0.429x \]  
\[ r^2 = 0.36 \]

Cascades  
\[ y = 129.43 + 0.513x \]  
\[ r^2 = 0.31 \]

Inland NW  
\[ y = 131.36 + 0.449x \]  
\[ r^2 = 0.31 \]

San Luis Valley, CO  
\[ y = 123.99 + 0.415x \]  
\[ r^2 = 0.27 \]
Coastal Cascades Inland NW San Luis Valley, CO

Autumn LOIN (cm)

\[ y = 3.59 + 0.316x \]
\[ r^2 = 0.10 \]

North: \[ y = 3.82 + 0.272x \]
\[ r^2 = 0.11 \]

South: \[ y = 1.96 + 0.597x \]

Spring LOIN (cm)

\[ y = 2.00 + 0.640x \]
\[ r^2 = 0.23 \]

North: \[ y = 3.75 + 0.339x \]
\[ r^2 = 0.17 \]

South: \[ y = 2.89 + 0.502x \]

Change LOIN over winter

\[ y = 3.34 + 0.348x \]
\[ r = 0.10 \]

\[ y = 1.23 + 0.773x \]
\[ r = 0.55 \]

Spring LOIN ADJ (cm)

\[ y = 3.53 + 0.358x \]
\[ r = 0.122 \]

\[ y = 3.90 + 0.272x \]
\[ r = 0.042 \]

\[ y = 2.00 + 0.640x \]
\[ r = 0.232 \]

North: \[ y = 1.96 + 0.597x \]

South: \[ y = 2.89 + 0.502x \]

Change LOIN over summer

\[ y = 3.75 + 0.339x \]
\[ r = 0.17 \]

\[ y = 2.89 + 0.502x \]
FIGURE 12

Coastal

Equilibrium maxima = 5.4%

Ingesta-free body fat (%)

Inland Northwest

Equilibrium maxima = 7.2%

South Cascades

Equilibrium maxima = 8.5%

North Cascades

Equilibrium maxima = 10.9%

Rocky Mountains (San Luis Valley, CO)

Equilibrium maxima = 5.1%
FIGURE 13

Nooksack, WA

White River, WA

Green River, WA

Steamboat/Toketee, OR

Sled Spring, OR

Springfield, OR

Wynoochee, WA

Willapa Hills, WA
FIGURE 14

Coastal
Equilibrium maxima = 225

North Cascades
Equilibrium maxima = 232

South Cascades
Equilibrium maxima = 219

Inland Northwest
Equilibrium maxima = 225

San Luis Valley, CO
Equilibrium maxima = 201

Equilibrium maxima:
- Coastal: 225
- North Cascades: 232
- South Cascades: 219
- Inland Northwest: 225
- San Luis Valley, CO: 201
Autumn ingesta-free body fat (%) of lactating cows

Roosevelt elk: $P = 0.5878$

Rocky Mtn elk: $P = 0.0213$

$y = 1.126x + 166.01; \ r^2 = 0.37$
FIGURE 18

Ingesta-free body fat (%) for different regions:
- Coastal
- Cascades
- Inland Northwest
- Rocky Mts.

Age estimated by canine annuli:
- 2-14
- 15+

Legend:
- Black: Pregnant
- Gray: Nonpregnant
FIGURE 19

Late autumn body mass (kg) vs. Frequency (%)

- Poor
- Marginal
- Good
- Excellent

Early spring body mass (kg) vs. Frequency (%)

- Coastal (22% pregnant)
- Cascades (40% pregnant)
- Inland NW (50% pregnant)
- Rocky Mtns (17% pregnant)
FIGURE 21

A Poor Marginal Good Excellent

B Poor Marginal Good Excellent

Frequency (%)

Body mass (kg)

Autumn ingesta-free body fat (%)

<90 90-105 106-125 >125

<8 8-12 12-16 >16

Yakima, WA Mt. St. Helens, WA San Luis Valley, CO
FIGURE 23

Autumn ingesta-free body fat (%) versus Cumulative APR - OCT precipitation (mm)
APPENDIX A

Herd number

Autumn LOIN thickness (cm)

Spring LOIN thickness (cm)

Lactators  Previously Lactating  Not Lactating at capture  Non-Lactators  Unknown