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A MULTI-SCALE TEST OF THE FORAGE MATURATION HYPOTHESIS IN A PARTIALLY MIGRATORY UNGULATE POPULATION

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Abstract. The forage maturation hypothesis (FMH) proposes that ungulate migration is driven by selection for high forage quality. Because quality declines with plant maturation, but intake declines at low biomass, ungulates are predicted to select for intermediate forage biomass to maximize energy intake by following phenological gradients during the growing season. We tested the FMH in the Canadian Rocky Mountains by comparing forage availability and selection by both migrant and nonmigratory resident elk (*Cervus elaphus*) during three growing seasons from 2002–2004. First, we confirmed that the expected trade-off between forage quality and quantity occurred across vegetation communities. Next, we modeled forage biomass and phenology during the growing season by combining ground and remote-sensing approaches. The growing season started 2.2 days earlier every 1 km east of the continental divide, was delayed by 50 days for every 1000-m increase in elevation, and occurred 8 days earlier on south aspects. Migrant and resident selection for forage biomass was then compared across three spatial scales (across the study area, within summer home ranges, and along movement paths) using VHF and GPS telemetry locations from 119 female elk. Migrant home ranges occurred closer to the continental divide in areas of higher topographical diversity, resulting in migrants consistently selecting for intermediate biomass at the two largest scales, but not at the finest scale along movement paths. In contrast, residents selected maximum forage biomass across all spatial scales. To evaluate the consequences of selection, we compared exposure at telemetry locations of migrant and resident elk to expected forage biomass and digestibility. The expected digestibility for migrant elk in summer was 6.5% higher than for residents, which was corroborated with higher fecal nitrogen levels for migrants. The observed differences in digestibility should increase migrant elk body mass, pregnancy rates, and adult and calf survival rates. Whether bottom-up effects of improved forage quality are realized will ultimately depend on trade-offs between forage and predation. Nevertheless, this study provides comprehensive evidence that montane ungulate migration leads to greater access to higher-quality forage relative to nonmigratory congeners, as predicted by the forage maturation hypothesis, resulting primarily from large-scale selection patterns.

Key words: Cervus elaphus; *digestibility of forage; elk; forage maturation; forage quality; forage selection; migration; MODIS; NDVI; partial migration; phenology; Rocky Mountains, Alberta, Canada.*

INTRODUCTION

Migration is thought to have evolved as a strategy to maximize fitness in the face of seasonal and spatial variation in resources (Boyce 1979, Swingland and Greenwood 1983). Large vertebrate herbivores, such as ruminant ungulates, are often migratory (Berger 2004). While migration can also reduce predation risk (Fryxell et al. 1988), selection for forage quality is proposed as the primary mechanism driving migration in ungulates (McNaughton 1985, Fryxell et al. 1988, Albon and Langvatn 1992). Migration allows ungulates to exploit forage quality to maximize intake rate over larger spatial scales than nonmigratory residents. This is because even modest increases in forage quality can increase nutrient intake for ruminants because of the multiplier effects of higher nutrients and accompanying reductions in rumination and passage time (White 1983). Forage quality is highest in new plant growth because of high cell soluble content, which declines as plants mature and fiber accumulates (Van Soest 1982). Thus, by following spatiotemporal patterns in new plant growth, migratory ungulates are expected to maximize energy intake rates (e.g., Fryxell et al. 2004).

Recent studies, however, suggest energy intake is not simply a function of quality, but of trade-offs between quality and quantity (Fryxell 1991). Daily intake rates are constrained by either plant cropping or handling time (Spalinger and Hobbs 1992, Gross et al. 1993), which change in importance as biomass increases. As plant biomass increases, encounters with potential bites

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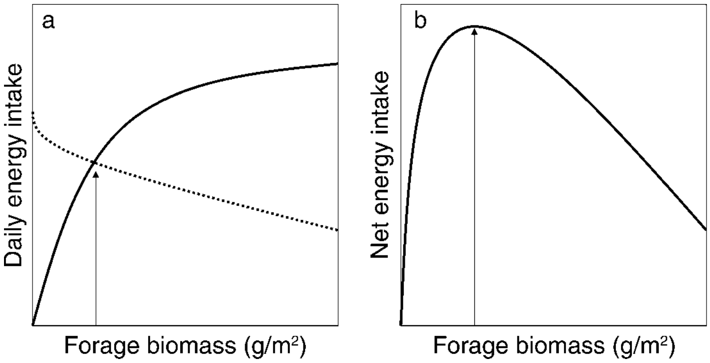


FIG. 1. Schematic showing general mechanisms of the forage maturation hypothesis (FMH). (a) Foraging constraints of daily cropping (solid line) and digestion (dotted line) that result in (b) maximum net daily energy intake at an intermediate forage biomass (IFB). The figure is adapted from Fryxell (1991).

are not limiting, and energy intake becomes constrained by processing (e.g., chewing; Spalinger and Hobbs 1992, Pastor et al. 1999). As plant biomass matures, however, digestibility and passage rates decline because of changes in cell-wall composition and structure (Spalinger and Hobbs 1992, Gross et al. 1993). The effects of the combined cropping and digestive constraints on net daily intake are shown in Fig. 1 (adapted from Fryxell 1991), which reveals that the maximum net intake rate occurs at an intermediate biomass where the two constraints intersect. The hypothesis that energy intake is maximized at intermediate forage biomass was coined the "forage maturation hypothesis" (FMH), and has been proposed as the main reason for observed patterns in ungulate migration (McNaughton 1985, Fryxell 1991).

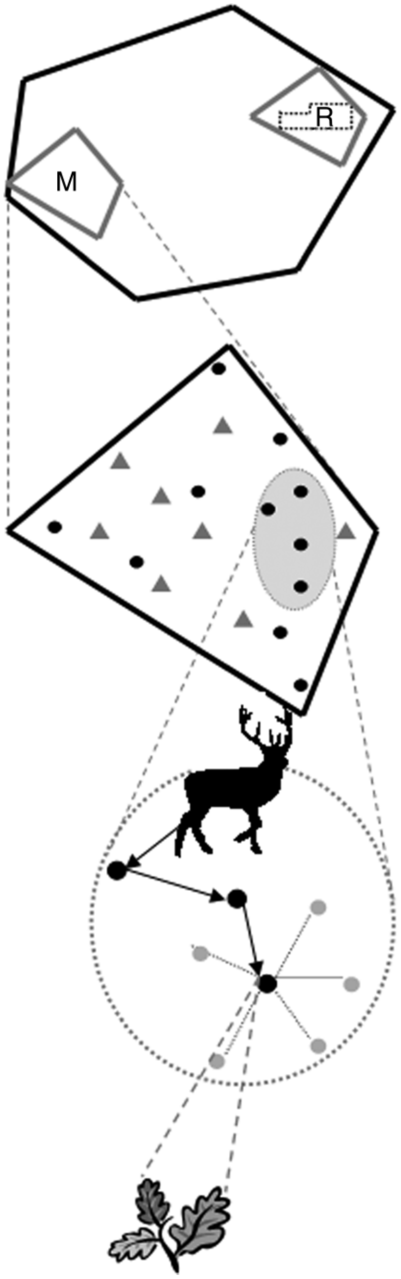
Empirical evidence that migratory ungulates select for intermediate forage biomass (IFB) comes primarily from savannah ecosystems, where forage growth is driven by seasonal rainfall (McNaughton 1985). Wilmshurst et al. (1999) showed migratory wildebeest (*Connochaetus taurinus*) in the Serengeti selected for IFB at landscape scales, but not at finer scales, revealing scale-dependence in selection for IFB. Wilmshurst et al. (1999) proposed that large-scale selection patterns constrained availability such that at smaller scales, only low biomass, high-quality forage was available.

In temperate montane ecosystems, forage phenology varies with topographic and elevational gradients that affect snowmelt and the start of plant growth (e.g., Bennett and Mathias 1984, Walker et al. 1993). Consistent with the FMH, migratory populations of montane ungulates often have access to higher diet quality (Oosenbrug and Theberge 1980, Albon and Langvatn 1992, Sakuragi et al. 2004). For example, Albon and Langvatn (1992) found crude protein was higher in plants available to red deer at higher elevations in Norway. And in a later study, Mysterud et al. (2002) confirmed that red deer at higher elevations in the same study area had higher body mass (Mysterud et al. 2002), inferential support for the importance of migration to ungulates. To date, however, there have been no direct tests in montane systems of selection for intermediate forage biomass, in part, because of the difficulties of quantifying mixed-plant community biomass at large scales in spatially complex environments (Merrill et al. 1993).

In this paper we examine evidence for the forage maturation hypothesis in a partially migratory elk (*Cervus elaphus*) population in the Canadian Rocky Mountains of Alberta, Canada. Partially migratory populations, where some individuals migrate seasonally and others are resident, have been largely overlooked in the study of migration (but see Nicholson et al. 1997, Ball et al. 2001). Yet these systems provide a powerful comparative experimental design to test for differences in forage selection by comparing migrant and resident forage selection (Kaitala et al. 1993). We test the general prediction of the FMH that migrant elk should show stronger selection for intermediate forage biomass, lower than that selected by nonmigratory residents. Our approach is comprehensive and multi-scale. We start by examining mechanisms of differences in plant phenology that dictate availability of forage quality available to migrant and resident elk. We use these mechanistic drivers of forage quality to build spatio-temporally dynamic models of forage biomass and quality available to elk at large, landscape scales. With the foundation of understanding the availability of forage biomass and quality to migratory and resident elk, we next examine multi-scale forage-selection patterns using advanced radio-telemetry methods to test predictions of the forage maturation hypothesis at different scales. Finally, we examine consequences of selection patterns to ask whether migrant elk have greater exposure to high forage quality based on our spatiotemporal forage models (sensu Albon and Langvatn 1992), and whether this results in higher quality plant species in the diet and higher fecal nitrogen content for migrant elk.

Multi-scale predictions of the forage maturation hypothesis

We develop specific predictions of the forage maturation hypothesis to test at each stage of our comprehensive and multi-scale approach. These are presented



Predictions of the forage maturation hypothesis, FMH

a) Landscape

Plant phenology of more nutritious forage classes and growth stages will be delayed in migrant ranges (M) compared to resident ranges (R), (Post et al. 2002) because of more complex, mountainous topography (Albon and Langvatn 1992, Mysterud et al. 2002).

Migrant elk will select intermediate forage biomass (IFB) by migrating away from high forage biomass winter ranges.

In contrast, resident elk, by remaining on winter ranges, will select for higher forage biomass (Wilmshurst et al. 1999).

b) Elk summer home range

Migrants should relax selection for IFB because of higher-scale selection (Boyce et al. 2003, Dussault et al. 2005).

In contrast, residents should display selection for IFB if they are selecting maximum forage quality.

c) Movement scale

Trends observed at summer range scale should continue at this fine scale with migrants showing less selection for IFB than residents.

d) Plant-patch level (diet)

Multi-scale selection should result in migrants being exposed to higher quality forage at telemetry locations, compared to residents (Albon and Langvatn 1992).

This is predicted to increase foraging quality in migrant diets (Morgantini et al. 1988), resulting in higher fecal nitrogen (Sakuragi et al. 2002) than for residents.

FIG. 2. Hierarchical framework for testing the forage maturation hypothesis at multiple spatial scales in a partially migratory elk (*Cervus elaphus*) herd, with scale-specific predictions made for elk forage selection and forage resources across scales. Black ovals represent telemetry locations, and gray triangles represent random locations.

here and summarized in Fig. 2. First, we start by testing whether the trade-off between forage biomass and quality, necessary for the FMH to hold (Fryxell et al. 1988), held in our montane study area. Second, we extend the approach of Albon and Langvatn (1992) to model the landscape-scale availability of forage biomass and quality (measured by percentage digestibility) by combining ground sampling, remote sensing, and geographic information systems (GIS) to make spatiotemporally explicit predictions of forage biomass available across the whole study area. We test phenological mechanisms for forage-quality differences between migrant and summer ranges with repeat sampling during the growing season. We test the prediction of the FMH that migrant ranges will have delayed phenology and higher forage quality because they occur at higher elevations and in more complex mountainous topography (Albon and Langvatn 1992, Post and Klein 1999, Post and Stenseth 1999, Mysterud et al. 2002). Next, we test whether migratory elk were more likely to select areas of intermediate forage biomass than resident elk using resource-selection functions (RSF; Manly et al. 2002) by contrasting used and available forage biomass across multiple spatial scales. We examine forage selection across scales because previous studies demonstrated ungulates can adopt selection strategies at more than one scale (Wilmshurst et al. 1999, Johnson et al. 2002, Boyce et al. 2003), and adopt Johnson's (1980) hierarchy of scales of selection to guide our analyses.

At the landscape or study-area scale (the second order of Johnson [1980]), we predicted migrant elk would select IFB (Wilmshurst et al. 1999), whereas resident elk would select higher forage biomass by remaining year-round on low-elevation winter range, foregoing benefits of migration (Fig. 2). Within summer home ranges and along movement paths (Johnson's [1980] third-order scale), we expected migrants to relax selection for IFB because selection at larger scales had already constrained availability of forage biomass to be low, and thus, forage quality to be high (e.g., Wilmshurst et al. 1999). In contrast, residents were expected to display stronger selection for IFB within summer home ranges and at the movement scale to attempt to compensate for lower availability of higher forage quality compared to migrants (Fig. 2). To test the consequences of selection at the plant-patch scale, we compared migrant and resident elk exposure to predicted forage biomass and percentage digestibility of forage at telemetry locations, with the prediction under the FMH that migrants should have significantly higher availability of high forage quality. Finally, because exposure, as measured by telemetry locations, may not reflect actual intake, we compared diet composition and quality indices between migrant and resident elk at the plant-patch scale (Fig. 2). We predicted the diet of migrants to have higher composition of high-quality forage classes, and thus higher fecal nitrogen (Fig. 2).

Study Area

The study area encompassed the front and main ranges of the eastern slopes of the Canadian Rocky Mountains in and adjacent to Banff National Park (BNP; 51°30′ N, 115°30′ W), and was defined by the movements of the Ya Ha Tinda (YHT) elk population over a 6000-km^2 area (Fig. 3, elk telemetry was buffered by 5 km [Hebblewhite et al. 2006]). Elevations range from 1600 m in valley bottoms to 3500 m in the western study area near the continental divide. Climate is cold continental, and strongly influenced by the North Pacific Climate Index (Trenberth and Hurrell 1994). The study area is dominated by pronounced east-to-west gradients in elevation, precipitation, and topographic complexity, all of which are greater in the western part of the study area (Holland and Coen 1983). Growing-season length is reduced at higher elevations and in the western part of the study area due to delayed snowmelt and reduced temperatures (Holland and Coen 1983).

Vegetation was classified into three ecoregions: montane, subalpine, and alpine (Holland and Coen 1983). The montane ecoregion is dominated by lodgepole pine (*Pinus contorta*) interspersed with Engelmann spruce (*Picea engelmanii*)–willow (*Salix* spp.), aspen (*Populus tremuloides*)–parkland, and grasslands. The principal winter habitat for this elk herd is the Ya Ha Tinda (YHT) montane winter range outside of BNP (Fig. 3). The YHT is dominated by rough fescue (*Festuca campestris*) grasslands, mixed with trembling aspen, open conifer forests, and willow–bog birch (*Betula glandulosa*) shrublands. The subalpine ecoregion consists of Engelmann spruce–subalpine fir (*Abies lasiocarpa*)–lodgepole forest interspersed with willow–shrublands, subalpine grasslands, and avalanche terrain, grading to open shrub–forb meadows in the alpine ecoregion (Holland and Coen 1983). The study area contained ~200 km^2 of prescribed and natural fires from 1970 as a result of Parks Canada and Alberta fire-restoration policy (White et al. 2003). Elk forage biomass was enhanced by fire in the study area (Sachro et al. 2005).

Elk were the most abundant ungulate, numbering between 1500 and 2500 individuals (Holroyd and Van Tighem 1983). This elk population was partially migratory. Migrant elk (~60%) left the winter range during summer in late May and early June and returned from late September to December. Most migrants (~90%) migrated into BNP and the main ranges during summer (Fig. 3, Hebblewhite et al. 2006). In contrast, resident elk (40%) remained year-round on the winter range (Hebblewhite et al. 2006). Accordingly, we considered the main ranges within BNP and the front ranges in the province of Alberta as migrant and resident ranges, respectively (Fig. 3). Although elk were the dominant ungulate, white-tailed deer (*Odocoileus virginanus*), moose, mule deer (*O. hemionas*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), and a remnant herd of 5–8 mountain caribou (*Rangifer tarandus*) also occurred. Elk were the most important prey for the area's large predators, comprising 40–70% of wolf diet (Hebblewhite et al. 2004) but were also important to grizzly bear (*Ursus arctos*) diet (Hebblewhite 2006). Other less important carnivores in the study area included black bears (*Ursus americanus*), cougars (*Felis concolour*), wolverines (*Gulo gulo*), and coyotes (*Canis latrans*) (Hebblewhite 2006).

Methods

Our methods are divided into three separate steps. First, we examined mechanisms driving patterns of forage biomass and quality, testing predictions of the forage maturation hypothesis (FMH) across the study area. We linked a spatial model of forage biomass availability to temporally dynamic forage availability using remote-sensing tools (Table 1). This allowed us to develop a spatiotemporally dynamic forage-biomass model for our study area. We also determined mecha-

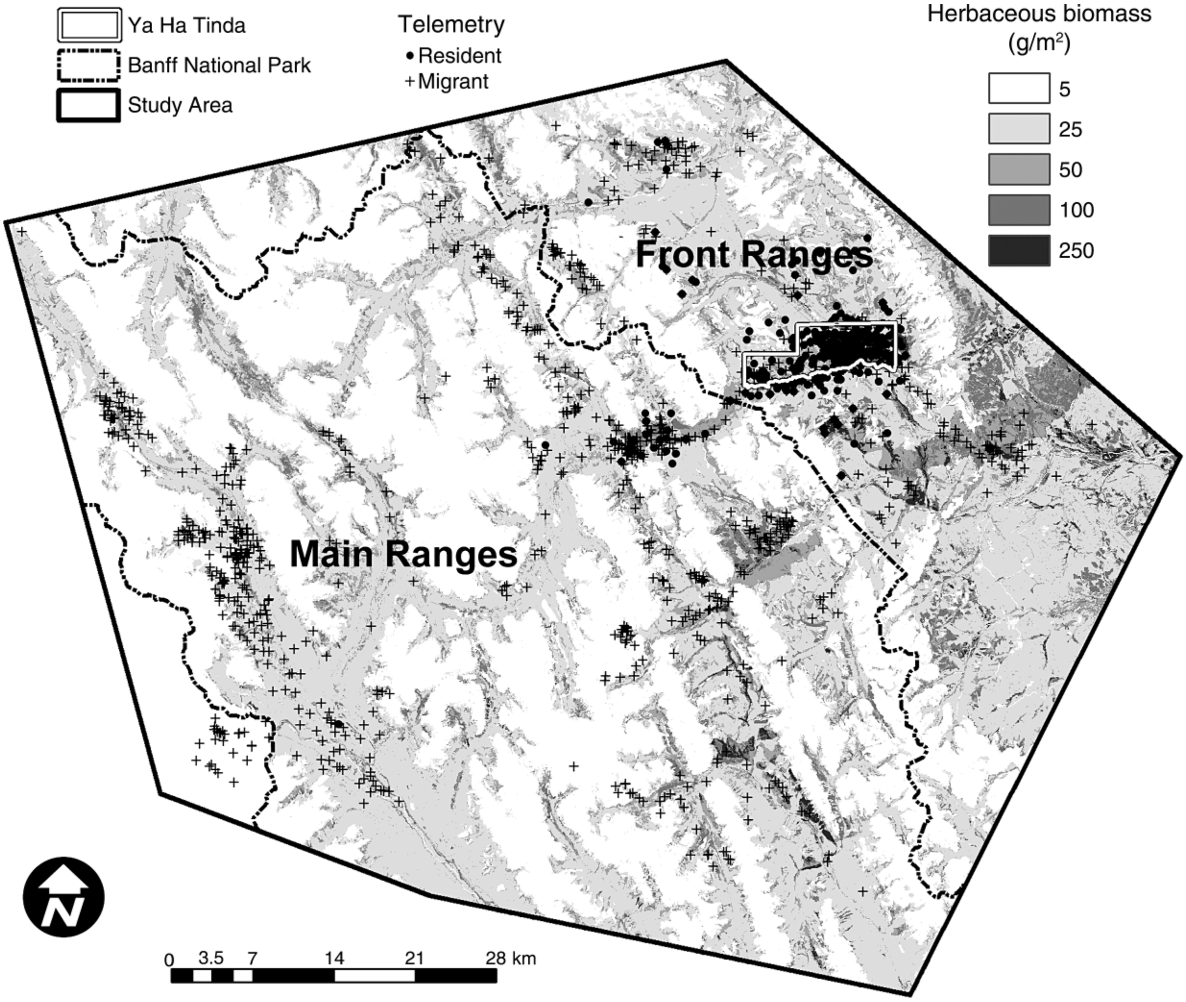


FIG. 3. Study area location on the eastern slopes of the continental divide in the front and main ranges of the Canadian Rockies, Alberta, Canada. Shown is an example of the spatially dynamic forage-biomass model, the predicted total herbaceous forage biomass (g/m^2) during 2003 at the peak of the growing season (4 August); darker areas signify higher herbaceous forage biomass. Each symbol represents an individual elk; resident elk (•) remain on or near the Ya Ha Tinda Ranch (outlined in white) during summer in the front ranges, while migrants (+) migrate throughout the 6000-km^2 study area, mostly to the main ranges in Banff National Park (BNP), as shown by VHF telemetry data for summer 2002–2004.

nisms driving differences in forage quality in our study area. In our second step, we used the dynamic forage biomass model to examine multi-scale elk selection for forage biomass across three different spatial scales for elk using radiotelemetry. Lastly, in our third step, we examined the consequences of selection to the exposure of migrant and resident elk to forage quality by looking at predicted forage biomass and quality at elk telemetry locations using the dynamic forage model combined with diet and fecal-nitrogen analyses.

Forage-maturation–biomass-quality relationships

A key prerequisite for the FMH is that forage quality declines with increasing forage biomass during growth (Fryxell et al. 1988). This allows digestible energy to be maximized at intermediate forage biomass above a threshold intake rate because of the trade-off between intake rate and declining quality (Fig. 1). In this section, we estimate the relationship between forage biomass and forage quality, measured by dry-matter digestibility (DMD) (Van Soest 1982) to confirm this relationship for plant communities during the growing season (Table 1). All herbaceous species were included because elk are herbaceous generalists (Cook 2002, Hebblewhite 2006), whereas only the 13 species of shrubs consumed by elk in this study were included (Hebblewhite 2006).

Forage growth.—Changes in forage biomass over the growing season were documented by repeatedly sampling 30 sites each month between 1 May (or after snowmelt) and 1 October, 2002–2004 (3.4 times/site/season, $n = 254$ total samples, Table 1). Sites were stratified by major factors influencing seasonal plant

TABLE 1. Description of steps used to develop a spatiotemporal model of forage availability to estimate forage biomass and dry-matter digestibility (DMD) at locations of migrant and resident elk (*Cervus elaphus*) in and adjacent to Banff National Park (Alberta, Canada) during the growing seasons of 2002–2004.

Forage-model component	General description of methods and data	Unit of measure
Forage biomass-quality model		
Forage growth	biomass of herbaceous and shrub measured repeatedly (3.4 times/site) at 30 plots growth from 1 May to 1 October	g/m^2
Forage quality	estimated percentage (DMD) of plant species over the growing season in four phenological classes	% digestibility (DMD)
Quality–quantity model	linear and exponential models for the growing season and within each 16-d MODIS interval; used to convert biomass exposure to DMD	DMD vs. g/m^2
Dynamic forage biomass model		
Peak forage biomass	forb, graminoid, and shrub biomass measured at July/August ($n = 983$ sites)	g/m^2
Peak forage model	modeled peak forage biomass using GLM to extrapolate to unsampled areas using a GIS	g/m^2
Seasonal growth adjustment		
Open habitats	ratio of forage growth from May through October to the maximum forage growth, indexed by NDVI derived from MODIS satellite data in 12, 16-d intervals	NDVI (−1 to 1)
Closed-canopy habitats	ratio of predicted forage biomass from May to October to predicted peak; developed using forage growth plots to estimate GLM model for study area; predictions made for midpoint of each 16-d interval.	g/m^2
Seasonal forage model	predicted herbaceous and shrub modeled for each growing season 2002–2004 using annual peak forage biomass model and fixed peak forage adjustments	g/m^2

ecology, including open/closed-canopied vegetation types (defined in Appendix A), low/high elevation (> or <2000 m), three aspect classes (north: 0°–112.5° and 292.5°–360°; south: 112.5°–292.5°; flat), and position in either the front or main ranges of the Canadian Rockies (Fig. 3). During each sampling period, total (green + dead) herbaceous forage biomass (g/m^2) was estimated within 10, 1-m^2 quadrats from the height of a disc pasture meter (Dorgeloh 2002) and a disc height–total biomass regression model (Hebblewhite 2006). The total herbaceous biomass then was converted to green biomass using percentage cover of green growth, which we visually estimated in each quadrat. Predicted herbaceous biomass values were averaged across the 10 quadrats for each site and sampling occasion.

Shrub leaf and twig biomass (current annual growth, g/m^2 up to 0.7 mm twig diameter) was estimated at the peak of the growing season in 2002 and 2003 as the product of stem density (no. stems/0.25 m^2) and biomass/stem (g/stem) measured in three 0.25-m^2 quadrats/site. Biomass/stem of each shrub species was estimated from allometric equations derived by Visscher et al. (2006) in an adjacent study area, supplemented by Hebblewhite (2006). Peak leaf and twig biomass was adjusted for seasonal changes using percentage of maximum leaf and twig biomass present during May to October that was derived from measurements of 5 stems/shrub species in 3 quadrats/site ($n = 15$ samples/site), and averaged for each time period.

Forage quality.—Dry-matter digestibility (DMD, in %; Van Soest 1982) was analyzed for the 64 most abundant plant species (72% of all plants consumed) found in the diets of elk (Hebblewhite 2006). We collected samples (≥2 cm in height) of each species in four phenological classes from 4–10 sites (total $n = 384$ samples) at forage growth plots across the study area (Table 1). Phenological classes were: previous year's growth, newly emergent, matured (included fruiting/flowering and mature growth), and cured (i.e., Griffith et al. 2002). Plant samples were combined into one composite sample per site and dried at <60°C for 48 h. DMD was determined using detergent fiber analysis (Van Soest 1982) at the University of Guelph (Ontario, Canada). For species known to be high in tannins ($n = 24$ species; Robbins 1994), tannin concentrations and crude protein were analyzed using a bovine serum assay (BSA) and Kjeldahl method (Van Soest 1982) at the Wildlife Habitat Nutrition Laboratory (Pullman, Washington, USA). We calculated DMD, adjusted for tannin content, using Eqs. 1 and 2 of Hanley et al. (1992:538); details are given in Hebblewhite (2006). This approach assumes constant tannin concentration during the growing season, which may not be valid (Hanley et al. 1987, Happe et al. 1990), a point to which we return in the *Discussion*. During each repeat-sampling period, DMD for a plot was calculated as a weighted average for the 10, 0.25-m^2 quadrats, with weights derived based on percent cover of species in each phenological stage and species-specific forage-quality estimates.

Forage biomass–quality relationships.—The relationship between DMD and biomass (g/m^2) was estimated separately for herbaceous and shrub biomass using linear and nonlinear regression (Table 1). DMD–quantity relationships were estimated for: (a) the entire

TABLE 1. Extended.

Time unit	Spatial unit
sampled 1/month from 1 May to 1 Oct, annually	30 m^2, measured with 1 plot of 10 × 0.25-m^2 quadrats
four temporal phenology classes	plant samples ($n = 64$ plants per class; $n = 256$ total plant samples)
growing season, 16-d interval	30 m^2
annually for 2001–2004 at 4 August	30-m^2 scale; measured with 1 plot of 3 or 5 × 0.25-m^2 quadrats
from 22 April to 15 October 2002	250 m^2
from 22 April to 15 October 2002	30 m^2, measured with 1 plot of 10 0.25-m^2 quadrats
22 April to 15 October 2002–2004	30 m^2 (open habitats adjusted for growth at 250 m^2)

growing season, (b) each 16-d MODIS (see *Spatial–temporal...: Adjusting for seasonal forage growth*, below) interval during the growing season, and (c) spatially between the front and main ranges of the Rocky Mountains.

Spatial–temporal dynamics of forage biomass

To determine elk selection for forage biomass at radiotelemetry locations of elk, we modeled the spatio-temporal dynamics of herbaceous and shrub biomass across the study area from 1 May 2002 to 30 October 2004 in two steps (Table 1). Our approach builds on the earlier pioneering work of Albon and Langvatn (1992) who predicted crude protein availability to red deer in Norway as a function of elevation. We extend this approach to multiple forage classes over the whole season as a function of multiple variables in addition to elevation. First, we modeled forage biomass available at the height of the growing season using an extensive random stratified design to sample many different habitat types throughout the study area to capture spatial variation in forage biomass (sensu Frair et al. 2005). Second, we used an intensive sampling design approach to link ground-based measures of forage biomass to remote sensing indices of primary productivity to adjust the spatial variation in peak biomass for temporal variation in closed and open habitats. We then related forage biomass from spatial models to predicted forage quality using biomass–quality relationships developed above to be able to evaluate forage-quality differences between strategies (Table 1, Fig. 4).

Peak-season forage biomass.—We modeled herbaceous and shrub biomass (g/m^2) at the peak of the growing season using a similar approach to Frair et al. (2005). We sampled 983 sites in 2001–2004 during the peak (July/August) of the growing season based on a proportional allocation design using key landcover and topographic strata (Table 1). Land cover type was based on Franklin et al. (2001) and is described in Appendix A and Hebblewhite (2006) in detail. Predictive generalized linear models (GLM) were then developed for forb, graminoid, and shrub biomass as a function of spatial covariates, and the top model was selected using backward-stepwise model selection. Spatial covariates included land cover type, year, aspect, hill shade (indexing xeric sites with high solar incidence), a soil drainage index (indexing the area draining into a pixel), slope (°), elevation (m), and distance to the continental divide in kilometers (see Hebblewhite [2006] for covariate details). A small portion of adjacent British Columbia (used by one elk) was not covered by land cover mapping, and so we did not estimate forage biomass for this area (Fig. 3). We then used the top GLM to spatially predict herbaceous (forb + graminoid) and shrub biomass (g/m^2) in a GIS at a 30-m^2 pixel resolution for 2002–2004 using RASTER calculator in ArcGIS 9.0 (ESRI 2002). We cross-validated predictions of herbaceous (forb + graminoid) and shrub biomass (g/m^2) using a randomly withheld 20% sample of the original data not used in model development. Top models for each biomass component are summarized in Appendix A – herein we only use forage models to predict biomass exposure for elk telemetry locations. Predicted and observed biomass was correlated for forbs

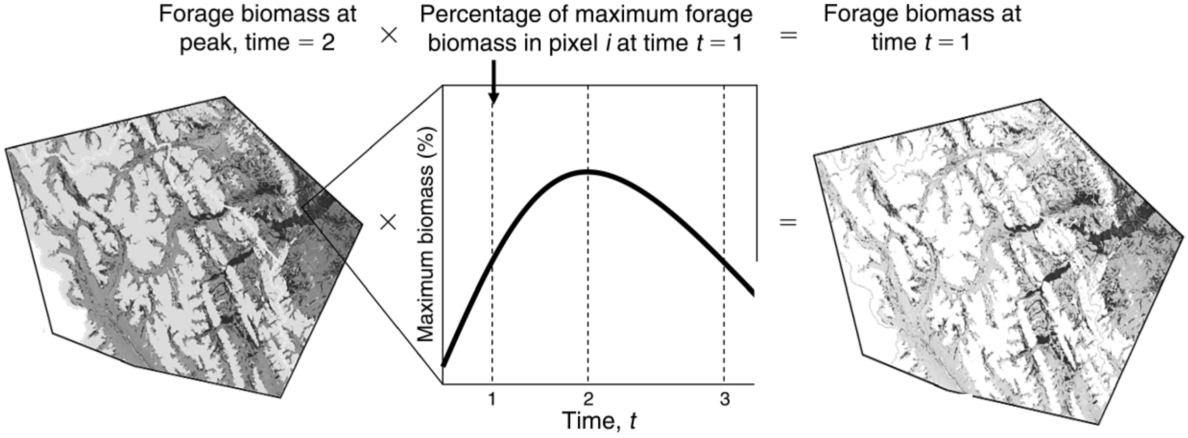


FIG. 4. Schematic of how modeling the spatial distribution of forage biomass in the study area at the peak of the growing season was adjusted for seasonal forage growth (percentage of maximum forage in the second panel) on a pixel-by-pixel basis using the relationships between ground biomass and NDVI to create a dynamic spatiotemporal model of forage biomass across the study area. In this example, peak biomass at 8 August 2004 (time 2) is adjusted for the lower percentage of maximum biomass at 8 May 2004 (time 1) to model lower forage biomass at time 1 across the study area, on a pixel-by-pixel basis. As in Fig. 3, darker areas signify higher herbaceous forage biomass.

(Pearson's $r = 0.55$, $P < 0.005$) and graminoids (Pearson's $r = 0.56$, $P < 0.005$). The total shrub biomass model showed weaker predictive capacity (Pearson's $r = 0.37$, $P < 0.001$) because of high variability in shrub biomass (Hebblewhite 2006).

Adjusting for seasonal forage growth.—Seasonal adjustments of biomass at peak season were made using different approaches in open- and closed-canopied cover types (Table 1). In open habitats we used the normalized-difference vegetation index (NDVI), an index of primary productivity (Tucker and Sellers 1986), derived from MODIS (moderate-resolution imaging spectroradiometry) satellite imagery (Huete et al. 2002) to predict forage growth. NDVI values from MODIS were obtained at a 250-m^2 resolution in 16-d interval composite images from 22 April to 30 October 2004 (see Appendix B; MODIS imagery *available online*).[4] To reduce noise caused by occasional cloud or other atmospheric attenuation factors present in the NDVI time series, we adopted a noise-reduction algorithm over a smoothing window of three time intervals for each MODIS pixel (Kawamura et al. 2005, Pettorelli et al. 2005*b*). Our smoothing algorithm consisted of first screening pixels of low quality using the MODIS data quality field (Huete et al. 2002). Next, we screened pixels in a three-window sequence based on pixel values before and after, and the trend in growth (i.e., whether the pixel was before or after the peak in NDVI) using a 25% decline threshold (Kawamura et al. 2005, Appendix B). The estimated biomass (B_{ij}) for a 30 m^2 pixel, i, for each 16-d interval, j, was then estimated as

$$B_{ij} = B_{pi}\frac{\mathrm{NDVI}_j}{\mathrm{NDVI}_{\max}} \qquad (1)$$

where B_{pi} was the modeled biomass at peak season in cell i, NDVI_j is the NDVI value for a 250-m^2 MODIS pixel encompassing the site pixel i for the 16-d time period j, and $\mathrm{NDVI}_{\max}$ is the maximum NDVI value observed for the pixel during a season j. B_{ij} was calculated for both herbaceous and shrub biomass. This approach was justified because ground estimates of herbaceous biomass were correlated with NDVI from MODIS (Appendix B), and the peak of shrub and herbaceous growth was correlated (Pearsons' $r = 0.51$, $P = 0.001$, $N = 311$ plots, Hebblewhite 2006). Additionally, our approach assumed that seasonal changes in forage growth in the year we obtained NDVI data (2004) were similar to 2002 and 2003. We test this assumption in the *Growing-season characteristics* section, below.

Because NDVI does not predict understory growth under closed forest canopies (Chen et al. 2004), we modeled forage growth in closed-canopied areas using data from the 30 repeatedly sampled vegetation sites described in the *Forage-maturation and biomass-quality. . .: Forage growth* section, above (Table 1). Green herbaceous biomass (Y) was modeled for a 30-m^2 pixel as a quadratic function of Julian sampling date (JD; day 1 is 1 January), year, and landscape covariates in a Gaussian GLM as follows:

$$\begin{aligned} Y_{ijk} = {} & \beta_0 + \beta_1(\mathrm{JD}_k) - \beta_2(\mathrm{JD}_k)^2 + \beta_3(\mathrm{YEAR})_{ij} \\ & + \beta_4 X_{4i} + \cdots + \beta_n X_{ni} + \varepsilon \end{aligned} \qquad (2)$$

where i = sites $1\ldots n$, and j = sampling year $1\ldots m$, and k = within-season sampling time $1\ldots p$, and X_i were elevation, slope, aspect class, and distance to continental divide. The top model was used to predict forage biomass in closed-cover pixels for the midpoint JD of each time 16-d interval, $i = 1$ to n. The ratio of predicted biomass at time interval i to the maximum value

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[4] ⟨http://modis.gsfc.nasa.gov⟩

observed at the peak of the growing season (i.e., $\text{Biomass}_i/\text{Biomass}_{\max}$) was then used to adjust peak biomass within season following Eq. 1 as for NDVI. Where predicted biomass <0 g/m^2, such as at high elevations early and late in the growing season, the value was set to 0 g/m^2. This functionally allowed the start and end date of the growing season to vary for each pixel until biomass >0.

Dynamic seasonal forage model.—To derive temporally dynamic estimates of herbaceous and shrub biomass (g/m^2) in a 30-m^2 pixel during the growing season, we combined the closed and open-habitat models (Table 1, Fig. 4). We multiplied peak biomass for each pixel for each growing season (2002–2004) by the appropriate percentage of maximum ratio for open and closed habitats for each 16-d MODIS interval (Table 1). Note that peak biomass was modeled at a fine scale (30 m^2), but adjusted in open habitats for seasonal growth using NDVI at a larger 250-m^2 scale. This allowed for spatial variation based on empirical NDVI measurements in open habitats (more important for elk foraging, Cook 2002) than the statistical approach for closed habitats which assumed similar relationships based on Eq. 2 across the study area.

Growing-season characteristics

To test for the phenological mechanisms of differences in plant forage biomass and quality, we compared characteristics of the growing season (start, end, duration) and plant phenology between migrant and summer home ranges of elk. We developed individual forage growth curves for green herbaceous biomass for each of the 30 repeat sampled sites using quadratic GLM's (identity link) of the following form:

$$Y_{ijk} = \beta_0 + \beta_1(\mathrm{JD}_{ijk}) - \beta_2(\mathrm{JD}_{ijk})^2 \quad (3)$$

where i = site $1 \ldots n$, j = sampling year $1 \ldots m$, and k = sampling occasion $1 \ldots p$. Growing-season start and end dates were defined following Jobbagy et al. (2002) (see Appendix C). Peak date of green forage biomass was estimated by taking the derivative of Eq. 3 with respect to Y for each site. The influence of environmental covariates on each of the four phenological parameters (start, end, peak, and length of growing season) was examined using the Gaussian GLM:

$$\theta_{ij} = \beta_0 + \beta_1(\mathrm{YEAR})_{ij} + \beta_2 X_{2i} + \cdots + \beta_n X_{ni} + \varepsilon \quad (4)$$

where θ_{ij} is the phenological parameter at site i in year j (start, end, peak, duration), and $X_{2..n}$ are the independent variables year, open/closed, north, south, and flat aspects, elevation (m), and distance to continental divide (km) for site i. The best predictive model with the highest r^2 was selected using backward-stepwise model selection, clustering on sites (Pendergast et al. 1996).

Plant phenology.—Differences between migrant and resident elk in the phenology of forbs, graminoids, and shrubs were tested using the 30 repeatedly sampled sites described above. The average percent species cover was recorded in 10 quadrats during each sampling occasion in four phenological classes: old growth, newly emergent, matured (included fruiting/flowering and mature growth), and cured. Following Griffith et al. (2002), each phenology class was assigned an ordinal score: 1 = previous year vegetation, 2 = newly emergent, 3 = mature, and 4 = senesced/cured. The frequency-weighted phenology score was then calculated for each species, and then by site, to derive the median phenology score by sampling date. Median phenology scores indexed younger plant growth, but not necessarily plant quality because old and cured plants would have similar quality, but phenology scores of 1 and 4. Differences in median phenology scores were tested using ANOVA with migrant summer range in the front or main ranges, open/closed, and month as categorical variables, clustered on sample sites as above. Two-way interactions were included, and Bonferroni post hoc tests were used to test which months and month–migratory status interactions were significant (Zar 1995). To test that differences in median phenology scores also translated to real differences in exposure to the most nutritious forage class, the proportion of newly emergent plants was compared between front and main ranges of the Rocky Mountains, open- and closed-canopied areas, and high and low elevations.

Elk forage selection at multiple scales

In the second major section of our methods, we use the dynamic model of seasonal forage biomass and elk telemetry locations to develop elk resource-selection functions for forage biomass by migrant and resident elk to test forage-selection predictions of the FMH at multiple spatial scales (Fig. 2).

Elk telemetry-data collection.—Elk were captured during winter (15 January to 31 March) from 2002 to 2004 at the Ya Ha Tinda winter range using corral traps baited with alfalfa hay (95% of all elk) or on secondary, more isolated winter ranges, using helicopter net gunning (5%) (University of Alberta [Edmonton, Alberta, Canada] Animal Care Protocol number 353112). We outfitted 119 individual female elk with 101 VHF (very high frequency) radio collars and 27 GPS collars (LOTEK, Aurora, Ontario, Canada); 9 elk wore both VHF and GPS consecutively during the study. Eighty percent of collared elk were adult females (>2.5 years old), 10% were subadults (<2.5 years old), and 10% were yearlings (<1.5 years old); 59% were migrant ($n = 70$ individuals) and 41% were resident ($n = 61$ individuals). Both GPS- and VHF-collared elk were located again aerially or from the ground weekly between 1 May and 31 October 2002–2004. Mean location error from the Cessna Skymaster 337 telemetry aircraft was 218 m ($n = 20$ blind trials). Using a Bessel function to model GPS collar error, we found 50% of locations were within 34 m of the true location, and 95% were within 113 m (Hebblewhite 2006). Habitat-induced

GPS bias was low enough with LOTEK GPS collars (<10%; Hebblewhite 2006) not to influence habitat analyses (e.g., Frair et al. 2004). VHF data were screened so that elk had ≥10 VHF locations per summer, and GPS-collar data were resampled to a consistent 2-h location schedule among individuals. We obtained an average of ~29 VHF locations per summer per elk from 57 and 44 VHF-collared migrant and resident elk, respectively, and an average of 1545 locations/summer/elk from 19 and 8 GPS collared migrant and resident elk, respectively. During each 16-d interval an average 2.6 VHF locations and 144 GPS locations were collected per elk. We defined "migration" as movements between nonoverlapping seasonal summer ranges (Craighead et al. 1972), and for nonmigratory resident elk, used the mean spring and fall migration dates of migrants to determine summer resident locations used in analyses.

Landscape-scale selection of summer home ranges.—Because both migrants and residents have equal availability of areas to select summer ranges at the scale of the study area, the decision to migrate reflects selection at Johnson's (1980) second-order scale (Fig. 2). To compare selection at the second-order scale, we contrasted landscape covariates of resident and migrant elk summer home ranges that were derived from a multiyear 100% minimum convex polygon for each individual elk using Hawthtools 3.19 (Beyer 2005). Landscape covariates included elevation (m), distance to the continental divide (km), herbaceous and shrub biomass on 4 August, growing-season length, start of growing season, and the richness of 100-m elevation classes and nine cardinal aspect classes surrounding each pixel (e.g., Mysterud et al. 2002). Elevation- and aspect-class richness (number of unique values) was calculated within a 1900-m radius (mean 24-h movement rate; M. Hebblewhite, *unpublished data*). Average growing-season start and length within each minimum convex polygon were estimated using GIS extrapolations of Eq. 3. Differences in multiple covariates between migrant and resident summer home ranges were tested using MANOVA (Zar 1995). Correcting for multiple comparisons, a one-way ANOVA was subsequently used to test each covariate for the magnitude of the difference (Zar 1995).

Selection within summer home ranges.—We assessed elk resource selection at two levels within summer home ranges: within the entire home range and along movement paths. For these finer scale analyses, we used only GPS locations from 18 migrant and 8 resident elk collared in 2002–2004. Within summer ranges, we evaluated selection for forage biomass using resource-selection functions (RSF) based on a use/availability design (Manly et al. 2002). We measured forage availability using a constant density of 10 random points/km^2 of elk summer range area for each elk's annual 100% minimum convex polygon. For time-specific covariates, like forage biomass, values were derived from the 16-d interval matching each elk location, or at random for the availability locations during the same period. The RSF was estimated as

$$\hat{w}(x) = \exp(\hat{\beta}_1 x_1 + \hat{\beta}_2 x_2 + \cdots + \hat{\beta}_n x_n) \tag{5}$$

where $\hat{w}(x)$ is the relative probability of use as a function of covariates $x_{1\ldots n}$, and $\hat{\beta}_{1\ldots n}$ are the coefficients estimated from logistic regression (Manly et al. 2002). See Manly et al. (2002) and Johnson et al. (2006) for discussion of the use of logistic regression to estimate the exponential RSF model.

Second, elk resource selection along movement paths (Fig. 2) was analyzed using conditional fixed-effects logistic regression (Hosmer and Lemeshow 2000). In conditional fixed-effects logistic models, responses (e.g., 0, 1) are constrained by pairing used and available sites (Hosmer and Lemeshow 2000, Compton et al. 2002). Five available sites were paired to each elk GPS location by generating random locations at the same distance as the observed step length for each individual GPS location using Hawthools 3.19 (Beyer 2005). Using the conditional logit model, the conditional RSF, $\hat{w}(x_{ij})$, was estimated following

$$\hat{w}(x_{ij}) = \exp(\hat{\beta}_1 x_{ij1} + \hat{\beta}_2 x_{ij2} + \cdots + \hat{\beta}_n x_{ijn}) \tag{6}$$

where $\hat{w}$ is the relative probability of the jth resource unit being selected at the ith group for covariates x_n, and $\hat{\beta}_{1\ldots n}$ are the coefficient estimates for each covariate. Each GPS location represents the ith group, at which an elk makes one of j choices from the five random points. In conditional logit (CLOGIT) models n is the number of groups of matched locations for model selection (Pendergast et al. 1996). We estimated CLOGIT models using STATA 8.0 (StataCorp 2003)

To test whether elk were selecting for intermediate levels of forage biomass at each spatial scale, we evaluated an a priori set of candidate models for resident and migrant elk selection for herbaceous and shrub forage biomass separately, and compared linear, quadratic, and the best-fitting nonlinear fractional polynomial (Hosmer and Lemeshow 2000) functions using AIC$_c$ (Burnham and Anderson 1998). Because of low model-selection uncertainty (all AIC weights $w_i >$ 0.85; Hebblewhite 2006), for brevity we only report the top overall summer and monthly models for both within home ranges and movement-path scales. We considered evidence for selection of intermediate forage biomass to be a positive quadratic function where selection peaks at intermediate biomass. We estimated the quadratic selection peak by taking the derivative with respect to forage biomass (Y) to determine the value of X (biomass) selected for by elk. Both herbaceous and shrub biomass were considered simultaneously in model selection. While assessing elk selection for intermediate biomass in this analysis, we controlled for the effects of the independent covariates of elevation, hill shade, soil moisture, slope, and land cover types, but report this

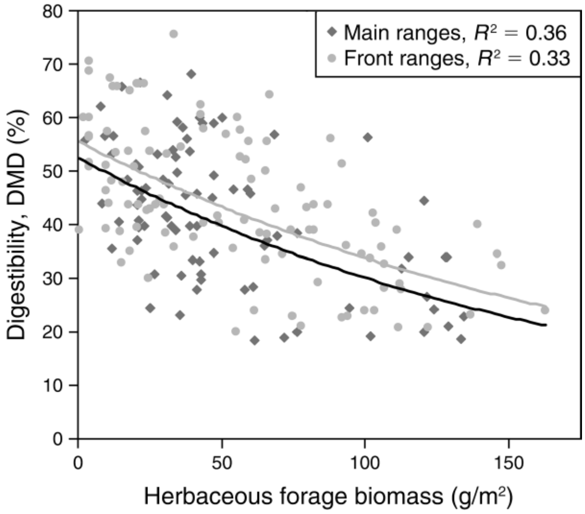

FIG. 5. Dry-matter digestibility (DMD) as a function of herbaceous forage biomass from phenology plots repeat-sampled over the course of growing seasons 2002–2004. Herbaceous biomass is shown with the best-fit exponential decline model for the entire growing season for the main ($R^2 = 0.36$, $P < 0.005$) and front ($R^2 = 0.33$, $P < 0.005$) ranges. There was no relationship between percentage digestibility and biomass for shrubs.

elsewhere (Hebblewhite 2006), herein focusing only on testing the FMH. Thus forage coefficients are the partial slopes of forage selection, holding all other covariates (including the other forage type, shrub or herbaceous) constant (Hosmer and Lemeshow 2000). At the summer home-range scale, we accounted for within-elk heterogeneity using clustering (Pendergast et al. 1996). At the path scale, however, because neither clustering nor random effects can be implemented in CLOGIT models, we controlled for unbalanced sampling between individual elk using sample weighting (Pfefferman 1993, StataCorp 2003).

Validating RSF models.—Model validation was used to assess the generality and predictive capacity of the top RSF models (Boyce et al. 2002). At both scales the top models for the summer and monthly periods were validated using VHF telemetry data from 58 migrant and 43 resident elk by comparing the area-adjusted frequency of used VHF locations to the area-adjusted frequency of available predicted probabilities within 10 equal availability "bins," similar to *k*-folds cross-validation (Boyce et al. 2002). The correspondence between the ranked RSF-availability bins and frequency of predicted VHF use was compared using Spearman's rank correlation (r_s).

Exposure of elk to forage biomass and digestibility

Ultimately, from the individual elk's perspective, what matters is not the mechanism of selection so much as the actual exposure to forage quality that occurs at the smallest scales. If residents were capable of compensating for foregoing migration by adopting forage selection strategies within the summer home range, final exposure to forage biomass and quality may not differ between migrants and residents. Thus, in the third major step in our methods, we examine the consequences of forage-selection patterns to elk's exposure to forage quality and biomass. Forage exposure was defined as the forage biomass (g/m^2) or DMD available at elk telemetry locations for all 67 collared migrant and 47 collared resident elk (including GPS and VHF collars) during the growing seasons of 2002–2004. First, we estimated exposure to herbaceous (forb + graminoid) and shrub forage biomass using forage models developed above by matching the location with the corresponding 16-d forage biomass prediction. Then, we converted total biomass to expected herbaceous forage quality (DMD) using forage quality–biomass relationships developed in the *Forage-maturation–biomass-quality relationships: Forage biomass-quality relationships* section, above. For herbaceous biomass we used quality–biomass relationships for each individual 16-d MODIS interval to convert corresponding biomass estimates to DMD (Appendix D). For shrub biomass, which did not vary in DMD within 16-d intervals (see *Results*, below), we used mean DMD values for each interval.

We tested for differences between migrant and resident elk for exposure to (a) herbaceous biomass, (b) shrub biomass, and (c) DMD using linear mixed-effects models (Skrondal and Rabe-Hesketh 2004). We tested for main effects of migratory strategy and time (16-d intervals), and their interaction. We also controlled, if necessary, for annual differences and open/

TABLE 2. Percentage dry-matter digestibility (DMD) for five phenological stages for forbs, graminoids, and shrubs, including twigs and leaves, during growing season 2004.

	Forb DMD (%)		Grass DMD (%)		Shrub twig DMD (%)		Shrub leaf DMD (%)	
Phenological stage	*n*	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD	*n*	Mean ± SD
New	55	66.1 ± 6.7	25	61.5 ± 9.8	19	66.4 ± 4.9	6	71.2 ± 5.9
Flower	40	65.0 ± 8.1	13	54.5 ± 4.8	9	68.3 ± 3.1	6	69.6 ± 4.9
Fruit	33	61.6 ± 8.9	24	47.7 ± 8.1	14	59.5 ± 6.7	3	71.4 ± 5.4
Mature	48	62.9 ± 9.1	22	48.3 ± 6.1	17	63.7 ± 9.1	3	65.4 ± 8.5
Cured	18	46.7 ± 9.8	29	38.7 ± 6.2	n.a.	58.0 n.a.	n.a.	n.a.
Mean		63.4		43.8		63.1		65.9

Notes: Percentage DMD was calculated following methods of Hanley et al. (1992) that account for tannin digestion inhibition of forbs and shrubs; n.a. = not applicable.

TABLE 3. Summary of top forage-growth models for the eastern slopes of Banff National Park, during the growing seasons, 1 May to 15 October 2002–2004.

					Variable estimates, mean (SE)			
Parameters	F	df	P	R^2	Intercept	Dist. divide (km)†	Elevation (m)	Open
a) Growing-season start	22.12	4, 9	<0.00005	0.59	65.5 (17.11)	−0.45 (0.095)	0.051 (0.008)	−16.7 (4.53)
b) Peak forage-biomass date	5.49	2, 26	0.0024	0.28	196.6 (5.88)	n.a.	n.a.	12.8 (4.37)
c) Growing-season end	0.01	9, 24	n.a.	n.a.	281.6 (1.79)	n.a.	n.a.	n.a.
d) Growing-season length	11.71	4, 24	<0.00005	0.51	262.6 (24.29)	0.59 (0.181)	−0.54 (0.010)	22.9 (7.02)

Notes: Parameter estimates for the top models are shown (with associated robust SE in parentheses). Coefficients are interpreted as delaying the start or date of peak biomass or lengthening the growing season if their coefficients are negative. Models were estimated clustered on individual plots across years to reduce autocorrelation. Reference categories for the intercepts of models are (a) the start of the growing season, for flat and north-facing closed-canopy habitats; (b) the date of peak, for flat closed-canopy habitats during 2002 and 2003; (c) the end of growing season, for flat/south-facing closed-canopy habitats; and (d) season length, for closed-canopy south-facing and flat habitats (n.a. = not applicable).

† Distance from the continental divide.

closed habitat type. A random intercept was included to account for heterogeneity between individual elk (Skrondal and Rabe-Hesketh 2004), and a term (AR1) to account for autocorrelation within elk (Baltagi and Wu 1999), using XTREGAR in STATA 8.0 (Baltagi and Wu 1999, StataCorp 2003). Herbaceous biomass was ln-transformed to satisfy normality assumptions, while shrub biomass and DMD was normally distributed (tested with normal *P–P* (probability–probability) plots). Backward-stepwise model selection was used to select the best model.

Diet composition and fecal nitrogen.—Because elk exposure to forage quality may not reflect actual intake, we also determined whether the above patterns in forage exposure reflected expected differences in diet quality observed in dietary composition and fecal nitrogen at the plant-patch scale. We were unable to observe individual plants that migrants and residents fed on, and thus consider diet composition and fecal nitrogen as aggregates at the plant-patch scale.

Pellet samples were collected for diet-composition analyses during June to September 2002. Each sample constituted a composite of five individual pellets selected from 10 pellet groups in a 2–5 ha area, stratified by migrant and resident ranges. Fecal plant-fragment analyses were conducted at the Wildlife Habitat Nutrition Laboratory (Pullman, Washington, USA). Plant species composition was collapsed to the forage class level (forb, graminoid, shrub) for resident and migrant elk (see Hebblewhite [2006] for species-specific details). Differences between migrant and resident elk plant composition were analyzed using ANOVA with main effects as migration status, month, and forage class, with all two-way interactions in Stata 8.0 (StataCorp. 2003). Percentage was arcsine square-root transformed to meet normality assumptions (Zar 1995). We used Bonferroni post hoc multiple comparisons with an experiment-wise error rate of $\alpha = 0.10$ to test for differences between migratory strategies by month and forage class, and their interaction (Zar 1995).

Monthly migrant and resident fecal nitrogen values were compared from pellets collected from June to August 2004 as an index of diet quality. Only fresh fecal samples (>50% were <10 min old, remainder <2 d old) were sampled from migrant and resident ranges, and represented composite collections from different individual pellet groups. Samples were immediately dried at 50°C for 48 h, and later analyzed for nitrogen content at the Wildlife Habitat Nutrition Laboratory (Pullman, Washington, USA). We tested for the main and interactive effects of month (June, July, August) and migratory strategy in a two-factor ANCOVA with distance to continental divide as a continuous covariate.

RESULTS

Forage-maturation—biomass-quality relationships

Digestibility of green herbaceous biomass declined exponentially as biomass increased (Fig. 5) over the entire growing season. Early in the growing season (before 25 June) when forage quality overall was high and biomass was low, there was a weak or no relationship between biomass and forage quality (Appendix D). There was no difference in the rate of decline in herbaceous-forage quality with increasing biomass between the front and main mountain ranges, ($P = 0.43$). Digestibility of total shrub biomass was a constant function of biomass over the growing season (linear regression $P = 0.55$) and within individual 16-d intervals (Appendix D). There was a small (1.5% higher, Appendix D) but significantly higher mean digestibility of shrub-leaf DMD (dry-matter digestibility) ($F_{1,17} = 3.47$, $P = 0.002$), but not twig DMD ($F_{1,17} = 0.32$, $P = 0.57$) in the main ranges. DMD was highest for forbs and shrub leaves and lowest for graminoids during almost all phenological stages (Table 2). Shrub leaves were consistently (average of 2.7%) higher in DMD than were twigs (Table 2).

Spatiotemporal dynamics of forage biomass

Seasonal forage growth.—Under closed canopies, herbaceous biomass peaked consistently on 7 August in every year of the study (no differences between years). The top combined herbaceous-forage growth model ($F_{6,24} = 16.2$, $P < 0.0005$, $n = 30$ plots) indicated that

TABLE 3. Extended.

Variable estimates, mean (SE)			
North aspect	South aspect	2004	2003
n.a.	−8.0 (4.25)	n.a.	n.a.
17.2 (6.28)	8.3 (6.29)	10.7 (5.89)	n.a.
n.a.	n.a.	n.a.	n.a.
−14.1 (5.55)	n.a.	n.a.	n.a.

herbaceous-forage growth decreased at higher elevations (Elev) and drier sites (Hillshade) but increased on south aspects (South), explaining 57% of the variation in herbaceous biomass (H, in g/m^2):

$$H = 37.7 + 1.90(\mathrm{JD}) - 0.0043(\mathrm{JD}^2) - 0.10(\mathrm{Elev}) + 20.3(\mathrm{South}) - 0.20(\mathrm{Hillshade}) \quad (7)$$

where JD = Julian date (day 1 = 1 January). Using Eq. 7 we predicted herbaceous biomass at the midpoint JD for each 16-d interval for each closed-canopy pixel.

Growing-season characteristics

Growing season.—Mean growing-season start date was JD = 124, or 3 May, and the top model explained 50% of the variance in start date (Table 3). Start dates were not different between any years of the study, confirming similar annual phenological trends. The growing season started 2.2 days earlier every 1 km east of the continental divide (Table 3), and was delayed by almost 50 days for every 1000-m elevation gain. The start of the growing season was 8 days earlier on south relative to flat and north aspects, and 17 days earlier in open habitats (Table 3). Mean peak of forage biomass occurred on 3 August (JD = 216). The linear regression model for peak date explained 28% of the variance in peak date (Table 3). Forage biomass peaked 17.2 days later on north aspects, and 8.3 days later on south relative to flat aspects, although south aspects were variable (Table 3). Biomass in open-canopied habitats peaked 12 days later than closed-canopied habitats. The only year that differed phenologically was 2004, when the growing season peaked 10.6 days later than in 2002 or 2003, but this difference was still <1 MODIS interval. Notably, elevation and distance to the continental divide did not influence the date of peak growth, indicating that growth peaked consistently across the study area, even though growth started earlier in the eastern portions of the study area. Most sites had not crossed the end of the growing-season threshold by 15 October of each year (71% of sites), and the best end-of-growing-season model predicted a constant end to the growing season of JD = 283, or ~9 October (Table 3). Modeling the length of the growing season was more successful, with the best model explaining 51% of the variance in growing-season length (Table 3). Growing-season length increased by ~1 day for every 2 km east of the continental divide and decreased almost 54 days with every 1000-m elevation gain. Growing-season length was almost 22 days longer in open habitats compared to closed, but was 14 days shorter on north-facing aspects compared to flat or south-facing aspects (Table 3).

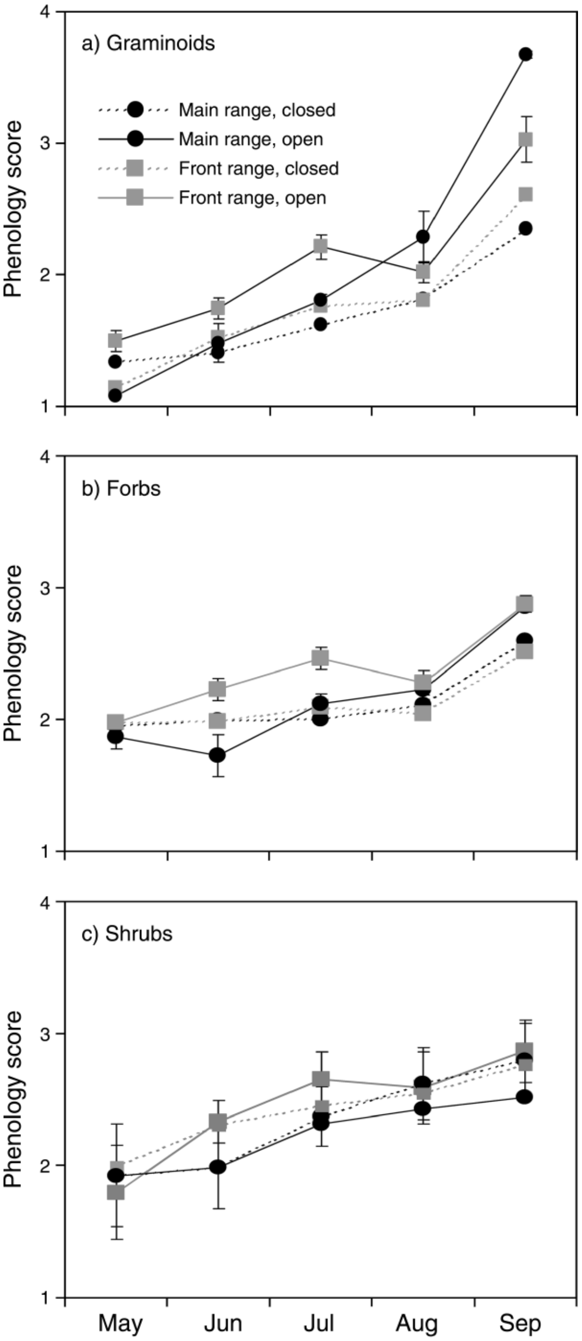

FIG. 6. Mean (a) graminoid, (b) forb, and (c) shrub forage species phenology scores (1 = old, 2 = newly emergent, 3 = mature, 4 = cured) in the front (resident elk area) and main (migrant elk area) ranges, by open vs. closed-canopy habitat type on the eastern slopes of Banff National Park, 2002–2004. Note that for clarity SE bars are only displayed for open habitats; varied shades of gray are used for legibility.

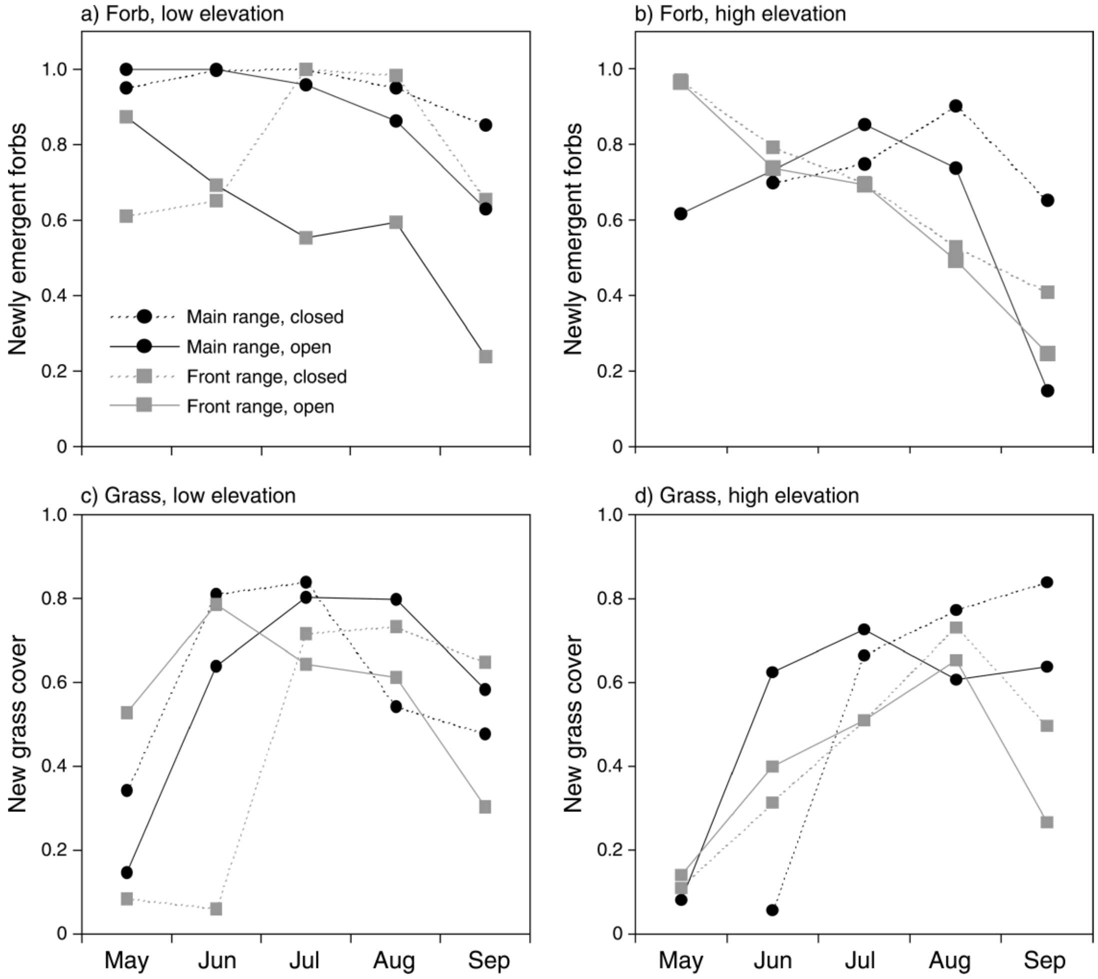

FIG. 7. Proportion of forage cover (biomass) in the newly emergent (highest forage quality) growth stage in the front (resident elk area) and main (migrant elk area) ranges for forbs at (a) low and (b) high elevations, and for graminoids at (c) low and (d) high elevations, on the eastern slopes of Banff National Park, summers of 2002–2004.

Average growing-season length was 157 days, or ~5.3 months.

Species phenology.—The best models for predicting the median phenology score of shrubs forb ($F_{9,18} = 62.8$, $P < 0.00005$), graminoid ($F_{11,18} = 573.1$, $P < 0.00005$), and shrub ($F_{6,19} = 69.1$, $P < 0.0005$) explained 71%, 49%, and 56% of the variance in each, respectively. The main ranges had consistently lower median phenology scores (e.g., delayed growth) than front ranges for forbs ($\beta_{\text{main}} = -0.52$, $P < 0.0005$), graminoids ($\beta_{\text{main}} = -1.09$, $P = 0.034$), and shrubs ($\beta_{\text{main}} = -0.15$, $P = 0.15$), although the difference was not significant for shrubs. Phenological differences in graminoids between main and front ranges remained during the entire growing season (Fig. 6) until September when graminoids cured rapidly on both ranges. Forb phenology was delayed in the main ranges in June ($P = 0.025$) and July ($P = 0.03$), but only in open-canopy habitats. Shrub phenology scores were the same in open- and closed-canopy habitats, and between the front and main ranges (Fig. 6).

Differences in median phenology scores translated to prolonged duration and higher proportion of newly emergent graminoid and forb biomass in the main ranges compared to the front ranges (Fig. 7). At low elevations in the front ranges, the proportion of newly emergent forbs had already peaked by May in open-canopied sites, while they peaked in July/August in closed-canopied sites (Fig. 7a). At high elevations, newly emerged forbs in both open- and closed-canopied sites in the front ranges peaked in May and declined steadily, whereas on the main ranges they peaked in July (open-canopied sites) and in August (closed-canopied sites) (Fig. 7c, d). The percentage of newly emerged graminoids at low elevations of the front ranges was most advanced in the open-canopied sites and declined rapidly at these sites, while graminoid growth was considerably delayed in the closed-canopied sites at low-elevation sites. In contrast, at the high-elevation sites in

TABLE 4. Differences in landscape and phenological covariates between migrant and resident elk summer ranges, 2002–2004, at the second-order home-range scale.

Parameter	Migrant (n = 44)		Resident (n = 67)		Univariate ANOVAs†		
	Mean	SD	Mean	SD	$F_{1,109}$	P	R^2
Elevation (m)	2045.6	186.19	1779.3	143.19	64.74	<0.00005	0.37
Distance from continental divide (km)	39	15.71	56.6	3.79	45.08	<0.00005	0.29
Aspect richness‡	5.11	0.89	3.79	0.91	57.59	<0.00005	0.35
Elevation richness‡	3.12	0.52	2.02	0.49	124.17	<0.00005	0.54
5 Aug. herbaceous biomass (g/m^2)	16.9	5.3	27.7	7.97	31.15	<0.00005	0.23
5 Aug. shrub biomass (g/m^2)	208.9	46.8	268.5	50.14	113.1	<0.00005	0.54
Growing-season length (d)§	172.98	15.32	200.53	7.07	105.9	<0.00005	0.49
Growing-season start (JD)§	160.45	19.32	137.22	9.53	55.4	<0.00005	0.55

Notes: Means are the average availability within the 100% summer range calculated using zonal statistics in ESRI's ArcGIS 9.0 (ESRI 2002); n is the number of radio-collared elk. The overall MANOVA for covariates indicated significant differences between migrants and residents.

† Univariate ANOVA results for each covariate. P values were evaluated at an experiment-wise error rate adjusting for multiple comparisons of $P = 0.05/8 = 0.00625$.

‡ Defined as the number of different aspect or 100-m elevation classes within 360 m of each pixel.

§ Defined based on growing-season parameter models. JD is Julian date, where day 1 is 1 January.

the main ranges there was little difference between phenological growth of grasses (Fig. 7c) while on the front ranges growth in closed-canopied sites was delayed.

Elk forage selection at multiple scales

Landscape-scale selection of summer home ranges.—Migrant and resident summer home ranges differed for all eight landscape covariates (MANOVA $F_{7,109} = 64.74$, $P < 0.0005$, Wilks' $\lambda = 0.349$) even after adjusting for multiple-comparisons (Table 4). Consistent with predictions of the forage maturation hypothesis (FMH; Fig. 2), migrant ranges had 30–40% lower total herbaceous and shrub biomass than residents, were ~266 m higher in elevation than residents, and had higher elevation and aspect richness (Table 4). The start of the growing season on migrant ranges was 23 days later and twice as variable (SD = 19.3 vs. SD = 9.5) than residents ranges (Table 4). Similarly, average growing-season length on migrant ranges was shorter (170 vs. 200 days), but again, twice as variable (SD = 15.5 vs. SD = 7.5) as on residents ranges (Table 4).

Selection within summer home ranges.—Within summer ranges, both migrants and residents selected for sites of intermediate herbaceous biomass in June to August, but not in September when elk selected low biomass (Table 5). Solving the quadratic selection function for the whole summer revealed migrants selected an intermediate herbaceous biomass of 70g/m^2, whereas residents selected a much higher intermediate herbaceous biomass of 114 g/m^2 (Table 5). Migrants consistently selected a lower intermediate herbaceous biomass than residents during every month and overall (Table 5, Fig. 8). When we considered frequency of use compared to availability, migrants used lower herbaceous biomass than residents at the summer home-ranges scale (Fig. 8), corresponding to selection analyses. In open habitats, migrant elk selected an optimum less than the expected maximum (35 g/m^2), whereas the predicted relative probability of use for residents was distributed across the range of available herbaceous biomass (see figures in Appendix E). In terms of selection for shrub biomass, migrant and resident elk showed similar shrub-biomass selection patterns within home ranges except during September. Instead of selecting for intermediate shrub biomass, migrant and resident elk avoided areas of high shrub biomass early in the growing season (June) and selected for sites of high shrub biomass during July and August (Table 5). During September residents selected maximum whereas migrants selected minimum shrub biomass. Out-of-sample VHF data closely matched predictions of resource-selection function (RSF) models at the home-range scale. Predictive capacity (r_s) of migrant models were all $r_s > 0.62$, and residents were $r_s > 0.81$, except during September when $r_s = -0.06$ (Table 5) for both migratory strategies.

At the movement-path scale, selection for intermediate herbaceous biomass was weaker for both migrants and residents (Table 5 vs. Table 6). Migrants selected sites with maximum herbaceous biomass in June and September. In contrast, during July and August migrants selected sites to minimize herbaceous biomass (Table 6; see also Appendix E). Over the entire summer, migrants selected for minimum, not intermediate, herbaceous biomass (Table 6). In contrast, resident elk consistently selected for sites of intermediate herbaceous biomass or minimal biomass at the peak of the growing season during July and August (Table 6). Solving the quadratic for the intermediate herbaceous biomass maximum showed, however, that residents really were selecting for very high (e.g., Table 6) herbaceous biomass near a maximum of 140g/m^2 (Appendix E, Table 6). In terms of shrub selection at the path scale, both strategies followed the same tactic as the home-range scale of selecting for the highest shrub biomass over the whole summer, and for all months except September. In September, they both switched to select

TABLE 5. Top-ranked RSF (resource-selection function) models within home-range scale, June–September 2002–2004.

Elk population and month	*n* used, *n* available†	r_S (SE)	Coefficient of biomass, β (SE)		
			Forage shrub biomass	Herbaceous biomass	(Herbaceous biomass)^2
Migrant elk					
Overall	18 736, 36 119	0.78 (0.01)	0.0024* (0.0001)	0.075* (0.001)	−0.0004* (0.00001)
June	5514, 9791	0.87 (0.03)	−0.0031* (0.0004)	0.133* (0.003)	−0.0006* (0.00003)
July	4970, 9811	0.62 (0.08)	0.0003 (0.0004)	0.186* (0.01)	−0.000831* (0.000049)
August	4412, 9676	9.77 (0.02)	0.006* (0.0003)	0.148* (0.004)	−0.0007* (0.00003)
September	3840, 9841	0.78 (0.01)	−0.001* (0.0003)	−0.0156* (0)	n.a.
Resident elk§					
Overall	8736, 26 966	0.97 (0.03)	0.0045 (0.0004)	0.0805 (0.0023)	−0.0004 (0.00002)
June	2601, 6730	0.89 (0.06)	−0.0017 (0.0009)	0.1697 (0.0074)	−0.0007 (0.00005)
July	2391, 6758	0.95 (0.04)	0.0051 (0.001)	0.1633 (0.0068)	−0.0006 (0.00003)
August	2072, 6650	0.81 (0.01)	0.0106 (0.0009)	0.1258 (0.0064)	−0.0005 (0.00005)
September	1672, 5288	−0.06 (0.09)	0.0012 (0.0006)	−0.0116 (0.0018)	n.a

Notes: Models were estimated using logistic regression, with the coefficient(s) for forage-biomass selection reported, holding effects of other covariates constant. Note that for all models the likelihood-ratio test indicated significant model fit, $P < 0.0005$. Shown for each season-strategy model are the *k*-fold Spearman rank correlation model-validation test (r_S) for VHF elk locations, the coefficients for shrub and herbaceous biomass selection, and their form, whether maximization, minimization, or selection for intermediate (quadratic); n.a. = not applicable.

* Coefficient significant at $P = 0.05$.

† The number of groups in the CLOGIT (conditional logit) model.

‡ Peak biomass was calculated by taking the derivative of the quadratic function, $\text{logit}(Y) = X + X^2$, where logit($Y$) is the relative probability of use and $X + X^2$ are the quadratic functions for forage biomass.

§ For resident elk, the number of parameters is 18 (see Appendix B).

minimum shrub biomass (Table 6). At the movement-path scale, for cross-validation of migrant models, all $r_s > 0.82$, and for residents all $r_s > 0.78$, except during September when $r_s = 0.24$ for migrants and $r_s = -0.333$ for residents (Table 6).

Exposure of elk to forage biomass and digestibility

Forage-biomass exposure.—Here we present only the details of differences between migrants and residents; full model details are given in Appendix F. Residents were exposed to higher overall forage biomass in a manner that varied seasonally (Fig. 9). The top model explained about 78% of the total variance in exposure to herbaceous biomass. Herbaceous-biomass exposure did not differ between migrant and resident elk prior to migration nor after elk returned to the ranch in the fall (Fig. 9a, Appendix F). On summer ranges, however, migrants were consistently exposed to 25–40% lower herbaceous biomass (biomass reduction for migrants $\beta = -11.5 \pm 1.84$ g/m^2 (mean ± SE); $P < 0.0005$) (Fig. 9a). Overall exposure to herbaceous biomass was also higher during 2004 (effect $+31.3 \pm 1.35$ g/m^2 (Fig. 7a), whereas biomass exposure in 2003 and 2002 was similar.

Exposure to total shrub (twig + leaf), and leaf-only shrub biomass was similar for both migrants and residents (overall resident effect $\beta = +0.67 \pm 1.16$ g/m^2, $P = 0.67$) except 9 June ($\beta = +7.54 \pm 3.24$ g/m^2, $P = 0.04$) and 25 June ($\beta = +6.67 \pm 2.46$ g/m^2, $P = 0.007$) when migrants had higher exposure to leaf forage biomass (Fig. 9b, Appendix F). The best linear mixed-effects shrub-biomass exposure models explained less variation than herbaceous models (overall total shrub $r^2 = 0.26$, overall leaf $r^2 = 0.36$) because of the higher variance in individual elk exposure to shrub biomass.

Forage-quality exposure.—Migrant elk had consistently higher exposure to forage of higher digestibility from 9 June through to the end of the 28 August 16-d interval (i.e., 12 September) in the top linear mixed-effects model for DMD exposure (β's for 9 June to 28 August intervals ranged from +3.7% to +10.4%, all P values <0.04, Fig. 9c). The greatest difference in forage-quality exposure occurred during the 25 June interval, when migrants had $+10.4 \pm 0.97\%$ (mean ± SE, $P < 0.0005$) higher forage quality (Fig. 9c). Exposure to DMD was more variable than herbaceous biomass; only 41% (overall r^2) of the variance in DMD was explained by the combination of migratory status, interval, and migrant × status interactions (see Appendix F for full model details). The reduced forage-biomass exposure of migrant elk translated to consistent exposure to higher forage quality, averaging 6.5% (range: 3.7–10.4%) higher forage digestibility in the six statistically different intervals (Fig. 9c). Decomposing DMD to its contributions from herbaceous and shrub components indicated little difference in shrub DMD exposure between strategies, but larger differences in herbaceous DMD that drove overall higher DMD for migrants (Fig. 9c).

Diet composition and fecal nitrogen.—Graminoids were the dominant forage class consumed by both residents and migrants, constituting ≥50% of the diet (Table 7). Diet composition changed seasonally by forage class ($P < 0.0005$) as well as between migratory strategies ($P < 0.06$; overall ANOVA $F_{13,76} = 35.84$, $P < 0.0005$, $r^2 = 0.84$). Migrants consumed less graminoids and more high-quality shrubs (Table 2) during June and July than residents (Table 7), but not during August when both resident and migrant shrub consumption increased to 30% at the expense of graminoid consump-

TABLE 5. Extended.

Herbaceous peak biomass (g/m^2)‡	Shrub selection by elk	Herbaceous selection by elk
90.4	maximize	intermediate
103.9	minimize	intermediate
111.6	maximize	intermediate
100.0	maximize	intermediate
n.a.	minimize	minimize
114.00	maximize	intermediate
116.10	minimize	intermediate
133.80	maximize	intermediate
115.7	maximize	intermediate
n.a.	maximize	minimize

tion. Besides this trade-off between shrub and graminoid, composition of high-quality forbs was higher for residents in July, but increased over summer for both strategies (Table 7).

Nitrogen concentration of feces (FN) of both migrants and residents declined over the growing season ($F_{2,32} = 3.77$, $P = 0.04$). While FN of migrant elk was always higher than residents, the difference was not statistically significant ($F_{1,32} = 1.01$, $P = 0.32$) except during the month of July where migrant FN was 15% higher than that of residents (interaction; $F_{2,32} = 5.63$, $P = 0.008$). Regardless of the nonsignificant main effect of migratory strategy, FN was lower in the eastern part of the study area ($F_{1,32} = 3.80$, $P = 0.05$) with FN declining by −0.8% ± 0.04% (mean ± SE, $P = 0.004$) for every 10 km east of the continental divide, confirming that elk that migrated to western portions of the study area benefited from increased diet quality.

DISCUSSION

Our study was among the first to demonstrate that fine-scale mechanisms of plant phenology, quality, and abundance can predict landscape-scale resource selection of migratory elk, consistent with predictions of the forage maturation hypothesis (FMH) that ungulates migrate to maximize forage quality (Fryxell et al. 1988). Using this approach, we confirmed that migratory elk used resource-selection strategies that exploited fine- and landscape-scale differences in the availability of forage quality to achieve an average of 6.5% higher forage-quality exposure by migrating, in comparison to nonmigratory resident elk. Certainly, other studies have shown migratory ungulates selected intermediate forage biomass in small-scale controlled studies (Wilmshurst et al. 1995, 1999), inferred higher diet quality arising from migration (Morgantini and Hudson 1989, Albon and Langvatn 1992, Yokoyama et al. 2000, Sakuragi et al. 2004), shown habitat-selection patterns that were consistent with migratory benefits (Oosenbrug and Theberge 1980, Mysterud et al. 2002), or used large-scale indices such as NDVI to infer migratory gain (Thomas et al. 2006). However, these previous studies often examined only one component of the link from plant-phenology mechanisms to the consequences of elk resource-selection strategies for forage-quality differences. And no previous studies compared migratory and resident animals to explicitly test the hypothesis against a suitable "control" group. In contrast, our study was unique in providing a comprehensive framework to test the FMH by (1) linking landscape differences in phenology to availability of forage quality for migrant and resident elk through spatial biomass modeling and bi-weekly (every two weeks) quality–quantity trade-off models, (2) evaluating resource-selection strategies of elk at multiple spatial scales to test for intermediate forage-biomass selection, and (3) employing a comparative approach using 119 elk where migrant foraging strategies were contrasted with nonmigratory residents to definitively test the FHM. Certainly, future studies could improve upon our approach by using improved spatio-temporal forage-quality predictions using recent advances in hyperspectral remote-sensing applications

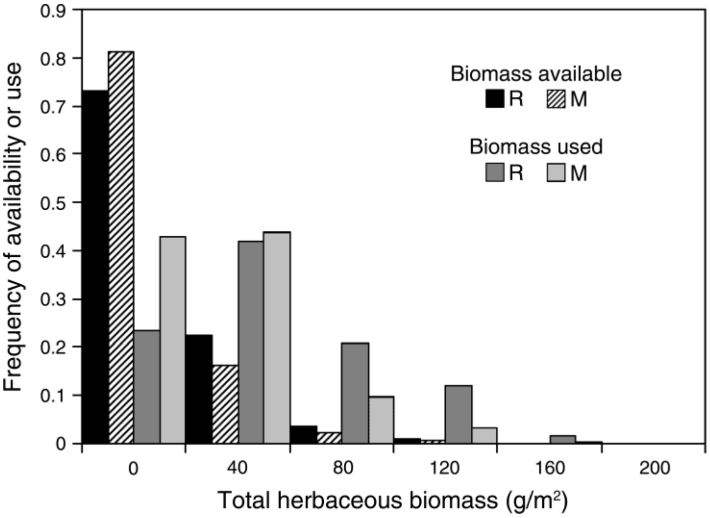

FIG. 8. Frequency of availability and use vs. herbaceous biomass for migrant (M) and resident (R) elk at the summer home-range scale in Banff National Park, Alberta, Canada. Migrant elk had lower biomass available to select at this scale in comparison to resident elk, which had greater forage availability from which they selected higher forage biomass.

TABLE 6. The top-ranked movement-path-scale RSF models, June–September 2002–2004.

Elk population and month	*n* used, *n* available	Likelihood ratio		Correlation		Coefficient of biomass, β (SE)		
		χ^2	P	r_S	P	Forage shrub	Herbaceous	(Herbaceous biomass)^2
Migrant elk								
Overall	18 736, 89 875	1698.8	<0.0005	0.987	<0.0005	0.005* (0.0002)	−0.002* (0.0008)	
June	5514, 26 500	309.9	<0.0005	0.984	<0.0005	0.002* (0.0003)	0.007* (0.002)	
July	4970, 24 255	1040.2	<0.0005	0.906	0.003	0.01* (0.0004)	−0.014* (0.002)	
August	4412, 20 885	1624.8	<0.0005	0.818	<0.004	0.014* (0.0004)	−0.02* (0.002)	
September	3850, 18 265	126.6	<0.0005	0.263	<0.56	−0.003* (0.0004)	0.006* (0.002)	
Resident elk								
Overall	2601, 12 575	474.1	<0.00005	0.987	<0.0005	0.01* (0.008)	0.008* (0.003)	−0.00003* (0.00001)
June	2391, 11 455	158	<0.00005	0.947	<0.0005	0.009* (0.0006)	0.015* (0.005)	−0.00005* (0.00003)
July	2072, 9605	154.5	<0.00005	0.794	<0.006	0.02* (0.0008)	−0.005 (0.005)	
August	1672, 8070	144.32	<0.00005	0.802	<0.005	0.02* (0.0008)	−0.02* (0.005)	
September	8736, 41 705	88.9	<0.00005	−0.333	<0.33	−0.004* (0.0006)	0.04* (0.007)	−0.0002* (0.00005)

Notes: Shown for each season-strategy model are the likelihood-ratio test (all $P < 0.0005$), the *k*-fold Spearman-rank correlation model-validation test (r_S) for the VHF elk locations, and the coefficients for shrub and herbaceous biomass selection and their form, whether maximization, minimization, or selection for intermediate (quadratic).

* Coefficient significant at $P = 0.05$.

† Peak biomass calculated by taking the derivative of the quadratic function.

(Mirik et al. 2005), by distinguishing foraging behavior from GPS collar data (Morales et al. 2005), or by examining diet selection at the individual plant level (Baker and Hobbs 1982). But no other study to date has tested the FMH from the plant-patch to the landscape scale, and none have empirically demonstrated the mechanisms of forage selection that translate to higher forage-quality exposure for migrants.

Starting at the plant-patch level, areas to which elk migrated had delayed and more variable phenological parameters, such as the start of the growing season, than did residents. This was because of strong elevation and topographic gradients in the study area that delayed the start of the growing season as much as 50 days for every 1000-m elevation gain, and half a day for every kilometer closer to the continental divide that elk migrated. Migrant home ranges were on average 240 m higher than resident home ranges, which itself would delay phenology of and provide access to early emergent vegetation by 10–15 days. Because herbaceous dry-matter digestibility (DMD) declined with plant maturation across vegetation communities, as expected under the FMH (Fryxell et al. 1988, Wilmshurst et al. 1995), this ensured that migrant elk would have higher exposure to forage quality merely from selecting home ranges in areas along these topographic gradients. Shrub DMD however, remained consistently high during the growing season, and did not decline with increasing shrub biomass, contrary to expectations under the FMH. However, the FMH was originally developed in savannah, not mixed-plant communities (McNaughton 1985), where shrub biomass contribution was minimal or absent. The absence of a trade-off between shrub biomass and DMD points to an underappreciated, yet important difference between montane and savannah systems revealed by our study. To maximize exposure to shrub forage quality under consistently high shrub DMD, ungulates would be expected to select sites with maximum, not intermediate, shrub biomass. The high DMD and structural features of shrubs combine to emphasize their importance. For example, leaves of deciduous shrub species, such as *Salix* spp. (the most prevalent shrub in elk diet in this system; Morgantini and Hudson 1989, Hebblewhite 2006) not only maintain high digestibility, but have high breakdown rates and permit large bite sizes by leaf-stripping, both of which can contribute to high daily intake rates (Hobbs et al. 1981, Baker and Hobbs 1982, Spalinger and Hobbs 1992). Thus, we would expect ungulates to be able to maximize shrub quality under such conditions by selecting areas of maximum shrub biomass, a novel, but nuanced prediction of the FMH in mixed-plant communities.

Regardless of these complexities, resource selection-analyses confirmed selection for intermediate herbaceous biomass by migrants, and selection for maximum shrub biomass by both migrants and residents. Resource-selection function (RSF) models indicated migrants selected for intermediate herbaceous biomass at the landscape and summer home-range scales, except in the fall when they avoided areas of high herbaceous biomass. While residents statistically selected for intermediate herbaceous biomass, in actuality the "maximum" selected for was much higher than that for migrants, and was at the higher end of availability across habitat types (Appendix A). This confirms residents essentially selected maximum herbaceous biomass. Results were confirmed when comparing simple measures of frequency of use between migrant and residents (Fig. 8). Along movement paths, migrants avoided herbaceous biomass, though the strength of selection was weaker (Tables 5 and 6). In contrast, residents selected intermediate herbaceous biomass along movement paths, but again, the "optimum" was essentially at

Table 6. Extended.

Herbaceous peak (g/m^2)†	Shrub selection by elk	Herbaceous selection by elk
	maximum	minimum
	maximum	maximum
	maximum	minimum
	maximum	minimum
	minimum	maximum
140.3	maximum	intermediate
141.4	maximum	intermediate
	maximum	minimum
	maximum	minimum
86.5	minimum	intermediate

the high end of availability. We interpret these multiscale comparisons to indicate that migrants were selecting for intermediate herbaceous biomass at the landscape and home-range scales. Migrants could therefore "relax" selection at the movement-path scale because overall biomass was low, and forage quality high, as a result of decisions made at larger scales. Wilmshurst et al. (1999) similarly reported stronger selection for intermediate forage biomass at larger spatial scales by Serengeti wildebeest. Similar to nonmigratory moose (Dussault et al. 2005), resident elk were forced to be more selective at finer spatial scales, but still showed selection for high herbaceous-biomass values. For shrub biomass, both migrants and residents consistently selected maximum shrub biomass (Tables 4–6), as expected to maximize energy intake. The only exception to shrub maximization was during June when they avoided areas with high shrub biomass, at a time when herbaceous biomass had the highest quality. Both migrants and residents also switched selection patterns in September, selecting areas with low herbaceous and shrub biomass.

However, shrub and herbaceous-biomass selection do not occur in isolation. The selection strategies of elk discussed here statistically represent the selection of herbaceous and/or shrub biomass given selection for the other biomass component is held constant (i.e., they are partial coefficients). Biologically, in our study area, areas of maximum selected shrub biomass were either shrub meadows or open coniferous stands, whereas selected herbaceous communities were burns, grasslands, and alpine herbaceous meadows (Appendices A and F). Thus, in the mixed-plant communities of our study area, elk were faced with two alternatives, maximize shrub biomass or "optimize" herbaceous biomass, compared to only one decision in homogenous savannah systems (e.g., Wilmshurst et al. 1999). Because shrubs comprised only a maximum of 30% of the diet (Table 7) and were patchily distributed, maturation of herbaceous forage still has the greatest influence on benefits of migration (e.g., Fig. 9c). In other words, because shrub quality was always high, migration in montane systems such as ours still appears driven by selection for intermediate forage biomass. However, in the fall when quality of herbaceous forage declined (Table 2), elk showed stronger selection for areas of shrub biomass (Appendix F) and shrubs increased to 30% of the diet of elk (Table 7). This suggests that leaf drop in the fall may be a contributing factor to fall migration date because after leaf drop, migrants would no longer benefit from higher shrub-forage quality.

These forage-selection strategies yielded migrant forage quality that peaked during late June, when migrants had 10% higher digestibility compared to residents, coinciding with peak lactation costs for female ungulates (Cameron et al. 1993, Cook et al. 2004). During the main migratory period from 9 June to 8 September, migrants were exposed to an average 6.5% higher forage quality. However, residents could have compensated for lower quality by selecting high quality forage at even finer scales than we investigated, for example, at the microsite or plant-part level (Hanley et al. 1992, Spalinger and Hobbs 1992). But fecal nitrogen (FN) for residents was still lower than for migrants during summer, similar to other dietary studies of migratory ungulates (Sakuragi et al. 2004). Dietary FN also increased closer to the continental divide, in agreement with landscape-scale phenology gradients. While FN is known to be sensitive to high tannin content (Robbins et al. 1987), resident consumption of tannin-containing forages (e.g., forbs and shrubs leaves) was lower than that of migrants, and mean tannin levels for forbs and shrub leaves were minimal, only ~0.04 mg BSA (bovine serum assay)/g forage (Hebblewhite 2006). Thus we interpret FN differences as real. Direct behavioral studies of plant-bite selection (e.g., Baker and Hobbs 1982), difficult to obtain for free-ranging elk in mixed landcover types, would be required to test for possible fine-scale dietary selection by residents that could compensate for foregoing migration. But based on the above logic, we maintain that resident diet quality would still be lower in this system even with such fine-scale selection.

In further support of our results of higher DMD for migrants, the way in which we estimated forage quality likely underestimated quality for migrants. We assumed a constant DMD given a particular species and phenological class, regardless of seasonal and spatial variation (e.g., Larter and Nagy 2001, Jorgenson et al. 2002). Forage quality for a species in a given phenology class would likely increase at higher elevations and western areas (Bennett and Mathias 1984, Walsh et al. 1997, Kudo et al. 1999). In addition, because migrants diets were higher in shrub leaves (Hebblewhite 2006), they would have benefited from reduced tannin content of newly emergent shrub leaves (e.g., Hanley et al. 1987, Happe et al. 1990). For these reasons, we consider the 6.5% higher forage digestibility for migrants as conservative. Migrant elk clearly had the nutritional advantage

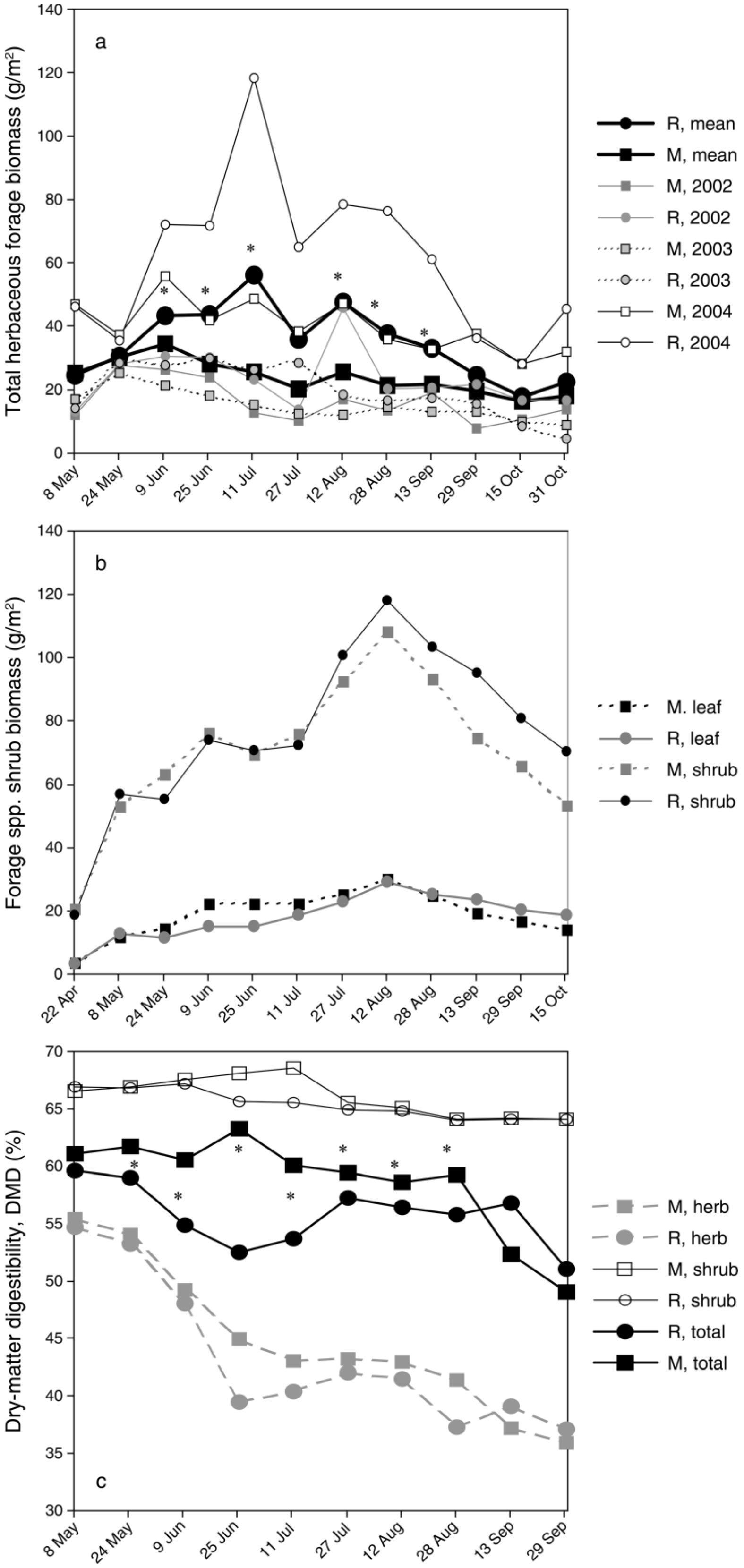
a
Total herbaceous forage biomass (g/m^2)
0
20
40
60
80
100
120
140
8 May
24 May
9 Jun
25 Jun
11 Jul
27 Jul
12 Aug
28 Aug
13 Sep
29 Sep
15 Oct
31 Oct
R, mean
M, mean
M, 2002
R, 2002
M, 2003
R, 2003
M, 2004
R, 2004
b
Forage spp. shrub biomass (g/m^2)
22 Apr
8 May
24 May
9 Jun
25 Jun
11 Jul
27 Jul
12 Aug
28 Aug
13 Sep
29 Sep
15 Oct
M. leaf
R, leaf
M, shrub
R, shrub
c
Dry-matter digestibility, DMD (%)
30
35
40
45
50
55
60
65
70
8 May
24 May
9 Jun
25 Jun
11 Jul
27 Jul
12 Aug
28 Aug
13 Sep
29 Sep
M, herb
R, herb
M, shrub
R, shrub
R, total
M, total

TABLE 7. Relative diet composition by major forage class for migrant and resident elk in the Ya Ha Tinda elk herd, summer 2002.

Elk status, by month	n	Forb (%)		Graminoid (%)		Shrub (%)		Shrub leaf (%)
		Mean	SE	Mean	SE	Mean	SE	
June								
Migrant	4	7.4^{a}	2.52	70.0^{a}†	10.72	22.6^{a}†	7.23	0.36
Resident	2	7.9^{a}	0.67	85.5^{a}†	0.20	6.6^{a}†	0.08	0.46
July								
Migrant	9	8.2^{a}†	1.52	70.8^{a}	3.77	21.0^{a}	2.89	0.41
Resident	5	12.4^{a}†	0.98	72.4^{a}	4.11	15.1^{a}	4.00	0.39
August								
Migrant	7	15.4^{b}	3.65	54.6^{a}	6.39	30.0^{a}	4.00	0.32
Resident	3	12.9^{b}	1.46	59.5^{b}	3.33	27.6^{b}	3.30	0.27

Notes: This analysis does not attempt to correct for bias against detecting forbs and shrub leaves in the diet. Lowercase superscript letters refer to post hoc comparisons following ANOVA within a migratory and forage class, between months; e.g., percentage of forbs in the diet of residents was significantly different between June/July and August, when it increased.

† Post hoc comparisons between migrant classes within a month and forage class; e.g., percentage forb in diet differed between migrants and residents in July. Experiment-wise error was set at 0.10 for post hoc Bonferroni multiple comparisons.

because of mountainous landscape gradients in phenology and herbaceous quality–biomass trade-offs.

But how significant, biologically, is exposure to forage that is 6.5% higher in digestibility? In the definitive test of this question for elk, Cook et al. (2004) experimentally fed captive elk diets of high, medium, and low forage quality during the summer months (with identical winter forage) over several years to isolate the effects of summer forage quality for elk survival and reproduction. Cook et al. (2004) showed that even when summer forage DMD was $>$55%, small increases of 5% were sufficient to significantly increase calf, yearling, and adult female weights, reduce pregnancy rates, reduce calf winter survival, and lead to important lagged effects on future reproduction and survival (Cook et al. 2004). Although Cook et al. (2004) admit their high-quality treatment (67% DMD) exceeded the average summer-forage quality available to elk in western North America, the $\sim$5% difference between their low and medium diets had significant consequences for survival and reproduction (Cook et al. 2004). These results were corroborated in other experimental settings for ruminants. In New Zealand, farmed red deer (males, females, and calves) fed experimental diets of red clover with 3–5% higher digestibility had higher body mass at the end of one year, and females on the high quality diet had increased milk yield than did a control group (Niezen et al. 1993, Semiadi et al. 1993). Domestic sheep foraging on summer diets of high-quality *Salix* spp. leaves (10% higher DMD than the control group) in New Zealand had greater body mass, and had higher pregnancy and lambing rates at the end of the winter (McWilliam et al. 2005). While few other studies empirically demonstrated the effect of a $\sim$5% difference in DMD to population characteristics, the relationship between nutrition and population parameters is well established in less controlled field and modeling studies (e.g., Thorne et al. 1976, Hobbs 1989). Based on these studies, the 6.5% higher DMD of migrant elk in this study should be expected to have important population consequences from a bottom-up forage perspective (Van Soest 1982, Cook et al. 2004).

As evidence of the population impacts of the higher forage quality observed in our study, Hebblewhite (2006) showed mid-winter body mass of 11 resident female calves in our study area were significantly ($P < 0.05$) lower than 8 migrant calves (a 20.6-kg difference), and adult pregnancy rates of 63 residents that were 7% lower than 78 migrants ($P < 0.05$). Differences in forage-quality exposure observed during our study appeared to have potentially important population consequences (Hebblewhite 2006). This is consistent with other empirical analyses linking duration of exposure to high-quality forage in spring to juvenile montane ungulate survival (Pettorelli et al. 2007).

The nutritional benefits of higher forage exposure for migrants will be mediated by environmental stochasticity, but with different effects between migrants and residents because of differences in spatial and temporal variation as a result of the migratory cycle. For example,

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FIG. 9. Average exposure of individual migrant (M) and resident (R) elk VHF and GPS locations in Banff National Park, Alberta, Canada, to (a) total herbaceous biomass, (b) forage and leaf-forage shrub biomass, and (c) percentage dry-matter digestibility (DMD) of herbaceous, shrub, and total forage estimated for migrant (M) and resident (R) elk during May–October, 2002–2004. Asterisks indicate intervals for which migrants and residents differed significantly ($P = 0.05$) in total measures (biomass or DMD) based on the linear mixed-effects model. Digestibility of herbaceous forage was calculated for average biomass values based on regressions between percentage digestibility and biomass from Fig. 4 and Table 2 for herbaceous forage. Digestibility of shrubs was calculated given average percentage digestibility for each MODIS interval from Table 2.

Wang et al. (2006) revealed opposing effects of increased variation in climate or forage productivity on the strength of density dependence in ungulate populations. Temporal variation in climate increased the strength of density dependence, whereas spatial variation in forage production weakened it (Wang et al. 2006). Migrants should thus experience weaker density dependence due to forage than residents because migration increased spatial heterogeneity in forage exposure at the landscape level (e.g., Table 4). The effects of temporal variability (i.e., climate) are more uncertain, because of complexities of how climatic variability play out in mountainous terrain and local climatic downscaling processes (Pettorelli et al. 2005*b*). For example, Petorrelli et al. (2007) showed strong effects of the rate of spring green-up on juvenile survival in montane ungulates. The relative tension between spatial and temporal heterogeneity on population dynamics of migrants and residents will ultimately depend on finer-scale mechanisms, such as whether spatial variability manifests in productivity (biomass) vs. quality (digestibility), and the interaction of temporal variability with predation (e.g., Lima et al. 2002).

Temporal variability could affect residents to decrease the strength of density dependence, for example, if greater variability provided residents greater flexibility in their foraging strategy. Poorer resident forage quality could potentially be counteracted by greater foraging choices provided by the relatively greater variation in peak biomass. Despite overall higher biomass on resident ranges, the temporal coefficient of variation in annual productivity was greater on resident compared to migrant ranges (in repeat-sample plots the temporal CV on the front ranges was 135%, $n = 19$ plots, vs. the main ranges of 69%, $n = 13$ plots). The temporal variability in biomass was driven by the strong correlation between summer rainfall and productivity ($r = +0.87$, $P = 0.09$, $n = 4$ years; see Hebblewhite 2006). In higher rainfall, and hence higher biomass years, residents may have had more opportunities to selectively forage for high-quality plants or plant parts, in effect providing more choices to residents in high-biomass years. Consistent with this hypothesis, Nicholson et al. (1997) found that in a semi-desert system, resident mule deer survival was lower than that of migrants in drought years but higher in years with high precipitation, with higher overall variation in resident survival rates. Thus, residents may be expected to benefit more from temporal environmental stochasticity during summer than migrants.

In contrast, increased temporal variability may increase the strength of density dependence more for migrants because of different localized climatic downscaling processes between migrants and resident ranges (Pettorelli et al. 2005*a*). Climate-change scenarios for the Rocky Mountains predict increased frequency of high spring precipitation or snowfall (April–May) and potentially drier later summers (Scott et al. 2002), but without a consistent trend, just more variation (Stenseth et al. 2002). High spring precipitation would manifest as snowfall at higher elevations on migrant ranges (Luckman and Kavanagh 2000), but as rainfall at the lower elevation winter range (sensu Pettorelli et al. 2005*a*). While this might benefit residents in terms of higher biomass production discussed above, migrants and their calves would be exposed to harsh conditions for calf survival. On the Isle of Rhum, cold, wet summers reduced calf survival (Clutton-Brock et al. 1987), presumably because of increased calf mortality during cold periods. We found similar evidence that cold, wet summers reduced elk population growth rate in this population (Hebblewhite et al. 2006). Temporal variability in plant phenology, which has the greatest impact on forage quality (Walsh et al. 1997), could also negatively influence migrant population dynamics (Post and Stenseth 1999, Pettorelli et al. 2005*a*). High spring snowfalls would delay phenology and migration (Pettorelli et al. 2005*a*, *c*, Hebblewhite 2006). Delayed migration would result in peak lactation demands occurring during adverse forage and climatic conditions. This could lead to reduced calving synchrony and benefits of predator swamping, with increased calf mortality (Post and Klein 1999). These postulated effects of climate on partial migration represent hypotheses that could be tested through simulation modeling by varying phenology in our spatial forage models and examining potential population consequences to migratory elk.

While delayed migration may just extend access to more nutritious forage for migrants, this ignores the interaction of predation risk and environmental stochasticity (Lima et al. 2002, Testa 2004), something not considered by Wang et al. (2006). Increased variability in spring climate will make it more difficult for migrant female elk to migrate before calving to reduce predation risk for calves (e.g., Bergerud et al. 1984). Instead, females with calves at heel will have to run the migration gauntlet past wolf dens and grizzly bears to high-elevation summer ranges (Hebblewhite and Merrill 2007). Indeed, Hebblewhite and Merrill (2007) revealed that wolf predation-risk exposure during migration was 1.7 times higher even than that for residents, and the highest mortality rates occurred during spring. Disentangling the interaction of stochasticity in top-down (predation) and bottom-up (forage biomass/quality) conditions remains a difficult but critical problem for ecologists (Lima et al. 2002, Testa 2004). Regardless, we hypothesize for the reasons above that increased stochasticity due to climate change in our montane system could be detrimental for migratory ungulates.

Conclusions

Large-scale topographic and climatic differences drove phenological patterns that promoted access to higher forage quality for elk that migrated to higher elevations, closer to the continental divide, and to areas of higher elevation and aspect diversity. The start of the growing season was delayed in these areas, which delayed plant growth. Because forage quality declined across the whole study area with increasing plant growth, forage quality was highest in these phenologically delayed areas. At the largest spatial scales, migrant elk selected to locate their home ranges at higher elevations and closer to the continental divide. As a result, migrant elk selected intermediate herbaceous biomass across spatial scales in accordance with the FMH to maximize exposure to higher forage quality than residents, and selection was the strongest at the largest landscape scale, in accordance with predictions (Table 3). Residents essentially selected for maximum herbaceous-forage biomass at all spatial scales, not compensating by selecting intermediate forage biomass at finer spatial scales as expected (Table 3). However, both resident and migrant elk switched to shrub biomass during late summer, likely to compensate for declines in herbaceous-forage quality. As a result of the difference in selection strategies for herbaceous biomass in particular between migrants and residents, migrant elk realized 6.5% higher forage quality than residents as predicted, peaking during late June at the time of highest lactation costs for females. The magnitude of these differences in forage quality between strategies is predicted to lead to significant differences in elk body mass, reproduction, and survival (Cook et al. 2004). Combined with results of previous studies of montane ungulates (Albon and Langvatn 1992, Mysterud et al. 2002, Pettorelli et al. 2005*a*), selection for forage quality as expected under the forage-maturation hypothesis (Fryxell et al. 1991) is a convincing mechanism driving elk migration in mountainous ecosystems. Despite evidence that elk benefited from migration from a foraging perspective, however, the decline of migrants in this system (Hebblewhite et al. 2006) driven by lower adult female and calf survival of migrants (Hebblewhite 2006) reveals forage does not determine fitness of migratory strategies in isolation. Elk must balance the benefits of migration from a foraging perspective with the costs of mortality from predation (e.g., Swingland and Lessels 1979, Nicholson et al. 1997, Testa 2004).

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APPENDIX A

Modeling peak of growing-season availability of forage-biomass components for elk (*Ecological Archives* M078-005-A1).

APPENDIX B

Modeling forage maturation using NDVI and ground maturation models (*Ecological Archives* M078-005-A2).

APPENDIX C

Estimating growing-season parameters for phenology modeling (*Ecological Archives* M078-005-A3).

APPENDIX D

Individual MODIS-interval quality–quantity regression equations (*Ecological Archives* M078-005-A4).

APPENDIX E

Predicted probabilities of use by migrant and resident elk as a function of herbaceous biomass at two levels within the home-range scale (*Ecological Archives* M078-005-A5).

APPENDIX F

Linear mixed-effects time-series models for forage (herbaceous and shrub) biomass exposure for migrant and resident elk GPS locations, 2002–2004 (*Ecological Archives* M078-005-A6).