

Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd

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Abstract. Migration is a striking behavioral strategy by which many animals enhance resource acquisition while reducing predation risk. Historically, the demographic benefits of such movements made migration common, but in many taxa the phenomenon is considered globally threatened. Here we describe a long-term decline in the productivity of elk (*Cervus elaphus*) that migrate through intact wilderness areas to protected summer ranges inside Yellowstone National Park, USA. We attribute this decline to a long-term reduction in the demographic benefits that ungulates typically gain from migration. Among migratory elk, we observed a 21-year, 70% reduction in recruitment and a 4-year, 19% depression in their pregnancy rate largely caused by infrequent reproduction of females that were young or lactating. In contrast, among resident elk, we have recently observed increasing recruitment and a high rate of pregnancy. Landscape-level changes in habitat quality and predation appear to be responsible for the declining productivity of Yellowstone migrants. From 1989 to 2009, migratory elk experienced an increasing rate and shorter duration of green-up coincident with warmer spring–summer temperatures and reduced spring precipitation, also consistent with observations of an unusually severe drought in the region. Migrants are also now exposed to four times as many grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) as resident elk. Both of these restored predators consume migratory elk calves at high rates in the Yellowstone wilderness but are maintained at low densities via lethal management and human disturbance in the year-round habitats of resident elk. Our findings suggest that large-carnivore recovery and drought, operating simultaneously along an elevation gradient, have disproportionately influenced the demography of migratory elk. Many migratory animals travel large geographic distances between their seasonal ranges. Changes in land use and climate that disparately influence such seasonal ranges may alter the ecological basis of migratory behavior, representing an important challenge for, and a powerful lens into, the ecology and conservation of migratory taxa.

Key words: carnivore recovery; *Cervus elaphus*; drought; elk; grizzly bears; migration; trophic mismatch; vegetation phenology; wolves; Yellowstone.

INTRODUCTION

Animal migration has long held the attention of ecologists and the public, partly because it is a means by which animals profitably exploit geographic gradients in resources and predation. The use by migratory animals of distinct and often distant seasonal habitats poses a unique challenge to research and conservation, particularly when migrations span modern political boundaries. This challenge grows as humans alter global patterns of habitat quality and predation.

Manuscript received 22 January 2012; accepted 10 January 2013. Corresponding Editor: M. Festa-Bianchet. For reprints of this Forum, see footnote 1, p. 1243.

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In ungulates, many taxa migrate seasonally across diverse biomes, from tropical savanna to northern temperate forests and grasslands. Migration is thought to have evolved in ungulates because in seasonal environments it affords prolonged access to high-quality forage and can reduce predator exposure (Fryxell and Sinclair 1988). In relatively pristine landscapes, such fitness benefits have promoted the abundance of migratory ungulates, which can outnumber their resident counterparts in some cases by an order of magnitude (Fryxell et al. 1988). In recent years, however, concern has grown over global declines in ungulate migration, including such diverse species as wildebeest (*Connochaetus taurinus*), saiga (*Saiga tatarica*), pronghorn (*Antilocapra americana*), and caribou (*Rangifer tarandus*) (Berger 2004, Bolger et al. 2008, Festa-Bianchet et al. 2011). Most of this attention has focused on habitat degradation and conspicuous physical barriers to migration (e.g., fences and roads), which have reduced prominent migratory populations (Harris et al. 2009). Comparatively little attention has been given to subtler changes in the spatial gradients of vegetation phenology and predation that migratory ungulates are known to exploit. This is an important avenue for new study and synthesis because climate and land-use change may influence the ecological basis of migration independently of physical barriers, with potentially important consequences for this ecological phenomenon.

Selection for ephemeral, high-quality forage is the primary driver of migration in ungulates (Fryxell et al. 1988, Fryxell and Sinclair 1988). For temperate species, the cold temperatures and deep snow of winter cause a steady decline in body mass (Parker et al. 2009), and though less harsh, the tropical dry season is also a period of low forage availability and declining fat reserves for ungulates (Sinclair et al. 1985). Following these periods of poor nutrition, feeding upon emergent vegetation at the onset of the growing season is adaptive because such highly digestible forage promotes fat gain and reproduction (Cook et al. 2004a, Parker et al. 2009). Accordingly, the migrations of species such as Serengeti wildebeest, and Greater Yellowstone elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) track vegetation green-up (Holdo et al. 2009, White et al. 2010, Sawyer and Kauffman 2011). After arriving on high-elevation summer ranges, northern temperate migrants continue to benefit from high forage quality associated with cool weather and prolonged snowmelt, allowing them to attain higher body mass and pregnancy rates than their resident counterparts (Albon and Langvatn 1992, Hebblewhite and Merrill 2007).

Reduced predation has been hypothesized as an important secondary benefit of ungulate migration. For a portion of the migratory period, dominant predators such as lions (*Panthera leo*) and wolves (*Canis lupus*) must tend their young at den sites that were established on the dry-season or winter range of

migratory prey, and are thus temporarily limited from following prey to the wet-season or summer range (Fryxell et al. 1988). For instance, in the Serengeti Ecosystem, predation was found to be lower for migratory than for resident wildebeest (Sinclair 1984), and in Alberta, migratory elk reduced their wolf exposure by 70% in comparison with resident elk (Hebblewhite and Merrill 2007). Thus, reduced mortality due to predation is thought to benefit migratory individuals by increasing juvenile survival (Bolger et al. 2008).

The Greater Yellowstone Ecosystem, USA (GYE), encompasses some of the most expansive wilderness areas in the United States, and retains seasonal migrations of 30–260 km by pronghorn, mule deer, moose (*Alces alces*), bison (*Bison bison*), and elk (Berger 2004, Sawyer et al. 2005). In this study, we evaluated the contemporary benefits of migratory behavior for a Yellowstone elk herd by comparing the reproductive performance of migratory and resident animals, then evaluating the ecological conditions that underlie observed demographic differences. Whereas prior research conducted from 1979 to 1980 found that 81% of elk in our study population were migratory (Rudd et al. 1983), surveys conducted from 2005 to 2009 indicated that $47.5\% \pm 0.03\%$ (mean \pm SE) are currently migratory. Long-term monitoring has revealed an associated shift in the spatial distribution of the population over 21 years, driven by high recruitment levels (see Fig. 2A) and eastward expansion in the resident subpopulation (Appendix A). Somewhat in contrast with the northern Yellowstone herd, which uses lower elevations in the park during winter and was considered overabundant during much of the 1900s, the migratory elk we studied use high-elevation wilderness areas of the park in summer and have historically been maintained at lower densities via human harvest on winter range. We show that two factors, large-carnivore recovery and a severe, long-term drought, appear to be reducing the benefits of migration in this population. In contrast, resident elk are likely subsidized by the removal of large carnivores and by irrigated agriculture, contributing to their recent expansion.

METHODS

Study area

We studied the Clarks Fork elk herd, a population of ~4500 individuals in the Absaroka Mountains of Wyoming, USA. Resident elk and ~10–15% of migratory elk spend their winters in the foothills northwest of Cody, Wyoming, and the remainder of the migrants winter further west (Fig. 1A). Migrants annually move 40–60 km to high-elevation summer range inside Yellowstone National Park (YNP; Fig. 1A, B). We delineated our study area (see *Landscape-level changes influencing Yellowstone migrants* below for details) into a migratory elk summer range (718 km², mean elevation 2588 m), characterized by open alpine and subalpine

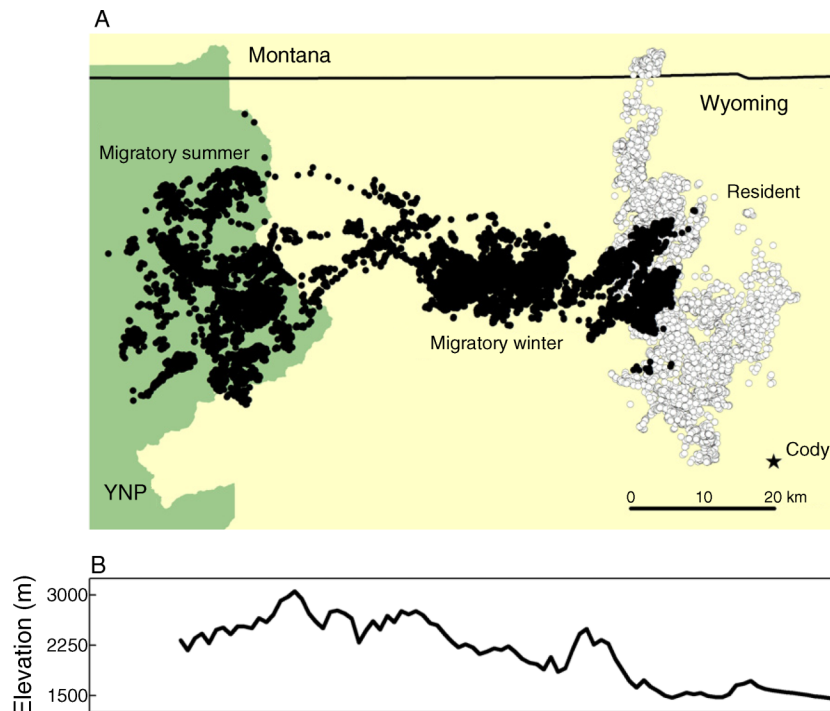


FIG. 1. (A) Global Positioning System (GPS) locations from a representative sample of migratory (black circles, $n = 10$) and resident (white circles, $n = 13$) elk (*Cervus elaphus*) used to delineate seasonal ranges for analyses of Normalized Difference Vegetation Index (NDVI), climate, and predator abundance in the Greater Yellowstone Ecosystem, USA. Yellowstone National Park (YNP) is shown in green. Approximately 10–15% of migratory elk commingle during winter with resident elk. Representative migration routes are shown. (B) Elevation on an east–west line through seasonal range center points.

meadows and spruce–fir or lodgepole forest, and a resident elk year-round range (1093 km², mean elevation 1769 m), characterized by subalpine meadows, sagebrush–steppe, and spruce–fir forest. Approximately 24% (173.5 km²) of the forest on the migratory summer range burned completely in the Yellowstone fires of 1988, and another 22% burned heterogeneously. Regeneration has generally been poor (Kashian et al. 2004). Resident elk may access a number of irrigated fields planted with alfalfa and grass hay, which constitute ~0.01% of their year-round range.

Comparative demography

We first sought to compare productivity indices for migratory and resident animals. Long-term patterns of productivity and distribution (1989–2009) were evaluated using winter surveys conducted via helicopter and ground observations by the Wyoming Game and Fish Department. Prior to 2005, ~20% of the population was surveyed annually. Since 2005, the agency has attempted to survey 70–80% of the population. Throughout this work, we define a “migratory” subpopulation or individual as having discrete seasonal ranges, and a “resident” subpopulation or individual as having non-discrete seasonal ranges (Fryxell and Sinclair 1988). Agency observations were classified at the subpopulation level based on winter range associations of

migratory and resident elk established previously via very high frequency (VHF) telemetry (Rudd et al. 1983), and validated through our own Global Positioning System (GPS) collaring during 2007–2010. We treated the ratio of calves (<1 yr) per 100 adult females (>1 yr) in each subpopulation as an index of recruitment. Though some studies have questioned the value of age ratios (e.g., Bonenfant et al. 2005), they are more reliable in the open habitats characteristic of our study area (Bonenfant et al. 2005); moreover, a recent modeling study based on the life history of a GYE elk population indicated that changes in elk calf survival explained 93% of the variation in calf : cow ratios (Harris et al. 2008). We evaluated trends in the calf : cow ratio using piecewise regression of the calf : cow ratio on year. To assess the timing of calf losses, we conducted summer recruitment surveys of migrants (via helicopter, 14–22 September) and residents (via ground, 15 August–15 October) from 2007 to 2009. We averaged the annual values, based on samples of 250–1000 individuals per subpopulation, and used a two-tailed t test to evaluate differences between subpopulations ($n = 6$).

We captured adult female elk via helicopter netgunning in January 2007 ($n = 60$) and 2008 ($n = 30$) and fitted them with GPS ($n = 70$; Telonics, Mesa, Arizona, USA) or VHF ($n = 20$; ATS, Isanti, Minnesota, USA) collars. Though we do not present detailed movement

data herein, monitoring of elk movements during the course of this work did not reveal any individuals switching between migratory strategies (this is similar to the <2% annual rate [$n = 109$] observed in Alberta by Hebblewhite and Merrill 2011). We recaptured a subset of GPS-collared individuals via helicopter darting to estimate body fat and pregnancy in winter (early March 2008–2010), and body fat and lactation status in autumn (early September 2008 and 2009). During these recaptures, elk were immobilized with a dart (Pneu-dart, Williamsport, Pennsylvania, USA) containing either a carfentanil–xylazine mixture or with Butorphanol–Azaperone–Medetomidine (BAM; ZooPharm, Fort Collins, Colorado, USA). During the initial captures, we determined pregnancy using pregnancy-specific protein B (PSPB) analysis of blood serum (BioTracking, Moscow, Idaho, USA). During the recaptures, pregnancy was determined via manual palpation. Non-pregnancies were independently verified using PSPB ($n = 14$), except when insufficient blood serum was available. We classified females as lactating if milk could be extracted from the udder. During captures, a vestigial canine was extracted for ageing via cementum annuli.

We used generalized linear mixed models (GLMM) to evaluate influences on elk pregnancy status ($n = 140$) while accounting for the repeated sampling of some individuals with random effects. We used Akaike's information criterion (AIC) to select the best model of pregnancy as a function of age (both linear and quadratic terms), migratory status, sampling year, and an interaction of age and subpopulation, and we used likelihood ratio tests to evaluate individual factors. We tested for differences in the 2007 age distribution of each subpopulation using a one-sided Kolmogorov-Smirnov (K-S) test ($n = 87$). We separately evaluated the influence of lactation on pregnancy, using Fisher's exact test, due to the low number of females for which both lactation and pregnancy were determined within the same year. In evaluating rates of lactator pregnancy, we included females that had been lactating in summer (migratory $n = 6$, resident $n = 14$) or winter (migratory $n = 8$, resident $n = 1$).

During the recaptures, two experienced investigators (R. C. Cook, J. G. Cook) collected a body condition score, measured rump fat thickness using ultrasonography, and measured chest girth (Cook et al. 2010). Nonpregnant body mass was calculated from chest-girth measurements using equations for immobilized, sternally recumbent female elk (Cook et al. 2010). Ingesta-free body fat was estimated using an arithmetic combination of rump body condition score and rump fat thickness allometrically scaled using nonpregnant body mass (Cook et al. 2010). We used two-tailed t tests to evaluate body fat differences between subpopulations.

Landscape-level changes influencing Yellowstone migrants

While we recognize the importance of winter conditions to ungulate vital rates (Parker et al. 2009), we

focused our investigation of declining migrant productivity on summer conditions, for three reasons. First, we detected no influence of density dependence (regression of calf : cow ratio on abundance, $F_{1,12} = 1.0$, $P = 0.34$) or winter severity (regression of calf : cow ratio on cumulative snow water equivalent [Wolverine Creek SNOTEL, 10 km northwest of the core winter range of migrants], $F_{1,21} = 3.02$, $P = 0.1$). Indeed, elk density and winter severity have been decreasing in the system for many years (Wilmers and Getz 2005, Eberhardt et al. 2007). Second, summer surveys from 2007–2009 indicated that few calves remained in the migratory subpopulation by the end of summer, highlighting a role of summer conditions. Third, much empirical evidence indicates that pregnancy of temperate ungulates is influenced primarily by growing-season nutrition (Langvatn et al. 1996, Cook et al. 2004a, Parker et al. 2009). Thus, we considered two broad mechanisms for the declining recruitment of the Yellowstone migrants: (1) declining summer habitat quality due to long-term drought, and (2) increasing calf predation due to large-carnivore recovery.

To evaluate long-term patterns in vegetation phenology, we used the Normalized Difference Vegetation Index (NDVI) obtained from Advanced Very High Resolution Radiometer (AVHRR) satellite imagery from 1989 to 2009 (1-km² resolution). Peak protein intake of temperate mountain ungulates has been shown to coincide with the annual maximum increment in NDVI (Hamel et al. 2009), and high annual NDVI increments (i.e., rapid vegetation emergence) have been negatively related to juvenile growth and survival (Pettorelli et al. 2007). To delineate the sampling range for each subpopulation, we created 100% minimum convex polygons (MCPs) using summer locations of GPS-collared migratory elk ($n = 10$) and year-round locations of resident elk ($n = 13$; Fig. 1A). Although we used a subset ($n = 23$) of the total collar sample ($n = 90$) obtained halfway through our study to describe seasonal ranges for NDVI analysis, we subsequently validated that the MCPs were representative of both subpopulations by determining that $83.8\% \pm 4.6\%$ of summer locations of migrants and $92.8 \pm 3\%$ of year-round locations of residents fell inside their boundaries. After excluding forested cover types (Hamel et al. 2009), we averaged NDVI pixels to obtain 26 measurements per range, per year. We then calculated six annual NDVI metrics for each subpopulation, which included peak NDVI and week of occurrence; maximum NDVI increment and week of occurrence; green-up duration (number of weeks between maximum increase and peak); and integrated (i.e., summed) June NDVI (June INDVI). We used two-tailed t tests to evaluate NDVI differences between subpopulations and linear regression to evaluate temporal trends within each subpopulation. When we found significant temporal trends in NDVI, we evaluated their relation to climatic variables associated with recent drought in the region (Westerling

et al. 2006, Barnett et al. 2008, McMenamin et al. 2008). Specifically, we evaluated the influence of spring precipitation (April–May) and spring–summer temperature (April–August). Climate data were obtained for 1989–2009 from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) mapping system (available online).¹⁰

We also evaluated a potential resource subsidy to resident elk ($n = 13$) via their use of irrigated fields. We used GPS locations collected eight times daily during July and August (i.e., months of irrigation that are important to elk nutrition and reproduction; Cook et al. 2004a). We digitized agricultural fields using 2009 maps of the National Agricultural Imagery Program (NAIP; available online),¹¹ and then calculated the percentage of each individual's summer locations that fell within them.

Because grizzly bears and wolves hunt young calves (Barber-Meyer et al. 2008) and many migratory elk calve prior to their spring migration, we used a year-round instead of summer-only migratory elk MCP to assess large-carnivore abundance. To evaluate patterns of grizzly abundance, we used a time series of bear group observations conducted in mid-summer flights by the Interagency Grizzly Bear Study Team (IGBST). To evaluate patterns of wolf abundance, we used a time series from the National Park Service (1996–1998) and U.S. Fish and Wildlife Service (1999–2009; available online).¹² We included packs that substantially overlapped with migratory or resident elk range, based on three years of recent wolf movements obtained via GPS collaring. Although territorial behavior probably limits packs in the migratory area from simultaneously hunting in elk-dense areas, migratory elk spend substantial portions of calving and summer seasons within all four wolf territories. We included wolves that were killed in management actions, because these removals typically occur in late summer and fall, after most elk calf predation in this system (Barber-Meyer et al. 2008). Although black bears (*Ursus americanus*) and mountain lions (*Puma concolor*) also occur in the study area, we were unable to document trends for these species.

RESULTS

Comparative demography

From 1989 to 2009, winter calf recruitment of migratory elk declined linearly by 73.5% ($F_{1,19} = 53.4$, $P < 0.001$; Fig. 2A). Calf recruitment of resident elk declined to a breakpoint (2002 ± 1.5 , $P < 0.001$), then steadily increased ($F_{1,19} = 5.71$, $P = 0.007$; Fig. 2A). Recent summer range surveys (2007–2009) revealed that the calf : cow ratio of the migratory subpopulation had declined approximately to the wintertime level by the

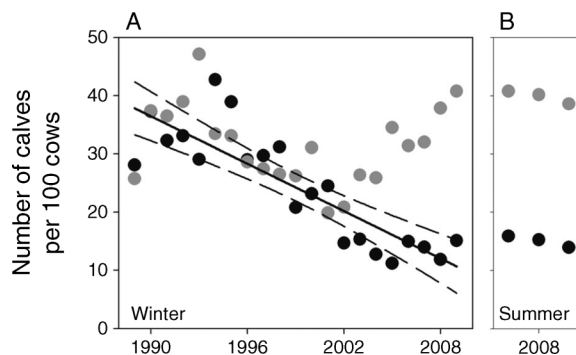


FIG. 2. (A) The number of calves observed per 100 adult females in each subpopulation during winter from 1989 to 2009 indicates a long-term decline in the recruitment of migratory elk (black circles with fitted solid line and 95% CI in dashed lines). The calf : cow ratio of resident elk (gray circles) declined to a breakpoint (2002 ± 1.5 , $P < 0.001$) and then steadily increased ($F_{1,21} = 5.71$, $P = 0.007$). (B) Comparable calf : cow ratios collected during summers 2007–2009 suggest that calf numbers had reached wintertime levels by the end of summer.

end of each summer ($15:100 \pm 0.58:100$, mean \pm SE; Fig. 2B).

Over four winters of sampling, the pregnancy rate of migrants was 70.6% ($n = 75$), vs. 89.2% ($n = 65$) for residents. Our best-fitting model indicated that pregnancy was a quadratic function of age (i.e., pregnancy probability was lowest for young and old females; $P < 0.001$), with an added effect of migratory status (i.e., pregnancy was lower for migratory elk independently of age; $P = 0.04$). Though our model included age as a continuous predictor, graphically we present the proportion of elk that were pregnant in young (1–3 yr), prime-age (4–9 yr), old (10–14 yr), and senescent (15+ yr) age classes (Fig. 3B; Cook et al. 2004b, Raithel et al. 2007). Consistent with a recent decline in recruitment, a one-sided K-S test indicated that the migratory subpopulation was older than the resident subpopulation ($D_{1,85} = 0.28$, $P = 0.03$; Fig. 3B). In the migratory subpopulation, the pregnancy rate of lactating females from 4 to 14 years old (21.4%, 3/14) was lower ($P < 0.001$) than that of non-lactating females (86.7%, 13/15; Fig. 3C). By contrast, the pregnancy rates of lactating (86.7%, 13/15) and non-lactating (100%, 6/6) residents did not differ ($P = 0.57$). Though these pregnancy results led us to expect lower body fat among migratory lactating females at the end of summer, lactator body fat levels did not differ ($P = 0.76$) between migrants ($10.5\% \pm 0.6\%$) and residents ($10.7\% \pm 0.5\%$) (Fig. 3D; Appendix B). Meanwhile, the percentage of body fat in September of non-lactating migrants ($17.4\% \pm 0.5\%$) was greater ($P < 0.001$) than that of non-lactating residents ($12.9\% \pm 0.5\%$; Fig. 3D; Appendix B).

Landscape-level changes influencing Yellowstone migrants

On average, migratory elk experienced higher and later peak NDVI values than resident elk (Fig. 4B;

¹⁰ <http://www.prism.oregonstate.edu/>

¹¹ <http://www.fsa.usda.gov/FSA/apfoapp?area=home&subject=prog&topic=nai>

¹² <http://www.fws.gov/mountain-prairie/species/mammals/wolf/>

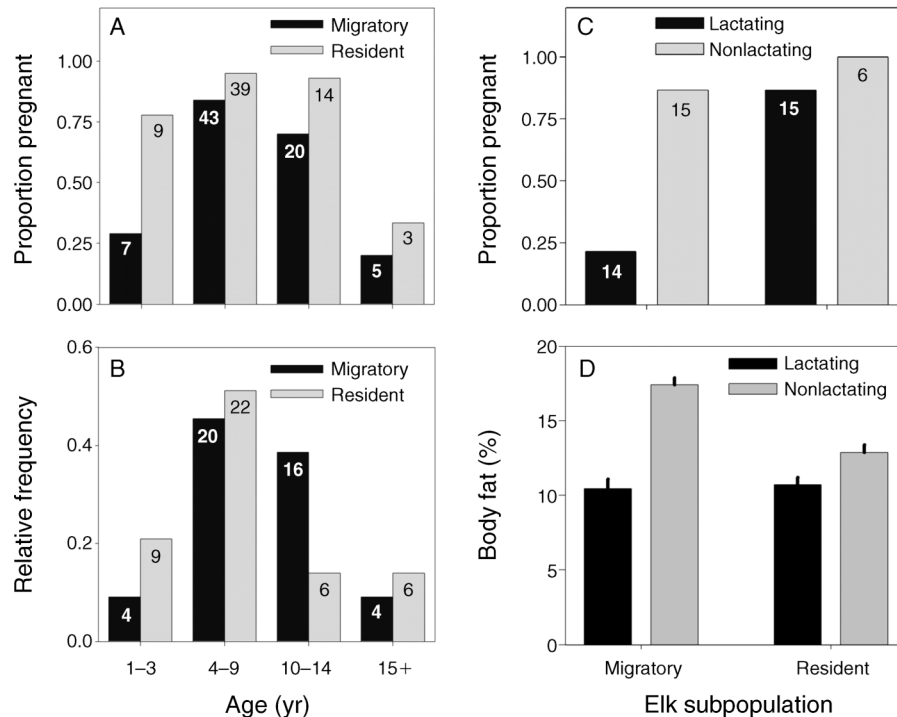


FIG. 3. (A) Pregnancy by age class and subpopulation. A generalized linear mixed model (GLMM) that accounted for individual recaptures (see *Results*) indicated that migrants had lower rates of pregnancy than residents after accounting for a quadratic function of age. (B) Age structure by subpopulation. A one-sided K-S test (see *Results*) indicated that migratory elk had a higher proportion of older individuals than the residents, consistent with recent reductions in calf recruitment. (C) Lactating females were pregnant at a lower rate than non-lactators in the migratory population, whereas lactation did not affect the pregnancy rate of residents. (D) The body fat (mean \pm SE) of lactating migrants was significantly lower than that of non-lactating migrants, but did not differ from that of lactating residents. Sample sizes are given at the top of each bar.

Appendix C), yet a 21-year reduction in habitat quality was evident only on the summer range of migratory elk (Fig. 4C–F; Appendix C). These include increasing trends in the maximum NDVI increment ($P = 0.04$; Fig. 4D) and peak NDVI ($P < 0.001$), as well as a reduction in green-up duration ($P < 0.001$; Fig. 4F) of 1.3 days per year, or a total of 27 days over 21 years. Not only did we fail to detect comparable phenological trends on the range of resident elk, but some residents appear to gain a nutritional subsidy from agriculture. Though only 0.01% of the residents' year-round range is irrigated, 23% (3/13) of resident females spent 47–52% of their time in irrigated fields during July and August. The remainder spent 0–8% of their time in irrigated fields.

Several climatic trends on the summer range of migratory elk may have caused the observed changes in plant phenology. Over 21 years, April–August temperatures increased markedly ($F_{1,19} = 10.93$, $P = 0.001$; Appendix D). Particularly striking was an increase in July temperature of approximately 4°C ($F_{1,19} = 5.87$, $P = 0.03$). Cumulative April–May precipitation also declined ($F_{1,19} = 5.11$, $P = 0.04$; Appendix D). These climatic trends were consistent with phenological changes. July temperature was

negatively related to the duration of green-up (July, $F_{1,19} = 6.47$, $P = 0.02$, $r^2 = 0.25$). Cumulative April–May precipitation was negatively related to peak NDVI ($F_{1,19} = 6.08$, $P = 0.02$, $r^2 = 0.24$) and weakly associated with a prolonged duration of green-up ($F_{1,19} = 2.63$, $P = 0.12$, $r^2 = 0.12$). Overall, warmer temperatures and reduced precipitation appear to facilitate rapid growth of vegetation and reduce the time in which it is available to Yellowstone migrants on their summer range. We detected a similar warming trend on the year-round range of resident elk, but no change in spring precipitation (Appendix D).

During summers from 1989 to 2009, the number of grizzly bear groups observed on the migrants' range increased fourfold ($F_{1,19} = 4.73$, $P = 0.05$; Fig. 5A), a trend consistent with the growth rate of Yellowstone grizzlies from 1983 to 2002 (Schwartz et al. 2006). In contrast, no grizzlies were detected on the year-round range of resident elk. Wolves were reintroduced into YNP in 1995 and 1996, during the study period, but did not establish on the range of resident elk until 2000. Since then, annual wolf numbers have, on average, been four times higher ($t = 9.39$, $P < 0.001$) on the range of migratory elk (35.2 ± 2.8 , mean \pm SE)

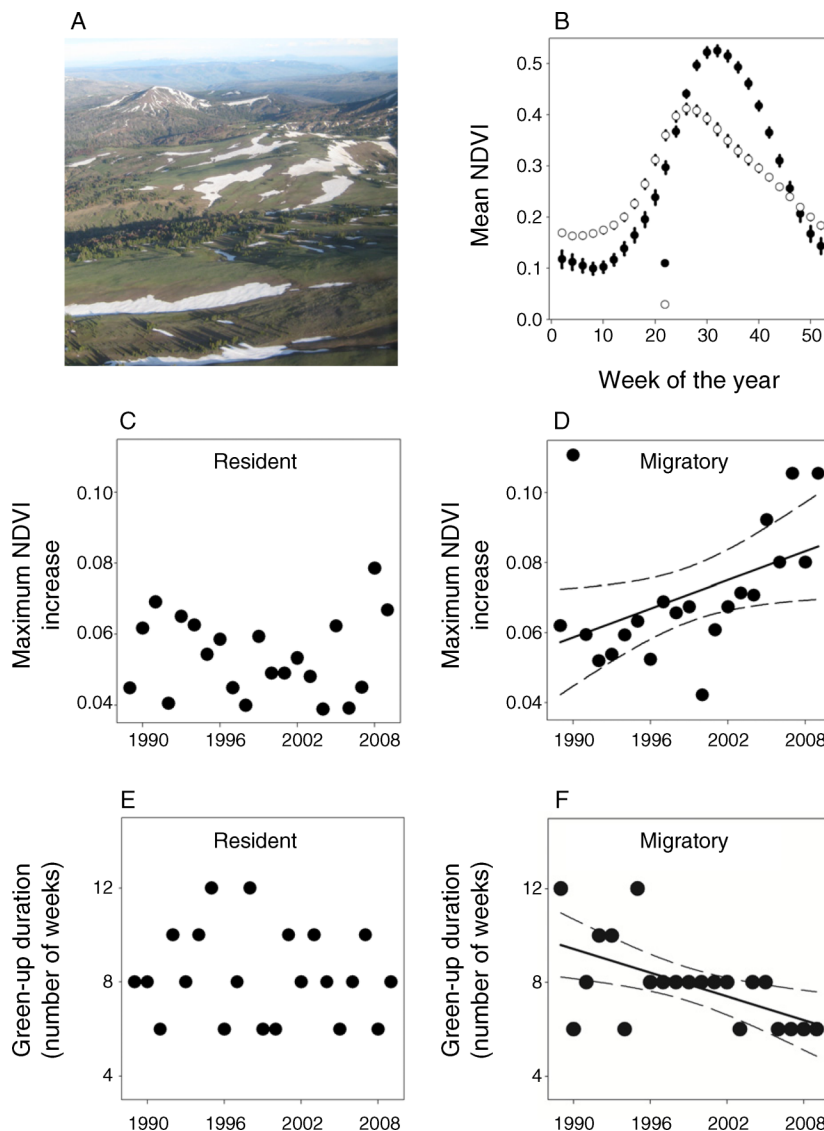


FIG. 4. Phenology on the summer range is influenced by recent drought. (A) Patchy snowmelt and greening in June typical of the high-elevation summer range of migratory elk. (B) Weekly Normalized Difference Vegetation Index (NDVI) values (mean \pm SE) from 1989 to 2009 for migratory (solid circles) and resident (open circles) ranges (see Appendix C for point estimates). (C, D) From 1989 to 2009, maximum NDVI increment (C) did not change on the resident range but (D) increased on the migratory range (shown with fitted solid line and 95% CI in dashed lines). (E, F) Over the same period, green-up duration (E) did not change on resident range but (F) decreased on migratory range (shown with fitted solid line and 95% CI in dashed lines). These phenological trends were related to reduced spring precipitation and warmer spring–summer temperatures (Appendix D: Fig. D1A, B).

than on that of resident elk (8.1 ± 0.7 ; Fig. 5A, B), probably because of a high rate of lethal removal (24% per year, due to chronic wolf–cattle conflict) on the range of resident elk.

DISCUSSION

In contrast to classic predictions of the benefits of migration in ungulates (Fryxell et al. 1988, Fryxell and Sinclair 1988), our analysis revealed poor performance of elk that migrate annually into wilderness habitats of YNP. Yellowstone migrants experienced declining calf recruitment and depressed pregnancy rates, indicating

lower annual reproductive success in recent years than that experienced by resident elk. This apparent decline in the demographic benefits of migration coincided with growing numbers of large carnivores that prey on elk calves and a severe, long-term drought that appears to have reduced habitat quality. Although concern over global declines in migratory ungulate populations has often focused on conspicuous barriers to migration that are associated with human development (Berger 2004, Bolger et al. 2008), our findings suggest that when the ecological conditions that favor migration are diminished, declines might occur even in wilderness land-

scapes that are highly protected. This study provides a lens through which to consider the persistence and decline of migratory taxa in the face of human activities that increasingly alter the geographic patterns of predation (Estes et al. 2011) and phenology (Parmesan and Yohe 2003) on which migration depends.

The declining productivity of migratory elk was associated recently with a pregnancy rate considerably lower than that of resident elk (Fig. 3A), and of Rocky Mountain elk in general (Raithel et al. 2007). The low pregnancy rate of migrants resulted in part from poor reproduction of young and lactating females (Fig. 3B, C), consistent with prior study of ungulates under nutritional limitation. In general, the fecundity of young females is highly sensitive to environmental variation (Gaillard et al. 2000), including climatic and phenological conditions similar to those we have documented (Fig. 4D, F). For instance, sexual maturity was delayed in populations of European red deer (*Cervus elaphus*) that experienced warmer springs and advanced phenology (Langvatn et al. 1996), probably because of reduced growth rates among calves and yearlings (Cook et al. 2004a). Although the fecundity of adult females is more stable (Gaillard et al. 2000), poor summer–autumn forage conditions can reduce pregnancy probability among adults carrying the high costs of lactation (Cook et al. 2004a, Parker et al. 2009). It is not clear to us why depressed pregnancy was not accompanied by lower body fat levels among lactating migrants. Fluctuations in short-term energy balance are known to influence the pregnancy probability of domestic ungulates (e.g., National Research Council 1985, Fitz-Rodriguez et al. 2009), and may occur without large changes in body fat levels. Thus, we suspect that a negative plane of nutrition associated with late-summer drought in the weeks prior to breeding may account for the low pregnancy of migrant lactators. An additional factor contributing to the reduced pregnancy rate of the migratory subpopulation was its older age structure (Fig. 3B), a likely result of sustained low recruitment in recent years.

For the migratory elk we studied, the reduced pregnancy of young and lactating females coincided with phenological changes (Fig. 4F, D) that are consistent with observations of a severe, long-term drought in Yellowstone and the surrounding region. Prior research has revealed diverse influences of recent drought on the region's wildfire activity and snowpack (Westerling et al. 2006), amphibian populations (McMenamin et al. 2008), and bat reproduction (Adams 2010). Our findings newly link the region's drought to changes in vegetation phenology and the demographic benefits of ungulate migration. Although determining the ultimate cause of this drought is beyond the scope of our own work, recent studies have described regional climatic changes as anomalous (within 1000-year [Pederson et al. 2011] and 14 000-year [Shuman 2011] contexts) and consistent with anthropogenic forcing (Barnett et al. 2008, Shuman

2011). Whether our work reveals the influence of an unusually severe drought or of directional climate change, we suggest that it can facilitate a fruitful discussion of some of the mechanisms by which climate change might influence migratory ungulates at individual, population, and landscape scales.

In temperate ungulates, parturition is timed to coincide with peak forage quality so that females can meet the high energetic demands of lactation (Parker et al. 2009). Therefore, one likely mechanism for a climate-induced reduction in the reproductive performance of migratory elk is a “mismatch” between vegetation green-up and the period of lactation (Post and Forchhammer 2008). In migratory birds in Europe, such a mismatch between the springtime arrival of migrants and the phenology of their breeding range may be linked to recent population declines (Both et al. 2006). In the only prior case for ungulates that we know of, recent arctic warming advanced vegetation green-up more rapidly than female caribou (*Rangifer tarandus*) advanced their parturition date, with negative effects on calf production (Post and Forchhammer 2008). The latter climate effect was thought to be mediated by a nutritional limitation on lactating females, similar to recent findings among Rocky Mountain bats, including migratory populations (Adams 2010). We found that poor performance of lactating females can also result from a reduction in the overall duration of optimal foraging opportunities associated with green-up. Thus, our work suggests a new mechanism by which large-scale changes in vegetation phenology may reduce a key benefit of ungulate migration. Future research is needed to explore whether phenological changes lead to trophic mismatches that are generalizable across migratory taxa, and conversely, what unique challenges will arise for migrants with reproductive strategies as diverse as those of ungulates, birds, fish, reptiles, insects, and cetaceans.

Recent research in the GYE raises the alternative possibility that the risk of wolf predation depresses elk pregnancy rates (Creel et al. 2007) by causing female elk to forage suboptimally in winter, hypothetically resulting in accelerated fat loss and, ultimately, intrauterine mortality (Creel et al. 2009). Although such nonconsumptive effects (NCE) have been commonly observed (Preisser et al. 2005), recent work found no differences in the body fat levels and pregnancy rates of Yellowstone elk before and after wolf reintroduction (White et al. 2011). This latter finding is consistent with the observations that elk in Yellowstone do not strongly avoid wolves during winter (Fortin et al. 2005, Mao et al. 2005) and do not avoid foraging on two preferred browse species, willow and aspen, even in high-risk areas of the ecosystem (Creel et al. 2009, Kauffman et al. 2010). In our own study, migratory elk experienced the higher risk of wolf predation (Fig. 6B, C), yet tended to be fatter in winter than resident elk (Appendix B), probably because so many migratory females lose their

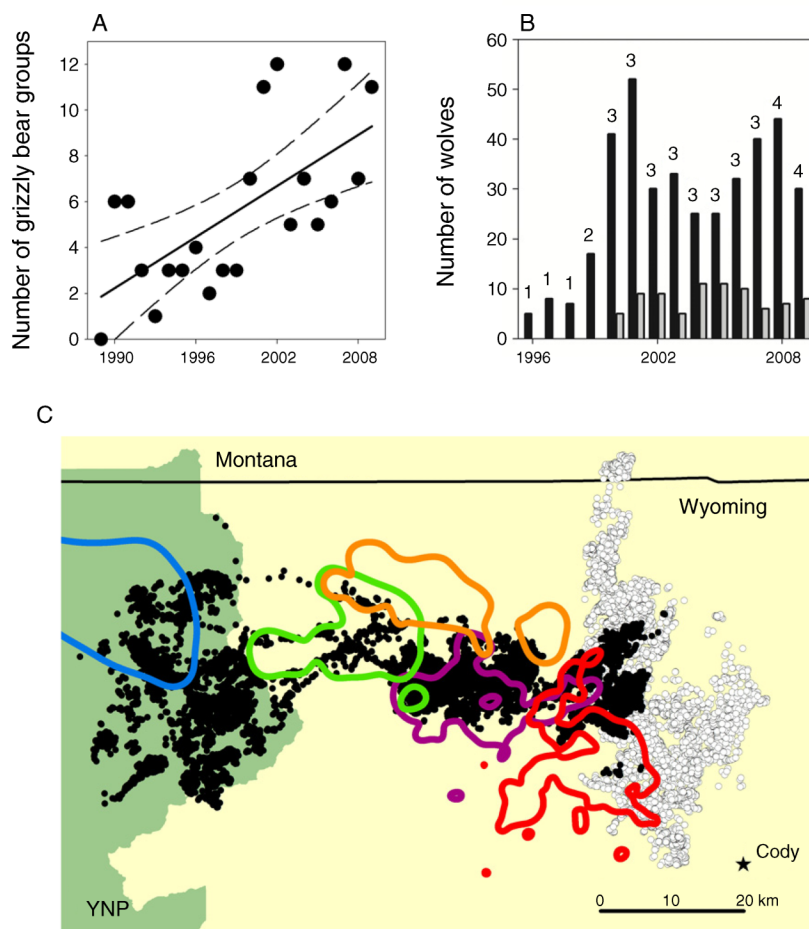


FIG. 5. (A) The number of grizzly bear (*Ursus arctos*) groups (shown with fitted solid line and 95% CI in dashed lines) counted during summer observation flights from 1990 to 2008 within the year-round range of migratory elk increased over 21 years (no grizzlies were observed in flights over the range of resident elk). (B) The number of wolves (*Canis lupus*) occupying migratory (black) and resident (gray) elk ranges since 1996. Several wolf packs now occupy the year-round range of migratory elk (pack numbers shown above bars), but only one pack has occupied the resident elk range. (C) The spatial distribution of wolf packs from 2007 to 2009, with pack boundaries represented by an 80% kernel home range. These include the Druid Peak (blue), Hoodoo (green), Beartooth (orange), Sunlight (purple), and Absaroka (red) packs. Migratory elk locations are shown with black circles, and resident elk locations are shown with white circles; as in Fig. 1).

nursing calves early in the growing season via direct predation (Barber-Meyer et al. 2008). Moreover, whereas the NCE of wolves is proposed to operate over the course of winter (Creel et al. 2009), we observed low pregnancy rates of migratory elk in early winter (e.g., as low as 57% in January 2007; Fig. 3A), suggesting a summer influence on the probability of conception that is at odds with the proposed mechanism. In light of the phenological and climatic changes these migratory elk have experienced, and because much evidence links ungulate pregnancy to summer forage conditions (Cook et al. 2004a, Parker et al. 2009), we interpret the reduced pregnancy of Yellowstone migrants as being caused primarily by drought-induced changes in habitat quality.

A secondary reason put forth for the historical dominance of migratory ungulates is that their seasonal movements reduce their exposure to predation (Fryxell et al. 1988, Fryxell and Sinclair 1988). Due to spatial patterns of large-carnivore recovery in the GYE, migratory elk in our study population now encounter far higher numbers of grizzly bears and wolves than do resident elk (Fig. 5A, B). Although we did not ourselves directly estimate rates of cause-specific elk calf mortality, a rigorous study of this question, one which included sampling of migratory calves from our study population, was conducted in an overlapping area from 2003 to 2005 (Barber-Meyer et al. 2008). During that study, bears (primarily grizzlies) caused 58–60% of calf deaths (Barber-Meyer et al. 2008), more than three times the proportion estimated 15 years earlier in the same area

(Singer et al. 1997). Additionally, newly reintroduced wolves caused 15–17% of calf deaths, favoring young calves in summer (Barber-Meyer et al. 2008). Here, we are assuming that rates of calf predation are very similar for the migratory elk we studied. Coupled with the low pregnancy rate of migratory elk, high rates of summer calf predation are consistent with the low numbers of migratory calves we observed at summer's end. Furthermore, the surprisingly high body fat levels of non-lactating females in the migratory subpopulation (Fig. 3D) are consistent with high levels of bear predation on neonates (Barber-Meyer et al. 2008) that free many females of lactation costs. An important consideration that we were unable to evaluate is whether the same nutritional limitation that depressed the pregnancy rate of migratory elk also rendered their calves more vulnerable to predators. Female elk under nutritional stress may give birth to lighter calves with reduced growth rates, which can increase the window of calf vulnerability and risk of calf mortality (Singer et al. 1997, White et al. 2010). By contrast, in the year-round habitats of resident elk, large carnivores are limited by management removals following livestock depredations, and bears may be further limited by a low tolerance for human activity. Recent increases in the recruitment of resident elk are consistent with a likely nutritional subsidy from irrigated fields, coupled with lower rates of calf predation by grizzlies and wolves.

Such disparate rates of predation on migratory ungulates, occurring across management jurisdictions along a wilderness frontier, are an unintended and little-recognized consequence of restoring large carnivores to the landscapes they once occupied. The influence of differential carnivore recovery and predation on the performance of partially migratory elk has previously been investigated in and around Banff National Park (BNP) in Alberta, Canada. There, lower predation on resident elk that benefited from wolf avoidance of urban habitat resulted in the dominance of resident over migratory elk by an order of magnitude (Hebblewhite et al. 2005). In a second study area, wolf removal, hay feeding, and prescribed burning outside the park subsidized resident elk, causing a fourfold increase in their numbers relative to migratory elk within BNP (Hebblewhite et al. 2006). In addition to experiencing similarly disparate patterns of predation and land use, migratory and resident elk in our study have experienced a divergence in the duration of the summer period when high-quality forage is available to them. Recent study of caribou populations (both migratory and resident) also highlights the importance of novel landscape changes (Festa-Bianchet et al. 2011). Beyond the conspicuous migration barriers and habitat conversion that often garner attention, some caribou declines may be linked to subtler changes in plant phenology, fire regimes, the accessibility of caribou to their predators, and densities of alternative prey (Vors and Boyce 2009, Festa-Bianchet et al. 2011).

Migratory ungulates in northern temperate regions generally move in summer to higher elevations (Fryxell and Sinclair 1988), where most of the parks and wilderness areas that sustain large-carnivore recovery occur (Joppa and Pfaff 2009) and where the effects of climate change are expected to be most pronounced due to strong associations between montane plant phenology and snow cover (IPCC Working Group I 2007). Meanwhile, cultivation in the lower elevation foothills brings human disturbance, predator control, and cropland irrigation that can function as subsidies to resident ungulates (Hebblewhite et al. 2006). Similar challenges have already become apparent for migratory birds. Though birds are also known to benefit from abundant resources (Levey and Stiles 1992) and reduced predation risk (McKinnon et al. 2010) on disparate seasonal ranges, population declines may be linked to trophic mismatch (Both et al. 2006), and human influences on seasonal resource availability and nest predation have long been a concern in studies of Neotropical migratory birds (Robinson et al. 1995).

As land migrants, ungulates appear particularly vulnerable to the physical obstruction of their migration routes in comparison with other migratory taxa. Thus, research and conservation have tended to focus on the impedance of ungulate migration corridors by human development (e.g., Berger 2004). Our findings suggest that landscape-level changes in vegetation phenology and predation pressure represent an important additional mechanism capable of reducing the demographic benefits of migration in ungulates. In revealing the declining productivity of migratory elk inhabiting one of North America's best protected wilderness areas, our findings also highlight a new and difficult challenge to the conservation of migratory ungulates. More broadly, the shifting fates of migratory elk in Yellowstone encourage us to consider the consequences for other migratory animals of human activities that increasingly, and ever more rapidly, alter the geographic variation in phenology and predation upon which migratory strategies so often depend.

ACKNOWLEDGMENTS

We thank P. J. White, D. Smith, and C. Hendrix of the U.S. National Park Service; C. Schwartz and M. Haroldson of the U.S. Geological Survey; J. Pehringer of USDA Wildlife Services; S. Woodruff of the U.S. Fish and Wildlife Service (USFWS); and C. Queen, C. Sax, and M. Bruscino of the Wyoming Game and Fish Department (WGFD) for assistance with data collection. We thank Quicksilver, Leading Edge, and Sky Aviation for assistance with animal captures and tracking. Our work was funded by WGFD, the USFWS, the Rocky Mountain Elk Foundation, the Wyoming Animal Damage Management Board, and the Wyoming Governor's Big Game License Coalition; and benefited from the cooperation of E. and B. Landmark, Heart Mountain, Mooncrest, Sunlight, Switchback, Trail Creek, and Two Dot ranches. A. D. Middleton received support from the University of Wyoming's Program in Ecology, the NSF-EPSCoR program (EPS-0447681), and the Buffalo Bill Historical Center. J. G. Cook and R. C. Cook

received support from the National Council for Air and Stream Improvement, Oregon Forest Industries Council, Washington Forest Protection Association, and several forest products companies. Comments by S. Buskirk, P. Cross, D. Doak, M. Festa-Bianchet, J.-M. Gaillard, J. Goheen, K. Monteith, S. Newsome, D. Skelly, P. J. White, and five anonymous reviewers improved the manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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SUPPLEMENTAL MATERIAL

Appendix A

Long-term spatial distribution of the study population as observed during winter recruitment surveys, 1989–2009 ([Ecological Archives E094-113-A1](#)).

Appendix B

Average percentage of body fat estimated for migratory vs. resident elk in winters 2008–2010 and summers 2008 and 2009 ([Ecological Archives E094-113-A2](#)).

Appendix C

A table of mean values and temporal trends for Normalized Difference Vegetation Index (NDVI) metrics used to compare phenological patterns on migratory summer and resident year-round range, 1989–2009 ([Ecological Archives E094-113-A3](#)).

Appendix D

Trends in spring–summer temperature and April–May precipitation in the study area, 1989–2009 ([Ecological Archives E094-113-A4](#)).