



Research Article

# Changing Migratory Patterns in the Jackson Elk Herd

ERIC K. COLE,<sup>1</sup> U.S. Fish and Wildlife Service, National Elk Refuge, PO Box 510, Jackson, WY 83001, USA

AARON M. FOLEY,<sup>2</sup> U.S. Geological Survey, Northern Rocky Mountain Science Center, 2327 University Way, Suite 2, Bozeman, MT 59715, USA

JEFFREY M. WARREN, U.S. Fish and Wildlife Service, Red Rock Lakes NWR, 27650B South Valley Rd., Lima, MT 59739, USA

BRUCE L. SMITH,<sup>2</sup> U.S. Fish and Wildlife Service, National Elk Refuge, PO Box 510, Jackson, WY 83001, USA

SARAH R. DEWEY, National Park Service, Grand Teton National Park, PO Drawer 170, Moose, WY 83012, USA

DOUGLAS G. BRIMEYER, Wyoming Game and Fish Department, PO Box 67, Jackson, WY 83001, USA

W. SUE FAIRBANKS,<sup>3</sup> Department of Natural Resource Ecology and Management, Iowa State University, 339 Science Hall II, Ames, IA 50011, USA

HALL SAWYER, Western Ecosystems Technology, Inc., 200 South 2nd Street, Laramie, WY 82001, USA

PAUL C. CROSS, U.S. Geological Survey, Northern Rocky Mountain Science Center, 2327 University Way, Suite 2, Bozeman, MT 59715, USA

**ABSTRACT** Migratory behavior in ungulates has declined globally and understanding the causative factors (environmental change vs. human mediated) is needed to formulate effective management strategies. In the Jackson elk herd of northwest Wyoming, demographic differences between summer elk (*Cervus elaphus*) population segments have led to changes in migratory patterns over a 35-year time period. The proportion of short-distance migrants (SDM) has increased and the proportion of long-distance migrants (LDM) has concurrently declined. The probability of winter-captured elk on the National Elk Refuge being LDM decreased from 0.99 (95% CI = 0.97–1.00) to 0.59 (95% CI = 0.47–0.70) from 1978 to 2012. We tested 4 hypotheses that could contribute toward the decline in the LDM segment: behavioral switching from LDM to SDM, differential survival, harvest availability, and calf recruitment. Switching rates from LDM to SDM were very low (0.2% each elk-year). Survival rates were similar between LDM and SDM, although harvest availability was relatively low for SDM that tended to use areas close to human development during the hunting season. Average summer calf/cow ratios of LDM declined from 42 to 23 calves per 100 cows from 1978–1984 to 2006–2012. Further, during 2006–2012, LDM summer calf/cow ratios were less than half of SDM (23 vs. 47 calves per 100 cows). Our data suggest recruitment is the driving factor behind the declining proportion of LDM in this region. Effectiveness of altering harvest management strategies to conserve the LDM portion of the Jackson elk herd may be limited. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

**KEY WORDS** *Cervus elaphus*, elk, Greater Yellowstone Ecosystem, migration, migratory distance, National Elk Refuge, predation, recruitment, summer range, survival.

Migration is a phenomenon exhibited by numerous genera and usually is a behavioral response to distribution of resources (Milner-Gulland et al. 2011). Ungulate migration is an adaptive behavioral strategy to obtain more nutritious forage resources and to avoid predation (McCullough 1985, Fryxell and Sinclair 1988, Bergerud et al. 1990). Some taxa have altered migratory behavior for a variety of reasons

including, but not limited to, anthropogenic activities, changing climate, and predation risk (Caccamise et al. 2000, Mbaiwa and Mbaiwa 2006, Wilcove and Wikelski 2008). Numerous partially migratory elk (*Cervus elaphus*) populations occur throughout western North America (Martinka 1969, Rudd et al. 1983, Woods 1991, Haggerty and Travis 2006, Robinson et al. 2010). Some advantages of migration may have been lost over time as climatic patterns have changed. For instance, Middleton et al. (2013a) suggested that elk migrating to high elevation areas in Yellowstone National Park (NP) were subject to drought induced changes in forage quality that resulted in lower fat reserves, lower pregnancy rates, and lower recruitment. Additionally, Hebblewhite and Merrill (2011) and Middleton et al. (2013a) found that migratory elk were subject to higher predation rates than non-migratory elk, perhaps because

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<sup>1</sup>E-mail: eric\_cole@fws.gov

<sup>2</sup>Present Address: 44 Duncan District Road, Sheridan, MT 59749.

<sup>3</sup>Present Address: Department of Natural Resource Ecology and Management, Oklahoma State University, 564 Agricultural Hall, Stillwater, Oklahoma.

<sup>†</sup>Eric K. Cole and Aaron M. Foley contributed equally to this work.

large predators like bears (*Ursus* spp.), wolves (*Canis lupus*), and mountain lions (*Puma concolor*) are easier to conserve in areas more distant from human habitation, which, in the United States, also tend to be higher elevation regions. The differential exposure to limiting factors between non-migratory and migratory elk groups is a concern because of the ecological and wildlife management consequences associated with conserving traditional migration behavior (Berger 2004, Wilcove and Wikelski 2008).

Many species of waterfowl, salmonids, and ungulates have mixed migration strategies (Allendorf et al. 2008). Managers often try to preserve the migratory behaviors of these species by adjusting hunting and fishing regulations in different regions, but this is difficult when migratory and sedentary segments of a population use a shared seasonal range during harvest seasons (Tacha et al. 1984, Caccamise et al. 2000, Wilson 2002, Reiss et al. 2009). Harvest via commercial fishing and recreational hunting can strongly influence annual population sizes (Solberg et al. 1999, Levin et al. 2006, Allendorf et al. 2008). Thus, understanding how subpopulations differ in use of space is important for quantifying the potential impact of harvest activities on each subpopulation (Mauritzen et al. 2002). For instance, resident Canada goose (*Branta canadensis*) populations are commonly hunted prior to and after migration to minimize harvest of migratory geese while maximizing harvest of residents (Caccamise et al. 2000). Surprisingly, little research has explored whether selective harvest could be partially driving different population growth trajectories between elk that display different migratory behavior (Smith 2007). For example, in their study of migratory and resident elk east of Yellowstone NP, Middleton et al. (2013a) did not consider differential harvest mortality between migratory and resident elk. Understanding whether differential harvest exists, and what the consequences may be, is critical for managing partially migratory populations.

The National Elk Refuge (hereafter termed the Refuge) hosts one of the world's largest concentrations of wintering elk, with an average of 7,300 elk occupying the Refuge from November to May each year, representing approximately 65% of the Jackson elk herd. Management of the Refuge and Jackson elk herd has been the subject of intense scrutiny and debate (Boyce 1989, U.S. Fish and Wildlife Service [USFWS] and National Park Service [NPS] 2007, Smith 2011). Elk receive supplemental feed on the Refuge operated by the USFWS and on 3 other feedgrounds northeast of the Refuge operated by the Wyoming Game and Fish Department (WGFD). Supplemental feeding has been employed in all but 9 winters on the Refuge since 1912. For the period of 1995–2014, elk were fed pelletized alfalfa at a mean daily rate of 3.6 kg per elk an average of 66 days a year. Supplemental winter feeding has minimized elk winter mortality, enhanced elk hunting opportunities, and reduced elk damage on private lands via maintaining elk on feedgrounds (Boyce 1989). However, supplemental feeding concentrates high numbers of elk in the same sites each winter, and elk density commonly exceeds 150 elk/km<sup>2</sup> on the Refuge (E. Cole, USFWS, unpublished data). Such

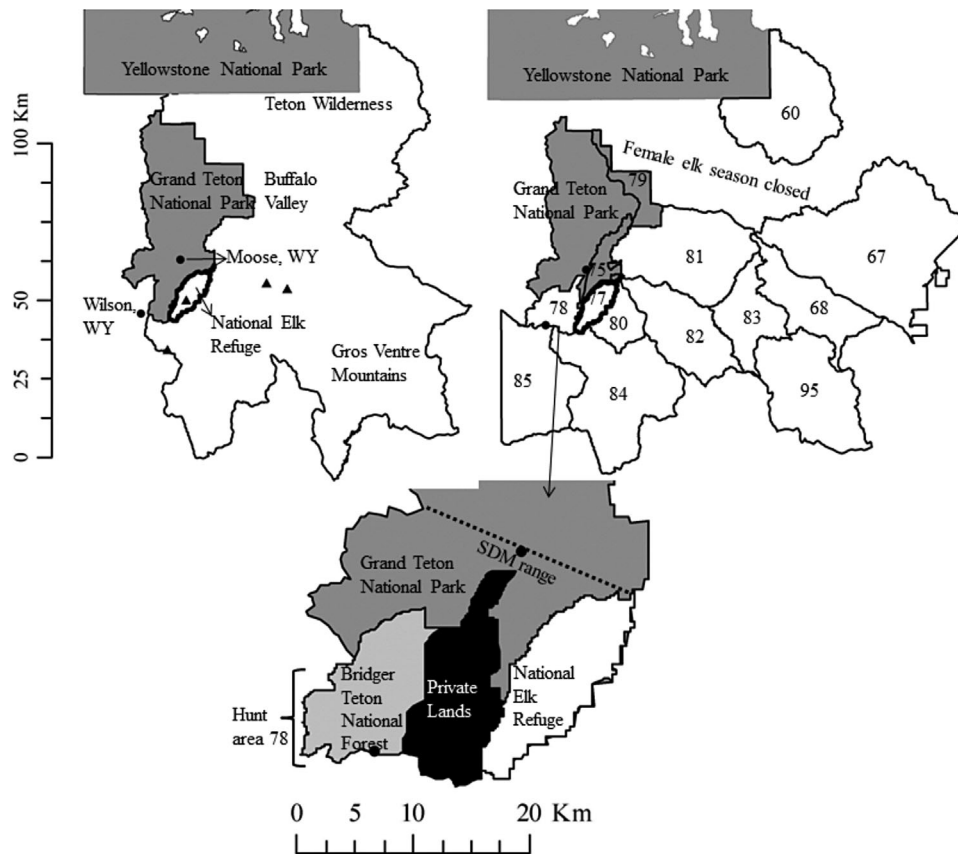
densities have resulted in loss of woody plant communities and bird habitat (Smith et al. 2004, Anderson 2007) and increased the prevalence of density-dependent diseases (Murie 1951, Franson and Smith 1988, Samuel et al. 1991, Herriges et al. 1992, Smith and Roffe 1997).

Migrations of elk from the Refuge to summer ranges in Grand Teton NP, the Gros Ventre Mountains, Teton Wilderness, and Yellowstone NP have been well documented (Anderson 1958, Cole 1969, Craighead et al. 1972, Boyce 1989, Smith and Robbins 1994). Boyce (1989) suggested that approximately 35% of the Jackson elk herd occupied summer ranges in southern Yellowstone NP in 1964, and Smith and Robbins (1994) estimated that 31% of cow elk captured on the Refuge between 1978 and 1982 summered in Yellowstone NP. In contrast, only <2% of elk sampled by Smith and Robbins (1994) summered between Wilson and Moose, Wyoming in southern Grand Teton NP (Fig. 1). Anecdotal observations by wildlife managers, hunters, and others suggested that the proportion of elk occupying the Wilson to Moose, Wyoming area had increased dramatically, whereas the proportion of elk that summer elsewhere (e.g., Yellowstone NP, Teton Wilderness, and Grand Teton NP; Fig. 1) had declined over 3 decades. We examined the changes in proportion of these elk captured in winter on the Refuge from 1978 to 2012 and evaluated the possible ecological and management factors that could be responsible for the observed changes. We then discuss the implications of these findings to meeting the Refuge and Jackson elk herd population objectives and the management strategies for conserving declining migratory populations where recreational harvest occurs.

## STUDY AREA

We conducted this study in and around the Jackson elk herd unit (approximately 8,000 km<sup>2</sup>) in northwest Wyoming, which included the Refuge, Grand Teton NP, Bridger-Teton National Forest (NF), and southern Yellowstone NP (Fig. 1). Herd unit boundaries were delineated by the WGFD to encompass a distinct group of elk from which there would be <10% annual interchange with surrounding elk herds (Gasson 1987). Elevations ranged from a low of 1,850 m in the Snake River flood plain to almost 4,200 m in the Teton Range. Boyce (1989) and Smith and Robbins (1994) described the herd unit's boundaries, geological features, and plant communities. Summer ranges of the elk occupied a wide range of topographic and vegetative features, from residential subdivisions and irrigated pasture, sagebrush (*Artemisia* spp.) grasslands, forests of lodgepole pine (*Pinus contorta*), and subalpine fir (*Abies lasiocarpa*), to alpine tundra in the highest elevations of the study area. The 98-km<sup>2</sup> Refuge was established in 1912 with a primary purpose of providing winter range for the Jackson elk herd. Boyce (1989), Smith and Robbins (1994), Smith et al. (2004), and Smith (2011) provided detailed descriptions of the history and management of the Jackson elk herd.

Elk hunting occurred throughout the study period, with season length, sex restrictions, and areas open to hunting varying by year. The Yellowstone NP was closed to hunting,



**Figure 1.** Elk capture sites, feedgrounds (triangles), and National Parks within the Jackson elk herd study area in northwestern Wyoming, USA (left) and hunt areas where female elk were legal for harvest (right). Note that hunt areas 75 and 79 are within Grand Teton National Park. The close-up image (bottom) depicts the summer range of short-distance migratory (SDM) elk south of the dotted line; black areas within hunt area 78 were privately owned and light gray areas were National Forest lands. Note the National Elk Refuge is hunt area 77.

but elk that summered there were subject to hunting during migration to winter range. In Grand Teton NP, elk were subject to harvest in areas east of the Snake River under Public Law 81-787. During the 1970s, elk management was focused on maximizing hunter opportunity to control elk populations in northern Grand Teton NP, and the Teton Wilderness. This was accomplished by extending hunting seasons into November for unlimited general license as well as limited quota license opportunities. Hunting was allowed on the Refuge and hunting opportunities on private lands south of Grand Teton NP were limited because of housing density, subdivision covenants, and land access. Despite these limitations, WGFD has worked with landowners to maximize elk harvest on private lands adjacent to the Refuge. In recent years, WGFD has designed hunting seasons to reduce harvest of migratory elk from Yellowstone NP and Teton Wilderness through bull-only seasons and reduced season length, quotas, and license types in areas east of the Refuge.

## METHODS

### Capture and Collars

We used radio-collar data of female elk from 3 distinct periods of study on the Jackson elk herd conducted by Grand Teton NP, Western Ecosystems Technology, Inc. (WEST),

the Refuge (Smith and Robbins 1994, Smith 2007, E. Cole, unpublished data), Iowa State University (ISU; Barbknecht et al. 2011), and WGFD. Winter (Jan–Mar) captures were on the Refuge, Buffalo Valley within and outside of Grand Teton NP, and 3 state feedgrounds in the Gros Ventre drainage (Alkali, South Park, and Patrol Cabin; Table 1, Fig. 1). Summer elk captures (Jul) were conducted within Grand Teton NP and Teton Wilderness Area (Table 1, Fig. 1). Capture activities were approved by WGFD (Chapter 33 permits #394 and #624) and ISU Animal Care and Use Committee (Protocol #8-05-5962).

Telemetry data were divided into 3 7-year periods to correspond with the independent studies comprising the data used here. The first period (P1) was 1978–1984, period 2 (P2) was 1994–2000, and period 3 (P3) was 2006–2012. Elk captured during P1 and P2 were fitted with very high frequency (VHF) radio collars (U.S. Department of Agriculture Denver Wildlife Research Center and Telonics, Inc., Mesa, AZ) and monitored via aerial and ground telemetry. Elk captured during P3 were fitted with global positioning system (GPS) radio collars (Lotek Inc., Newmarket, ON, Canada; Advanced Telemetry Systems, Inc., Isanti, MN; and Telonics, Inc.). Average number of locations per elk was 55 (range = 6–156) and 46 (range = 5–103) during P1 and P2, respectively. Elk with GPS collars during P3 had varying fix rates (range = 2–24 hr) that

**Table 1.** Years of elk capture, study publication or agency, capture methods and collar type, and number of collared female elk used for analysis in northwestern Wyoming during 1978–2012. Collar types were very high frequency (VHF) and global positioning system (GPS). NER refers to National Elk Refuge. NPS refers to National Park Service. WGFD refers to Wyoming Game and Fish Department.

Capture years	Project	Method and collar type	<i>n</i>
1978–1982	Smith and Robbins (1994)	Trapping/darting; VHF	68
1994–1997	Smith et al. (2007)	Darting; VHF	42
2005–2007	NER, unpublished	Trapping/darting; VHF	31
2008–2011	NER, unpublished	Darting; GPS	51
2007–2010	NPS, unpublished	Darting; GPS	45
2008–2010	WGFD, unpublished	Darting; GPS	4
2006–2010	Barbknecht et al. (2011)	Net-gun; GPS	10
2010–2012	WGFD, unpublished	Darting; GPS	29

resulted in considerably more locations per individual (mean number of locations per elk = 1,004, range = 69–4,416). Only adult females were collared except during P2 when all captured females were 1-year-old.

### Summer Range Classification

The summer range between Wilson and Moose, Wyoming is only 8–10 km west and northwest of the Refuge, and we defined elk that summered in this area as short-distance migratory elk (SDM). We did not classify these elk as resident elk (Hebblewhite and Merrill 2011, Middleton et al. 2013a) because these elk do not reside on winter ranges year-round. The SDM occupying the area between the towns of Wilson and Moose, Wyoming (Fig. 1) are distinct from long-distance migratory elk (LDM) because of 1) shorter migratory distance between summer range and the Refuge, 2) greater anthropogenic influences such as housing development and agricultural activity, and 3) relatively late seasonal migration to winter range (Fig. S1, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). Three elk that summered within 8–10 km northeast of the Refuge in the Bridger-Teton NF were considered LDM elk in our analyses because they did not meet criteria 2 and 3 in our definition of SDM.

We classified elk as LDM or SDM based on the location of summer-range centroids relative to the SDM–LDM boundary (Fig. 1). We estimated summer home ranges using locations obtained 1 July to 30 September, except for 2 elk that were still migrating after 1 July. For these elk, we used locations after the net squared displacement reached an asymptote (when the distance between the winter range and the elk became consistent). We used minimum convex polygons (MCP; Worton 1987) to identify centroid locations for each individual-year summer ranges. Because the VHF-collared elk during P1 and P2 had relatively fewer locations compared to GPS radio-collared elk, we randomly selected *X* locations per GPS elk with the caveat that *X* was within the range of VHF locations ( $n = 6–156$ ) with the intention to reflect intensity of data acquisition during P1 and P2.

### Proportion Migratory

We tested for a declining probability of a marked female elk on the Refuge being LDM using generalized linear models in R 3.0.3 (R Development Core Team 2005), binomially-distributed errors, and a logit link. We assessed model goodness-of-fit assuming a  $\chi^2$  distribution for the estimated

deviance with  $n-k$  degrees of freedom, where  $n$  is the sample size and  $k$  is the number of estimated parameters (Neter et al. 1996). We calculated standard errors using the delta method (Oehlert 1992).

We used radio-collar data from all elk captured on the Refuge to assess the frequency of elk that switched from LDM to SDM. We divided the number of switches from SDM to LDM (or vice versa) by the total number of elk-years. To further evaluate whether movement behaviors have changed over time, we computed average distance between each summer home-range centroid of elk captured on the Refuge and the Refuge centroid during P2 and P3. Behavioral switching may be a function of distance because elk that summer on the periphery of the SDM–LDM boundary area may be more likely to become SDM relative to elk that summer elsewhere (e.g., Yellowstone NP). We used a subset of individuals from P3 to graphically test for monotonically declining distance between consecutive summer centroids per individual and the Refuge. Lastly, we obtained the switching rate and estimated elk population sizes for both LDM and SDM to model how many years of consistent switching would result in the current proportion of LDM to SDM assuming constant rates of birth, death, emigration, and immigration. The number of SDM or LDM elk in year  $t$  are  $SDM_{t+1} = SDM_t(a+1)$  and  $LDM_{t+1} = (1-a)LDM_t$ , where  $a$  is the net proportion that switched from LDM to SDM.

We used radio-telemetry data from all female elk from all 3 periods to estimate annual survival of LDM and SDM. We defined an elk-year as 1 January to 31 December. We chose 1 January as our start date because the earliest captured elk occurred on 17 January. The first study period concluded on 21 November 1984, the final year of P1; we ended P2 and P3 on the same day of their final years. We right censored individuals that switched from LDM to SDM, or vice versa, and created a new encounter history with the new status starting the year switching occurred. We used Kaplan–Meier staggered entry survival analysis (Heisey and Patterson 2006) via R package *wild1* (Sargeant 2011).

For the harvest availability analyses, we limited our scope to P3 when GPS radio-collar data were available. We compared proportional use of hunt areas among elk captured on different sites (e.g., Refuge, Buffalo Valley, etc.) and did not detect differential proportional use. Habitat-induced bias (Frair et al. 2004, Nielson et al. 2009) due to different terrain

features among hunt areas was not an issue because GPS fix-rate success during open rifle season was 97%. Lastly, because elk may have moved among hunt areas to avoid hunting pressure, we examined differences in day-time and night-time use of hunt areas; we found no statistical differences in averaged individual elk-year proportional use of hunt areas. Thus, all GPS data of elk during P3, regardless of capture location, were combined for this analysis.

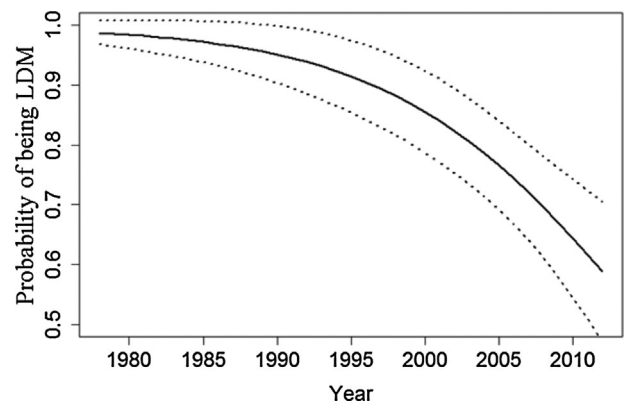
For both LDM and SDM, we computed proportion of locations spent within 14 hunt areas during open rifle seasons (18 Aug to 31 Jan) during P3 (Fig. 1). We then used a mixed effects Cox proportional hazards model (Cox 1972, Therneau et al. 2003) to evaluate relative harvest hazard of each hunt area. This type of analysis uses locational data (which hunt areas elk were within during open rifle season) of all elk during a given date of harvest (month, day, and year) to assess risk. We randomly selected 1 location per elk-day only when individual elk visited multiple hunt areas during 1 day. We excluded non-harvest mortalities, which were mostly of unknown causes, and used hunt area as a random effect in R package *coxme* (Therneau et al. 2003).

We collected summer (Jul–Aug) calf/cow ratios from multiple sources (Smith and Robbins 1994, Smith and Anderson 1996, NPS and WGF, unpublished data) which were grouped by migratory status based on locations of aerial surveys. We summed number of calves and cows observed throughout the migratory range for each year surveyed and plotted the calf/cow ratios for each period. We used analysis of variance (ANOVA) to test for differences in mean calf/cow ratios among periods for LDM. We also used a *t*-test with the Welch degrees of freedom modification (Welch 1938) because of the assumption of unequal variances when testing for statistical difference in calf/cow ratios between LDM and SDM during P3. There were insufficient ratios for SDM during P1 and P2 because the presence of a small SDM population in the Wilson to Moose, Wyoming area did not warrant summer surveys at that time.

## RESULTS

During 1978–2012, 191 monitored females provided data suitable for analysis. Multiple years of summer range selection data were collected on 129 females, ranging from 2 ( $n = 49$ ) to 16 years ( $n = 1$ ; Table S1, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). Only 3 individuals switched between LDM and SDM. The model testing for a change in the proportion of females being LDM fit the data well ( $\chi^2_{189} = 152.2$ ,  $P = 0.98$ ). There was a strong support for a decrease in the probability of a marked female on the Refuge being LDM during the years data were available (Table S1; Fig. 2); the probability of a marked female being LDM declined from 0.99 (95% CI = 0.97–1.00) to 0.59 (95% CI = 0.47–0.70) between 1978 and 2012 (Fig. 2).

We amassed data on 553 elk-years and only 3 (0.5%) elk switched summer ranges. Of these 3 elk, 2 switched from LDM to SDM, an annual switching rate of 0.2%. Both elk that switched from LDM to SDM came from Grand Teton NP. The relationship between centroids in consecutive summers was not correlated with distance to the Refuge



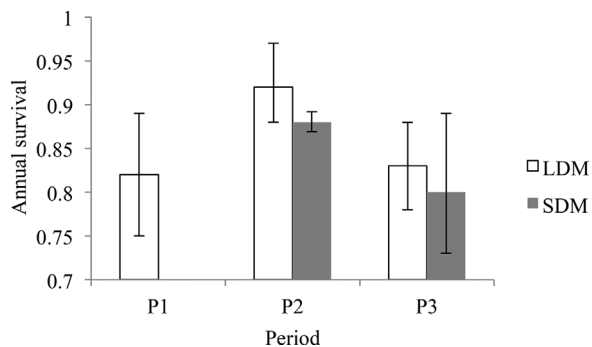
**Figure 2.** Probability with 95% CI of a female elk marked during winter on the National Elk Refuge, Wyoming, being from a long-distance migratory (LDM) population segment, 1978–2012.

among the subset of 88 GPS-collared elk captured between 2006 and 2012 (Fig. S2, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)).

We further assessed the plausibility of behavioral switching as a primary driver of the observed change in LDM and SDM behaviors using the observed switching rate in a simple coupled geometric growth model assuming equal birth and death rates between LDM and SDM. Given starting populations of 8,000 and 100 in 1978, a net switching of 0.2% would result in a proportion LDM ( $SDM_t / (SDM_t + LDM_t)$ ) of 93% in 2012 which is higher than the observed 59% (Fig. S3, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)).

Periods 1–3 contained 154, 143, and 244 LDM elk-years, respectively. Only 2 SDM elk-years were observed during P1; P2 and P3 contained 28 and 115 SDM elk-years, respectively. Eighty-one percent (71/88) of mortalities were due to harvest, including 2 wounding losses. Point estimates of annual survival probability were lower, but not significantly, during P1 (0.82, 0.75–0.89 95% CI) and P3 (0.83, 0.78–0.88 95% CI) than P2 (0.92, 0.88–0.97 95% CI) for LDM elk (Fig. 3). Further, survival probabilities were not significantly different between LDM and SDM elk during any period.

During P3, we used 130,177 hunting-season GPS locations to assess proportional use in hunt areas among LDM and SDM elk. We used 231 elk-years and 30 harvest mortalities in conjunction with 9,458 un-duplicated hunting-season elk GPS locations to assess hunt area-specific hazard risks with hunt area 78 as the baseline. There was variation in harvest availability; elk in hunt area 77 (the Refuge) were the most available for harvest, whereas elk in hunt area 78 were the least available (Fig. 4). The SDM spent a high proportion of their time within the least hazardous region, hunt area 78 (Fig. 5), but only 2% of hunting-season locations were within the Bridger-Teton NF, a public hunting tract within hunt area 78 (Fig. 1, Fig. S4, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). Compared to SDM, LDM more often used multiple hunt areas (Fig. 5) and were most likely to be found in hunt areas 75 and 77, which were the most hazardous (Fig. 4).

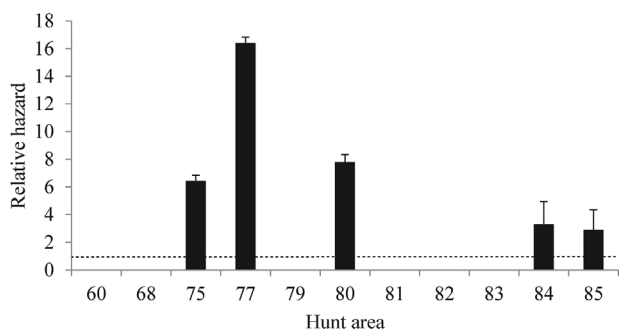


**Figure 3.** Annual survival rates of long-distance migratory (LDM) and short-distance migratory (SDM) female elk during 3 temporal periods in northwestern Wyoming. Only 2 SDM elk-years were available during period 1 (P1). Period 1 = 1978–1984, P2 = 1994–2000, and P3 = 2006–2012. Error bars show 95% confidence intervals.

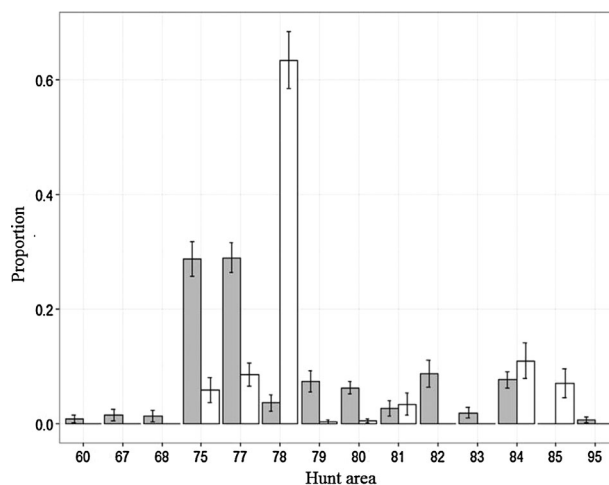
There was an obvious decline in summer calf/cow ratios in the LDM segments through time (Fig. 6); during P1 and P2, LDM averaged 42 (SD = 7) and 40 (SD = 5) calves per 100 cows, respectively ( $F_2 = 24.1$ ,  $P < 0.001$ ). During P3, the number of calves per 100 LDM cows decreased to 23 (SD = 5), which was less than half of the 47 (SD = 7) calves per 100 cows in the SDM segment during the same time period ( $T_{6,09} = -6.25$ ,  $P < 0.001$ ).

## DISCUSSION

We found an increase in the proportion of short-distance migrants and a decrease in the proportion of long-distance migrants captured from 1978 to 2012 on the Refuge, suggesting commensurate changes in elk distribution in the southern portion of the Greater Yellowstone Ecosystem (GYE) and a decrease in the number of elk that undertake long-distance migrations in the Jackson elk herd. We tested 4 hypotheses that could potentially influence the opposite population growth trajectories between LDM and SDM of the Jackson elk herd: behavioral switching rates, adult female survival, harvest availability, and recruitment.

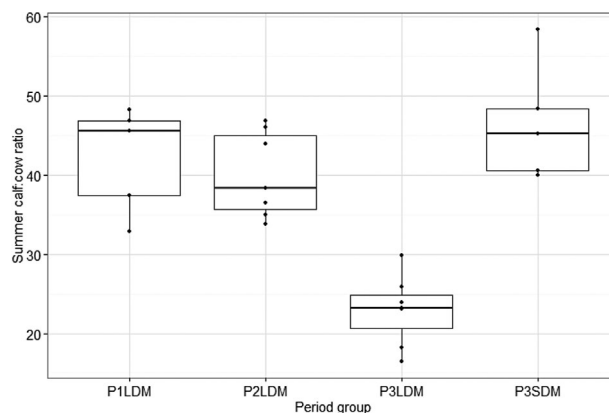


**Figure 4.** Relative hazard of hunt areas derived from a combination of global positioning system (GPS) data during open hunting seasons and harvested female elk during 2006–2012 in northwestern Wyoming. Coefficient estimates are relative to hunt area 78 and the horizontal dotted line indicates 1 where there is no difference. Error bars are standard error. Histogram bars are not visible for several hunt areas because of very low relative hazard values.



**Figure 5.** Average proportional use of hunt areas by long-distance migratory (gray) and short-distance migratory (white) individual female elk in northwestern Wyoming during 2006–2012. Classification of long and short distance migratory elk were based from centroids of summer (Jul–Sep) home ranges. Error bars denote standard deviations.

Annual survival rates of both LDM and SDM adult female elk were 80–92%, which is similar to the average survival rates of 85% from 26 studies (see Webb et al. 2011b). Most of the change in survival rates appeared to be associated with the time period rather than migration status because LDM and SDM survival during a given time period were separated by only a few percentage points. Smith’s (2007) finding that Grand Teton NP elk had higher survival rates than elk from elsewhere (i.e., Yellowstone NP, Gros Ventre, and Teton Wilderness) during the 1990s may be attributed to including both LDM and SDM elk from Grand Teton NP in his analysis. Even though survival was comparable between both elk segments during our study, harvest availability varied.



**Figure 6.** Box plots of summer calf/cow ratios from long-distance migratory (LDM) and short-distance migratory (SDM) elk during 3 periods in northwestern Wyoming. Periods (P) 1, 2, and 3 were during 1978–1984, 1994–2000, and 2006–2012, respectively. The dark line inside of boxes indicates the median and the top and bottom of the boxes are 25th and 75th percentiles, respectively (the entire box contains 50% of the data). Outliers, defined as being outside of the inter-quartile range times 1.5, are represented by dots outside of the box.

The SDM spent a high proportion of time within hunt area 78, an area with a large amount of privately owned lands with limited hunter access. However, when SDM elk left summer ranges to enter the Refuge (hunt area 77), vulnerability increased and survival rates likely decreased. In recent years, wildlife managers have structured hunts to limit harvest of the northern migrants (e.g., Yellowstone NP and Teton Wilderness elk) and secure public access to private lands to improve harvest rates and decrease numbers of SDM elk that occupy the Wilson to Moose, Wyoming area. Although there is opportunity to direct harvest activities toward hunt areas based on the proportional use of various hunt areas by elk, the highly consistent survival rates among both subpopulations indicate this management strategy may not be sufficient to reverse trends in the proportional change between SDM and LDM.

Hunting mortality of calves may affect recruitment rates because calves are an important element of elk population dynamics (Raithel et al. 2007). Work done by Smith and Anderson (1998) indicated hunting mortality did not differ between calves and adult elk; however, this was during the early 1990s when number of hunters was 3 times greater associated with the relatively large Jackson elk herd population size (D. Brimeyer, WGFD, personal communication). During the early 1990s, hunting seasons promoted harvest of LDM elk through hunting seasons that extended into November for general and limited quota licenses. Between 1993 and 1997, an average of 1,920 limited quota any elk licenses were offered each year in the northern hunt areas of the Jackson elk herd unit, in which LDM elk migrate. Hunter numbers in the Jackson herd averaged over 9,190 hunters during this time period. In recent years, hunting seasons have been designed to protect LDM elk while increasing harvest of SDM elk. Since 2012, no limited quota any elk licenses have been offered in the hunt areas that focused hunting pressure on LDM. Hunter numbers since 2012 (2012–2014) averaged 2,985 hunters. Although hunting seasons and quotas have become more conservative for the areas where LDM are more vulnerable, the hunt units for the SDM have been liberalized through the addition of license types and extending season lengths to the end of January (Hunt Area 78).

We also explored whether elk switched from LDM to SDM summer ranges and whether the switching rates were high enough to alter population growth trajectories during the 35-year study period. Switching from LDM to SDM was extremely low (0.002 elk-years), which supports the general consensus that female elk exhibit high site fidelity (Irwin and Peek 1983, Edge et al. 1986, Webb et al. 2011a). Further, elk herds elsewhere with resident and migratory segments also exhibited low switching rates (Hebblewhite and Merrill 2007, Middleton et al. 2013a). However, juvenile elk in the Jackson elk herd had high dispersal rates in the early 1990s, which may be attributed to density effects when the population peaked at approximately 18,000 elk (Smith and Anderson 2001). Additionally, the authors did not test whether dispersing elk were relocating to the Wilson to Moose, Wyoming area or to other summer ranges within our

study area. Our model also indicated that the switching rate from LDM to SDM was not sufficient to account for the observed declines in the proportion of LDM. Similarly, Smith and Anderson (2001) determined that switching (dispersing) did not differentially influence population growth of summer herd segments within the Jackson elk herd.

Recruitment, a key driver in elk population dynamics (Gaillard et al. 1998, Raithel et al. 2007), appears to be the primary driver of the decline in LDM. Recruitment, as indexed by summer calf/cow ratios, in LDM declined and during recent years was half of summer calf/cow ratios observed in SDM elk (Fig. 6). The current 23 calves per 100 cows in LDM is considered low recruitment (White et al. 2010) and is nearly half of historical LDM summer calf/cow ratios (Fig. 6). Potential effects on summer calf/cow ratios include pregnancy rates influenced by winter range conditions (Thorne et al. 1976, Weber et al. 1984), spring weather conditions (Lubow and Smith 2004, Smith et al. 2006), forage quality and quantity through summer climate (Cook et al. 2004), elk density (Stewart et al. 2005), sex and age composition (Albon et al. 1986, Noyes et al. 1996), and predators, both directly and indirectly (Barber-Meyer et al. 2008, Creel and Christianson 2008).

We did not have sufficient data to model influences on summer calf/cow ratios although we conducted exploratory analyses to examine changes in environmental covariates throughout the study period (Supplementary Material 1, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). There is likely a differential exposure to predation between SDM and LDM elk because SDM are likely partially buffered from predators (Hebblewhite and Merrill 2007). Neonate predation by grizzly bears (*Ursus arctos*) has increased since the 1980s (Middleton et al. 2013b) and winter calf/cow ratios were significantly negatively correlated with grizzly bear density at a herd-unit scale in the southern portion of the GYE (Foley et al. 2015). Wolves also prey on neonates but probably to a lesser extent than grizzly bears (Barber-Meyer et al. 2008, Griffin et al. 2011). Wolves can affect recruitment in 2 ways—directly and indirectly. Wolves directly predate calves but also may increase anti-predator behavior in cow elk (see Garrott et al. 2005) that results in reduced pregnancy rates (Creel and Winnie 2005, Christianson and Creel 2010). In 2006–2007, only 70% (53/76) of adult female elk sampled during January–March in Buffalo Valley, within the LDM summer range of the Jackson herd unit, were pregnant (S. Fairbanks, Iowa State University, unpublished data), and 71% of migratory elk in Clark's Fork herd unit were pregnant when sampled during winters of 2008–2010 (Middleton et al. 2013a). These pregnancy rates were considerably lower than the 89% (141/158) rate from 3 feedgrounds (Bench Corral, Soda Lake, and Scab Creek) in the Pinedale, Piney, and Upper Green River herd units during 2006–2007 (Barbknecht et al. 2011, S. Fairbanks, unpublished data) personal communication; Fig. S6, available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). During the years when pregnancy data were collected, Jackson and Clark's Fork had 79% higher indices of wolf densities than

the 3 feedgrounds (Foley et al. 2015). Further, during 1976–1982 when wolves were not present on our study area, the Refuge had an 87% pregnancy rate (Smith and Robbins 1994) that did not differ from the 86% rate in 1998–2002 when wolves were colonizing Jackson Hole (Smith et al. 2006). The inverse relationship between pregnancy rates and wolf density might suggest that anti-predator behavior affects pregnancy rates. Comparing pregnancy rates between elk with and without supplemental feed via winter feedgrounds may not be appropriate, but the phenomenon of lower pregnancy rates in relation to higher predation risk has been observed throughout the GYE (Creel et al. 2011).

However, lower recruitment rates may also be manifested through weather conditions (Proffitt et al. 2014) and forage quantity and quality (Cook et al. 2001, 2004) via changes in climate patterns (Middleton et al. 2013a) and weather-mediated predisposition of neonates to predation and disease (Smith et al. 2006). Foley et al. (2015) found a positive correlation in winter calf/cow ratios with previous year summer rainfall and a negative correlation with previous year maximum snow-water equivalent. Climate and predation data at a finer spatial and temporal scale are required to better understand their relative impacts on elk recruitment.

## MANAGEMENT IMPLICATIONS

The proportional decline of LDM compared to SDM has significant management implications for the Jackson elk herd. This change suggests that long-distance migratory elk have declined over a 35-year time period, and short distance migrants that summer immediately adjacent to the Refuge winter range have increased dramatically. Long-distance migratory elk populations are biologically and economically important, and strategies designed to protect long-distance migratory elk may limit the ability of elk managers to reduce the Refuge population to objective levels. Population objectives are 11,000 elk for the Jackson elk herd, with 5,000 of these wintering on the Refuge (USFWS and NPS 2007), but 2014 surveys enumerated approximately 11,600 elk in the Jackson elk herd with 8,300 of these wintering on the Refuge (WGFD 2014). Current harvest strategies such as modified hunt area boundaries and hunting season dates designed to protect LDM may have little effect because survival rates of adult female elk, which are mostly determined by harvest, were comparable between LDM and SDM population segments based on our data. Low recruitment rates appear to be driving the decline of the LDM segment, which limits remedial options of wildlife managers. Conversely, strategies to maximize harvest of SDM have proved insufficient to offset high recruitment among SDM and meet the Refuge population objectives. Failure to reduce elk numbers to the Refuge population objective will necessitate continued reliance on supplemental feeding, higher prevalence, and risk of density-dependent disease outbreaks throughout the Jackson elk herd, and continued loss of shrub and woodland communities on the Refuge due to browsing by large numbers of elk (Smith et al. 2004, USFWS and NPS 2007).

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## LITERATURE CITED

- Albon, S., B. Mitchell, B. Huby, and D. Brown. 1986. Fertility in female red deer (*Cervus elaphus*): the effects of body composition, age and reproductive status. *Journal of Zoology* 209:447–460.
- Allendorf, F. W., P. R. England, G. Luikart, P. A. Ritchie, and N. Ryman. 2008. Genetic effects of harvest on wild animal populations. *Trends in Ecology & Evolution* 23:327–337.
- Anderson, C. C. 1958. The elk of Jackson Hole: a review of Jackson elk studies. *Bulletin* 10, Wyoming Game and Fish Commission, Cheyenne, Wyoming, USA.
- Anderson, E. M. 2007. Changes in bird communities and willow habitats associated with fed elk. *Wilson Journal of Ornithology* 119:400–409.
- Barber-Meyer, S. M., L. D. Mech, and P. J. White. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildlife Monographs* 169:1–30.
- Barbknecht, A. E., W. S. Fairbanks, J. D. Rogerson, E. J. Maichak, B. M. Scurlock, and L. L. Meadows. 2011. Elk parturition site selection at local and landscape scales. *Journal of Wildlife Management* 75:646–654.
- Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. *Conservation Biology* 18:320–331.
- Bergerud, A., R. Ferguson, and H. Butler. 1990. Spring migration and dispersion of woodland caribou at calving. *Animal Behaviour* 39:360–368.
- Boyce, M. S. 1989. *Elk management in North America: the Jackson herd*. Cambridge Press, Cambridge, United Kingdom.
- Caccamise, D. F., L. M. Reed, P. M. Castelli, S. Wainright, and T. C. Nichols. 2000. Distinguishing migratory and resident Canada geese using stable isotope analysis. *Journal of Wildlife Management* 64:1084–1091.
- Christianson, D., and S. Creel. 2010. A nutritionally mediated risk effect of wolves on elk. *Ecology* 91:1184–1191.
- Cole, G. F. 1969. The elk of Grand Teton and southern Yellowstone National Parks. Research Report GRTE-N-1, and manuscript for Fauna of the National Parks of the United States. U.S. National Park Service, Office of Natural Science Studies, Washington, D.C., USA.
- Cook, R. C., J. G. Cook, and L. D. Mech. 2004. Nutritional condition of northern Yellowstone elk. *Journal of Mammalogy* 85:714–722.
- Cook, R. C., D. L. Murray, J. G. Cook, P. Zager, and S. L. Monfort. 2001. Nutritional influences on breeding dynamics in elk. *Canadian Journal of Zoology* 79:845–853.
- Cox, D. R. 1972. Regression models and life tables. *Journal of Royal Statistical Society, Series B* 34:187–220.
- Craighead, J. J., G. Atwell, and B. W. O'Gara. 1972. Elk migrations in and near Yellowstone National Park. *Wildlife Monographs* 29:3–48.
- Creel, S., and D. Christianson. 2008. Relationships between direct predation and risk effects. *Trends in Ecology & Evolution* 23:194–201.
- Creel, S., D. A. Christianson, and J. A. Winnie Jr. 2011. A survey of the effects of wolf predation risk on pregnancy rates and calf recruitment in elk. *Ecological Applications* 21:2847–2853.



- Creel, S., J. Winnie Jr, B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86:3387–3397.
- Edge, W. D., C. L. Marcum, S. L. Olson, and J. F. Lehmkuhl. 1986. Nonmigratory cow elk herd ranges as management units. *Journal of Wildlife Management* 50:660–663.
- Foley, A.M., P.C. Cross, D.A. Christianson, B.M. Scurlock, and S. Creel. 2015. Influences of supplemental feeding on winter elk calf:cow ratios in the southern greater Yellowstone ecosystem. *Journal of Wildlife Management* 79:in press.
- Frair, J. L., S. E. Nielsen, E. H. Merrill, S. R. Lele, M. S. Boyce, R. H. M. Munro, G. B. Stenhouse, and H. L. Beyer. 2004. Removing GPS collar bias in habitat selection studies. *Journal of Applied Ecology* 41:201–212.
- Franson, J. C., and B. L. Smith. 1988. Septicemic pasteurellosis in elk (*Cervus elaphus*) on the United States National Elk Refuge, Wyoming. *Journal of Wildlife Diseases* 24:715–717.
- Fryxell, J., and A. Sinclair. 1988. Causes and consequences of migration by large herbivores. *Trends in Ecology & Evolution* 3:237–241.
- Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution* 13:58–63.
- Garrott, R. A., J. A. Gude, E. J. Bergman, C. Gower, P. White, and K. L. Hamlin. 2005. Generalizing wolf effects across the Greater Yellowstone Area: a cautionary note. *Wildlife Society Bulletin* 33:1245–1255.
- Gasson, W. 1987. Managing elk the Wyoming way. *Wyoming Wildlife* 9:16–25.
- Griffin, K. A., M. Hebblewhite, H. S. Robinson, P. Zager, S. M. Barber-Meyer, D. Christianson, S. Creel, N. C. Harris, M. A. Hurley, D. H. Jackson, B. K. Johnson, W. L. Myers, J. D. Raithel, M. Schlegel, B. L. Smith, C. White, and P. J. White. 2011. Neonatal mortality of elk driven by climate, predator phenology and predator community composition. *Journal of Animal Ecology* 80:1246–1257.
- Haggerty, J. H., and W. R. Travis. 2006. Out of administrative control: absentee owners, resident elk and the shifting nature of wildlife management in southwestern Montana. *Geoforum* 37:816–830.
- Hebblewhite, M., and E. H. Merrill. 2007. Multiscale wolf predation risk for elk: does migration reduce risk? *Oecologia* 152:377–387.
- Hebblewhite, M., and E. H. Merrill. 2011. Demographic balancing of migrant and resident elk in a partially migratory population through forage-predation tradeoffs. *Oikos* 120:1860–1870.
- Heisey, D. M., and B. R. Patterson. 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. *Journal of Wildlife Management* 70:1544–1555.
- Herriges, J. D., T. E. Thorne, and S. L. Anderson. 1992. Vaccination to control brucellosis in free-ranging elk on western Wyoming feed grounds. Pages 107–112 in R. D. Brown, editor. *The biology of deer*. Springer-Verlag, New York, New York, USA.
- Irwin, L. L., and J. M. Peek. 1983. Elk habitat use relative to forest succession in Idaho. *Journal of Wildlife Management* 47:664–672.
- Levin, P. S., E. E. Holmes, K. R. Piner, and C. J. Harvey. 2006. Shifts in a Pacific Ocean fish assemblage: the potential influence of exploitation. *Conservation Biology* 20:1181–1190.
- Lubow, B. C., and B. L. Smith. 2004. Population dynamics of the Jackson elk herd. *Journal of Wildlife Management* 68:810–829.
- Martinka, C. 1969. Population ecology of summer resident elk in Jackson Hole, Wyoming. *Journal of Wildlife Management* 33:465–481.
- Mauritzen, M., A. E. Derocher, Ø. Wiig, S. E. Belikov, A. N. Boltunov, E. Hansen, and G. W. Garner. 2002. Using satellite telemetry to define spatial population structure in polar bears in the Norwegian and western Russian Arctic. *Journal of Applied Ecology* 39:79–90.
- Mbaiwa, J. E., and O. I. Mbaiwa. 2006. The effects of veterinary fences on wildlife populations in Okavango Delta, Botswana. *International Journal of Wilderness* 12:17–23.
- McCullough, D. R. 1985. Long range movements of large terrestrial mammals. Pages 444–465 in M. A. Rankin, editor. *Contributions in marine science*. University of Texas Marine Science Institute, Port Aransas, Texas, USA.
- Middleton, A. D., M. J. Kauffman, D. E. McWhirter, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver. 2013a. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. *Ecology* 94:1245–1256.
- Middleton, A. D., T. A. Morrison, J. K. Fortin, C. T. Robbins, K. M. Proffitt, P. White, D. E. McWhirter, T. M. Koel, D. G. Brimeyer, and W. S. Fairbanks. 2013b. Grizzly bear predation links the loss of native trout to the demography of migratory elk in Yellowstone. *Proceedings of the Royal Society B: Biological Sciences* 280:20130870.
- Milner-Gulland, E., J. M. Fryxell, and A. R. E. Sinclair. 2011. *Animal migration: a synthesis*. Oxford University Press, Oxford, United Kingdom.
- Murie, O. J. 1951. *The elk of North America*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. *Applied linear statistical models*. Fourth edition. McGraw-Hill, New York, New York, USA.
- Nielson, R. M., B. F. Manly, L. L. McDonald, H. Sawyer, and T. L. McDonald. 2009. Estimating habitat selection when GPS fix success is less than 100%. *Ecology* 90:2956–2962.
- Noyes, J. H., B. K. Johnson, L. D. Bryant, S. L. Findholt, and J. W. Thomas. 1996. Effects of bull age on conception dates and pregnancy rates of cow elk. *Journal of Wildlife Management* 60:508–517.
- Oehlert, G.W. 1992. A note on the Delta method. *American Statistician* 46:27–29.
- Proffitt, K., J. Cunningham, K. L. Hamlin, and R. A. Garrott. 2014. Bottom-up and top-down influences on pregnancy rates and recruitment of Northern Yellowstone Elk. *Journal of Wildlife Management* 78:1383–1393.
- R Development Core Team. 2005. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Raithel, J. D., M. J. Kauffman, and D. H. Pletscher. 2007. Impact of spatial and temporal variation in calf survival on the growth of elk populations. *Journal of Wildlife Management* 71:795–803.
- Reiss, H., G. Hoarau, M. Dickey-Collas, and W. J. Wolff. 2009. Genetic population structure of marine fish: mismatch between biological and fisheries management units. *Fish and Fisheries* 10:361–395.
- Robinson, B. G., M. Hebblewhite, and E. H. Merrill. 2010. Are migrant and resident elk (*Cervus elaphus*) exposed to similar forage and predation risk on their sympatric winter range? *Oecologia* 164:265–275.
- Rudd, W. J., A. L. Ward, and L. L. Irwin. 1983. Do split hunting seasons influence elk migrations from Yellowstone National Park? *Wildlife Society Bulletin* 11:328–331.
- Samuel, W., D. Welch, and B. Smith. 1991. Ectoparasites from elk (*Cervus elaphus nelsoni*) from Wyoming. *Journal of Wildlife Diseases* 27:446–451.
- Sargeant, G. A. 2011. wild1: R tools for wildlife research and management. R package version 1. <<http://cran.r-project.org/web/packages/wild1/vignettes/csm.pdf>>. Accessed 18 Apr 2013.
- Smith, B. L. 2007. Migratory behavior of hunted elk. *Northwest Science* 81:251–264.
- Smith, B. L. 2011. *Where elk roam: conservation and biopolitics of our national elk herd*. Lyons Press, Guilford, Connecticut, USA.
- Smith, B. L., and S. H. Anderson. 1996. Patterns of neonatal mortality of elk in northwest Wyoming. *Canadian Journal of Zoology* 74:1229–1237.
- Smith, B. L., and S. H. Anderson. 1998. Juvenile survival and population regulation of the Jackson elk herd. *Journal of Wildlife Management* 62:1036–1045.
- Smith, B. L., and S. H. Anderson. 2001. Does dispersal help regulate the Jackson elk herd? *Wildlife Society Bulletin* 29:331–341.
- Smith, B. L., E. K. Cole, and D. S. Dobkin. 2004. Imperfect pasture: a century of change at the National Elk Refuge in Jackson Hole, Wyoming. Grand Teton Natural History Association, Moose, Wyoming, USA.
- Smith, B. L., and R. L. Robbins. 1994. *Migrations and management of the Jackson elk herd*. National Biological Survey Resource Publication 199, Washington, D.C., USA.
- Smith, B., and T. Roffe. 1997. Evaluation of studies of Strain 19 *Brucella abortus* vaccine in elk: clinical trials and field applications. National Elk Refuge and U.S. Fish and Wildlife Service Final Report, Jackson, Wyoming, USA.
- Smith, B. L., E. S. Williams, K. C. McFarland, T. L. McDonald, G. Wang, and T. D. Moore. 2006. Neonatal mortality of elk in Wyoming: Environmental, population, and predator effects, Biological Technical Publication BTP-R6007-2006, Washington, D.C., USA.
- Solberg, E. J., B. E. Saether, O. Strand, and A. Loison. 1999. Dynamics of a harvested moose population in a variable environment. *Journal of Animal Ecology* 68:186–204.

- Stewart, K. M., R. T. Bowyer, B. L. Dick, B. K. Johnson, and J. G. Kie. 2005. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. *Oecologia* 143:85–93.
- Tacha, T. C., P. A. Vohs, and G. C. Iverson. 1984. Migration routes of sandhill cranes from mid-continental North America. *Journal of Wildlife Management* 48:1028–1033.
- Therneau, T. M., P. M. Grambsch, and V. S. Pankratz. 2003. Penalized survival models and frailty. *Journal of computational and graphical statistics* 12:156–175.
- Thorne, E. T., R. E. Dean, and W. G. Hepworth. 1976. Nutrition during gestation in relation to successful reproduction in elk. *Journal of Wildlife Management* 40:330–335.
- U.S. Fish and Wildlife Service [USFWS] and National Park Service [NPS]. 2007. Bison and Elk Management Plan: National Elk Refuge, Grand Teton National Park. USFWS and NPS, Lakewood, Colorado, USA.
- Webb, S., M. Dzialak, S. Harju, L. Hayden-Wing, and J. Winstead. 2011*a*. Influence of land development on home range use dynamics of female elk. *Wildlife Research* 38:163–167.
- Webb, S. L., M. R. Dzialak, J. J. Wondzell, S. M. Harju, L. D. Hayden-Wing, and J. B. Winstead. 2011*b*. Survival and cause-specific mortality of female Rocky Mountain elk exposed to human activity. *Population Ecology* 53:483–493.
- Weber, B. J., M. L. Wolfe, G. C. White, and M. M. Rowland. 1984. Physiologic response of elk to differences in winter range quality. *Journal of Wildlife Management* 48:248–253.
- Welch, B. L. 1938. The significance of the difference between two means when the population variances are unequal. *Biometrika* 29:30–362.
- White, C. G., P. Zager, and M. W. Gratson. 2010. Influence of predator harvest, biological factors, and landscape on elk calf survival in Idaho. *Journal of Wildlife Management* 74:355–369.
- Wilcove, D. S., and M. Wikelski. 2008. Going, going, gone: is animal migration disappearing. *PLoS biology* 6:e188.
- Wilson, R. M. 2002. Directing the flow: migratory waterfowl, scale, and mobility in western North America. *Environmental History* 7:247–266.
- Woods, J. G. 1991. Ecology of a partially migratory elk population. Dissertation, University of British Columbia, Vancouver, Canada.
- Worton, B. 1987. A review of models of home range for animal movement. *Ecological Modelling* 38:277–298.
- Wyoming Game and Fish Department [WGFD]. 2014. Annual big game herd unit job completion reports. WGFD, Cheyenne, Wyoming, USA.

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