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Migration can enhance survival and recruitment of mammals by increasing access to higher-quality forage or reducing predation risk, or both. We used telemetry locations collected from 140 adult female elk during 2000–2003 and 2007–2008 to identify factors influencing the migration of northern Yellowstone elk. Elk wintered in 2 semidistinct herd segments and migrated 10–140 km to at least 12 summer areas in Yellowstone National Park (YNP) and nearby areas of Montana. Spring migrations were delayed after winters with increased snow pack, with earlier migration in years with earlier vegetation green-up. Elk wintering at lower elevations outside YNP migrated an average of 13 days earlier than elk at higher elevations. The timing of autumn migrations varied annually, but elk left their summer ranges at about the same time regardless of elevation, wolf numbers, or distance to their wintering areas. Elk monitored for multiple years typically returned to the same summer (96% fidelity, $n = 52$) and winter (61% fidelity, $n = 41$) ranges. Elk that wintered at lower elevations in or near the northwestern portion of the park tended to summer in the western part of YNP (56%), and elk that wintered at higher elevations spent summer primarily in the eastern and northern parts of the park (82%). Elk did not grossly modify their migration timing, routes, or use areas after wolf restoration. Elk mortality was low during summer and migration (8 of 225 elk-summers). However, spatial segregation and differential mortality and recruitment between herd segments on the northern winter range apparently contributed to a higher proportion of the elk population wintering outside the northwestern portion of YNP and summering in the western portion of the park. This change could shift wolf spatial dynamics more outside YNP and increase the risk of transmission of brucellosis from elk to cattle north of the park. DOI: 10.1644/08-MAMM-A-252.1.

Key words: brucellosis, *Canis lupus*, *Cervus elaphus*, elk, migration, wolves, Yellowstone

Migration places animals under favorable conditions for survival and recruitment by increasing access to higher-quality forage or reducing predation risk, or both (Dingle 1996; Hebblewhite et al. 2008). Migratory movements in response to changes in population density and climate have been reported for ungulate populations (Ball et al. 2001; Forchhammer et al. 1998; Mahoney and Schaefer 2002). Migration of wildebeest (*Connochaetes taurinus*) in response to rainfall (Maddock 1979) is a classic example, but many other large herbivores also follow forage productivity gradients and migrate in response to climate variation (D'Eon and Serrouya 2005; Igota et al. 2004; Leimgruber et al. 2001; Mysterud et al. 2001).

Individual variability in migratory behavior has been documented in many ungulates, including caribou (*Rangifer tarandus*—Bergerud et al. 1990), elk (*Cervus elaphus*—Morgantini and Hudson 1988; Woods 1991), horses (*Equus caballus*—Berger 1983), moose (*Alces alces*—Ball et al. 2001), mule deer (*Odocoileus hemionus*—Kufeld et al. 1989; Nicholson et al. 1997), pronghorn (*Antilocapra americana*—Hoskinson and Tester 1980; White et al. 2007), sika deer (*Cervus nippon*—Sakuragi et al. 2003), Tibetan chiru (*Pantholops hodgsonii*—Schaller 1998), and white-tailed deer (*Odocoileus virginianus*—Nelson and Mech 1991). Migration can be facultative, wherein individuals adopt movement

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strategies that differ according to demographic class (e.g., age and sex), environmental suitability (e.g., forage availability and predation risk), or social cues (e.g., density of conspecifics—Alerstam et al. 2003; Hebblewhite and Merrill 2007; Sakuragi et al. 2003; Sutherland 1998).

Migratory elk are generally found in mountainous regions where animals move in response to seasonal changes, particularly changes in availability and quality of forage (Boyce 1991; Irwin 2002; McCullough 1985). The largest elk herd in Yellowstone National Park (YNP) spends the winter on grasslands and shrub steppes along the northern boundary of the park and nearby areas of Montana (Houston 1982; Lemke et al. 1998). Northern Yellowstone elk have long been known to migrate seasonally, with the timing of migration and length of time spent on the summer and winter ranges being related to weather (Craighead et al. 1972; Houston 1982; Skinner 1925; Vore 1990). Also, wolves (*Canis lupus*) were restored to YNP in 1995–1996, and predation risk is an important variable driving many behavioral decisions by elk, the primary prey of wolves (Creel et al. 2005; Fortin et al. 2005; Gower et al. 2009). Wolf presence could affect migration behavior of elk because areas preferred by ungulates and wolves tend to correlate in this and other wolf–ungulate systems (Bergman et al. 2006; Garrott et al. 2009; Kauffman et al. 2007; Mao et al. 2005).

We documented the movements of northern Yellowstone elk to identify factors affecting the timing of migration, selection of migratory routes and summer ranges, and individual fidelity to a migratory strategy. We expected to find a range of migratory strategies in the population, with flexibility exhibited by individuals (e.g., timing and destination) from year to year based on demography (e.g., age and pregnancy status), environmental suitability (e.g., predator density and forage green-up), and social cues (e.g., ungulate density). We predicted that migration patterns before and after wolf restoration would be similar because of overriding nutritional demands for quality forage during both summer and winter (Cook 2002; Cook et al. 2004); spatial structuring on the winter range would affect the timing of migration and selection of summer ranges (Craighead et al. 1972; Hamlin 2006); elk would have lower mortality during migration and summer than during winter because of lower predator densities away from the northern winter range (Barber-Meyer et al. 2008; Smith 2005); elk summering in areas of higher risk of wolf predation and higher elevations might depart from summer ranges earlier; and elk migrating to areas outside YNP might delay migration to reduce risk of harvest during the autumn hunting seasons.

Materials and Methods

Yellowstone National Park encompasses 8,991 km² in northwestern Wyoming and adjacent portions of Montana and Idaho (44°N latitude, 110°W longitude). Elk that spend winter in the Yellowstone River and Lamar River valleys in and adjacent to the northern portion of YNP (1,520 km²) are known as the northern Yellowstone herd (Houston 1982; Fig. 1). Approximately 65% (995 km²) of their winter range is located within YNP, whereas the remaining 35% (525 km²) extends north of the park (Lemke et al. 1998). The climate is characterized by short, cool summers and long, cold winters (Houston 1982). Vegetation is principally montane forest (44%; e.g., lodgepole pine [*Pinus contorta*] and Douglas fir [*Pseudotsuga menziesii*]), open sage–grassland (37%; e.g., Idaho fescue [*Festuca idahoensis*], blue-bunch wheatgrass [*Pseudoroegneria spicata*], and big sagebrush [*Artemisia tridentata*]), and upland grasslands, wet meadows, and nonvegetated areas (19%—Despain 1990).

Northern Yellowstone elk migrate seasonally, moving to higher-elevation summer ranges in spring and returning to the winter range in autumn (Skinner 1925). Their summer range includes the majority of YNP and extends outside the park to the north (Craighead et al. 1972). Elk from 6 or 7 other discrete winter herds—Madison–Firehole, Clarks Fork–Sunlight Basin, Cody (i.e., North Fork Shoshone and Carter Mountain), Jackson, Sand Creek–Bechler, and Gallatin River—occupy portions of YNP during the summer, and overlap occurs among herds (Houston 1982). Counts of northern Yellowstone elk decreased from a mean of 16,664 (range = 12,859–19,045) during the decade before wolf restoration to 13,400 in winter 2000–2001 and 6,279 in 2007–2008. This decrease was due to predation by wolves and other large predators, concurrent human harvests of antlerless elk, and, possibly, drought effects on maternal condition and recruitment (Barber-Meyer et al. 2008; Hamlin et al. 2009; Varley and Boyce 2006; Vucetich et al. 2005; White and Garrott 2005). Elk that spent winter outside YNP were exposed to archery and rifle hunts during September through February, with approximately 700–1,300 elk killed annually during 2001–2003 and 100–130 killed during 2007–2008 (Lemke 2008; Vucetich et al. 2005; White and Garrott 2005). Grizzly (*Ursus arctos*) and black (*Ursus americanus*) bears accounted for 58–60% of deaths of neonates and wolves accounted for an additional 14–17% of deaths during 2003–2005 (Barber-Meyer et al. 2008).

We captured and radiocollared 140 adult female elk aged 1–18 years on the northern winter range using helicopter net gunning and darting, including 41 elk in 2000, 24 in 2001, 18 in 2002, 19 in 2003, 11 in 2007, and 27 in 2008. We handled all elk in compliance with requirements of the Institutional Animal Care and Use Committees for the United States Geological Survey (2000–2003) and Montana Fish, Wildlife, and Parks (2007–2008) and guidelines recommended by the American Society of Mammalogists (Gannon et al. 2007). We fitted captured elk with very-high-frequency (VHF) and global positioning system (GPS) telemetry collars (Advanced Telemetry Systems, Isanti, Minnesota; Telonics, Mesa, Arizona; LOTEK, Newmarket, Ontario, Canada) and obtained locations during March 2000–March 2004 and February 2007–January 2009. We monitored 60 elk for 1 winter, 14 elk for 2 winters, and 27 elk for 3 winters. We monitored 77 elk for 1 summer, 24 elk for 2 summers, 12 elk for 3 summers, and 16 elk for 4
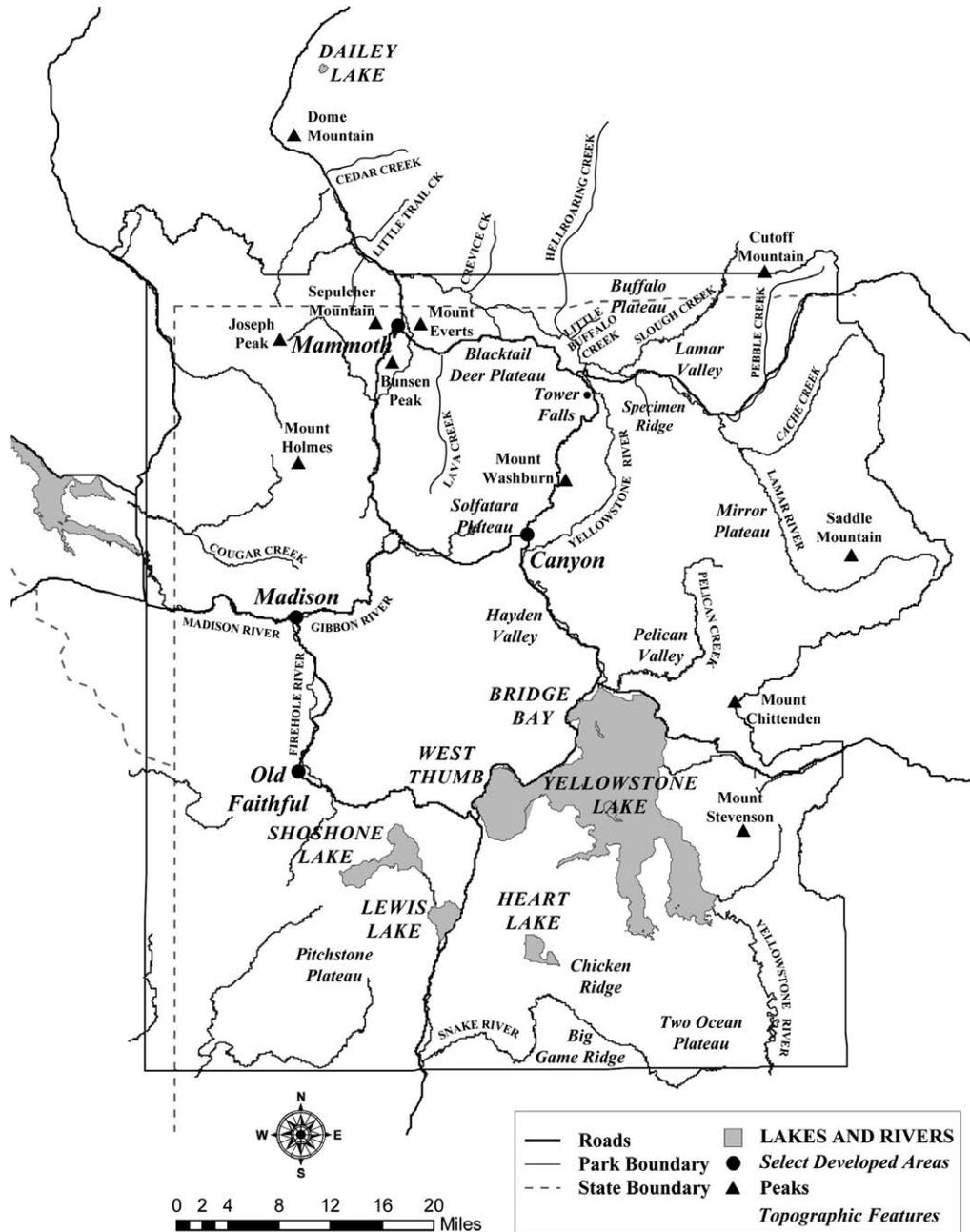
Fig. 1.—Names of areas used by northern Yellowstone elk during summer and winter in Yellowstone National Park and nearby areas of southwestern Montana during 2000–2003 and 2007–2008.

summers. We obtained about 4,600 VHF (n = 80 elk) and 676,000 GPS (n = 60 elk) telemetry locations. The mean interval between successive VHF locations for an individual elk was 12 days (SE = 0.11 days—Mao 2003). We compared causes and timing of deaths for radiocollared elk during migration, summer, and winter using the same data as Evans et al. (2006), plus data from 57 additional female elk radio-collared in 2003, 2007, and 2008.

We defined migration as seasonal movement between allopatric home ranges and identified the timing of migration separately for each elk fitted with a GPS collar (n = 59). We defined the start of spring migration as the date that the animal began a directed movement toward the summer range. For the few animals that did not have well-defined winter and summer ranges, we considered the start of spring migration as the day an individual departed the winter range elevation sector (defined as lower outside, lower inside, middle, or upper) containing the individual's winter locations. The upper sector was located inside YNP and included the Lamar River Valley and Slough Creek, where winter snow depths tend to average 0.6–0.7 m. The middle sector was located inside YNP and included the portion of the Yellowstone River valley from the confluence of the Lamar and Yellowstone rivers near Tower Junction through the Blacktail Deer

Plateau, where snow depths are only slightly less (i.e., ~0.5 m). The portion of the lower sector located inside YNP included the southern portion of the Yellowstone River valley between Mt. Everts near Mammoth Hot Springs and Reese Creek at the northern park boundary near Gardiner, Montana, where snow depths are <0.3 m. The portion of the lower sector located outside YNP included United States Forest Service and private land north of the park boundary along the Yellowstone River valley, where snow depths are <0.3 m (Coughenour and Singer 1996).

We considered individual covariates for age and pregnancy status and annual covariates indexing snow-pack severity (snow water equivalent [SWE]; i.e., amount of water in snow), landscape-level primary productivity on 15 April (normalized difference vegetation index [NDVI]), land ownership or management jurisdiction (Outside Park versus Inside Park), and elk and wolf densities on the winter range. We indexed snow-pack severity by summing daily SWE values for the Blacktail Deer Plateau and Lamar Valley areas of the northern range during 1 October through 30 April using the Langur snow-pack model (Watson et al. 2009). We indexed vegetation greenness based on 15 April weekly averaged NDVI values for grassland and meadow areas and averaged values across the winter range (Bartlette et al. 2006; http://www.wfas.net). We intended NDVI to represent an annual metric of environmental variability, so we averaged values over the entire range and applied 1 NDVI value to all elk on all elevation sectors. Wolf density was estimated annually for each elevation sector of the northern winter range as the total number of adult wolves per square kilometer in December based on repeated counts of packs, the majority of which contained radiocollared animals (Smith 2005). Elk density was estimated annually for each elevation sector of the northern winter range from single-day airplane counts conducted during December in 2000–2002 and 2007 and during February in 2008 (Eberhardt et al. 2007). We evaluated 27 competing a priori linear models explaining variations in timing of spring migrations. We used Akaike's information criteria corrected for small sample size (AIC_c) to identify competitive models ($\Delta AIC_c < 2$) and model weights (w_i) to address model selection uncertainty (Burnham and Anderson 2002). To assess the relative importance of each predictor variable we calculated a predictor weight for each of the R predictors, $w_{+(j)}$, by summing Akaike weights for all a priori models containing predictor x_j, for $j = 1, ..., R$ (Burnham and Anderson 2002).

We defined the start of autumn migration as the date an animal began a directed movement toward its winter range. We considered individual covariates for age, timing of spring migration, and winter range sector, and annual covariates for previous winter snow-pack severity and autumn snow pack. We estimated the mean SWE value averaged across the Hayden and Pelican valleys on 15 October of each year as an annual index of autumn snow pack (Watson et al. 2009). We also used the Canyon Snowpack Telemetry (SNOTEL) site to define daily variations in snow pack, and we calculated the daily increase in SWE as a metric of storm events, which we defined as a daily increase in SWE of 0.5 cm (www.wcc.nrcs. usda.gov; elevation 2,623 m). We evaluated landscape covariates including wolf numbers on an elk's summer range, elevation at the centroid of the summer range, and land ownership status of the range used during the preceding winter. Because wolves moved through elk summer ranges during summer but were not monitored daily, we were unable to calculate wolf density on the summer range. Also, monitoring effort (e.g., proportion collared and location frequency) for wolves varied substantially among elk summer ranges within and outside of YNP, which limited our ability to construct comparable utilization distributions for wolves across the various summer ranges for elk. Instead, we calculated an arguably weaker measure of predation risk as the number of adult wolves known to use an individual elk's summer range during the course of the summer. We evaluated 13 competing a priori linear models explaining variations in the timing of autumn migrations.

We used telemetry locations from elk fitted with GPS collars and a Brownian bridge movement model to obtain probabilistic estimates of spring migration routes used by northern Yellowstone elk. The Brownian bridge movement model is a continuous-time stochastic movement model in which the probability of being in an area is conditioned on the distance and elapsed time between successive locations, the location error, and an estimate of the animal's mobility (Horne et al. 2007). From each GPS-collared animal we used a Brownian bridge movement model to estimate a utilization distribution for the migration route. We used a sequence of GPS locations that occurred between the winter and summer range and locations during the 24-h period before and after spring migration. Brownian bridge movement model calculations were restricted to sequential locations, and we used a 20-m location error (Sawyer et al. 2009). The interval between locations was 30 min for animals collared outside of YNP and 5 h for animals collared inside the park. We used a program developed in the R language for statistical computing (R Development Core Team 2007) provided by Sawyer et al. (2009).

Next, we calculated a population-level migration route. For each pixel of the landscape we summed the utilization distribution value of each individual and then rescaled the cumulative pixel values to 1. We categorized the utilization distribution values for the population-level route into 25% quartiles. The top 25% were classified as high use and represented areas along migratory corridors where animals spent the most time, presumably resting or foraging, and moved slowly. The lower-use areas represented movement corridors between stopover sites (Sawyer et al. 2009).

We used telemetry locations from all elk to evaluate the selection of summer ranges and fidelity to particular ranges. We compared elk migration patterns and use areas to previous studies of northern Yellowstone elk conducted during 1963–1966 (Craighead et al. 1972) and 1984–1987 (Vore 1990).

TABLE 1.—Primary winter areas used by northern Yellowstone elk marked with individualized neck collars during 1963–1966 (Craighead et al. 1972) and fitted with telemetry collars during 1984–1987 (Vore 1990) and 2000–2003 and 2007–2008 (this study) while on their winter range in and near Yellowstone National Park, Montana and Wyoming. Elk were captured on portions of the northern winter range inside the park during 1963–1966 and 2000–2003 and outside the park during 1984–1987 and 2007–2008.

	1963–1966		1984–1987		2000–2003		2007–2008	
Winter areas	No. elk	% elk	No. elk	% elk	No. elk	% elk	No. elk	% elk
Lamar River valley								
Lamar Valley (including Cache Creek and Pebble Creek)	367	21	0	0	6	10	0	0
Specimen Ridge to Crystal Creek	302	18	0	0	2	3	0	0
Tower Falls	0	0	0	0	2	3	0	0
Little Buffalo Creek to Slough Creek (including Garnet Hill, Pleasant Valley, and Junction Butte)	293	17	1	4	25	40	0	0
Yellowstone River valley								
Hellroaring Creek to Crevice Creek	741	43	0	0	4	6	0	0
Blacktail Deer Plateau (including Oxbow Creek, Mt. Everts, and Lava Creek)	0	0	1	4	11	17	0	0
Mammoth (including Gardners Hole and Bunsen Peak)	0	0	1	4	3	5	1	3
Sepulcher Mountain foothills (including Stephens Creek drainage)	19	1	4	14	7	11	3	8
North of Yellowstone National Park (including Little Trail Creek, Cedar Creek, Dome Mountain, and Dailey Lake)	0	0	21	75	3	5	34	89
Total	1,722		28		63		38	

RESULTS

Elk were distributed across the northern portion of YNP during winter, with some evidence of spatial segregation or subgrouping between elk that tended to spend the winter in the upper-elevation Lamar River valley or the lower-elevation Yellowstone River valley (Table 1). Twenty-five (61%) of the 41 radiocollared elk monitored for 2 or 3 winters demonstrated fidelity to a specific winter area in each river valley, but other elk changed the portion of the northern range they used by 8–55 km between winters (straight-line distance between median winter locations). Also, 2 elk migrated to entirely different winter ranges closer to their summer areas. The proportion of elk that spent winter in the lower-elevation portions of the Yellowstone River valley inside and outside of YNP (i.e., Blacktail Deer Plateau, Mammoth, Sepulcher Mountain foothills, and Dome Mountain–Dailey Lake) apparently increased between 1963–1966 and 1984–1987 (prewolf reintroduction) and remained higher through 2000–2003 and 2007–2008 (post–wolf reintroduction; Table 1).

Initiation of spring migration differed with environmental variables across years of our study. Mean date of the start of spring migration was 18 May in 2001 (SD = 10 days, n = 9), 4 June in 2002 (SD = 10 days, n = 8), 6 May in 2007 (SD = 17 days, n = 12), and 3 June in 2008 (SD = 23 days, n = 26). Estimated SWE was 10.8 m in 2001, 16.9 m in 2002, 11.6 m in 2007, and 23.7 m in 2008. Average NDVI was 92 in 2001, 105 in 2002, 122 in 2007, and 106 in 2008. Elk density averaged 3.8/km^2 in the upper, 6.4/km^2 in the middle, 5.8/km^2 in the lower inside, and 6.9/km^2 in the lower outside sector. Wolf density averaged 70/1,000 km^2 in the upper, 80/1,000 km^2 in the middle, 30/1,000 km^2 in the lower inside, and 30/1,000 km^2 in the lower outside sector.

Both precipitation and forage green-up appeared to influence timing of spring migration by northern Yellowstone elk. The most-supported model explaining variation in timing of spring migrations included the covariates SWE ($w_{+(j)}$ = 0.89) and Outside Park ($w_{+(j)}$ = 0.51; Table 2; R^2_{adj} = 0.24, w_i = 0.26). The top model predicted that spring migrations occurred 2.2 days later for every 1-m increase in SWE (β_{SWE} = 2.2, 95% confidence interval [95% CI] = 1.2–3.2) and 13 days earlier for animals wintering in the lower outside-the-park elevation sector (β_{Owner} = −13.5, 95% CI = −1.5–25.5). The 2nd-ranked model contained the covariates SWE and NDVI ($w_{+(j)}$ = 0.28) and received some support from the data (R^2_{adj} = 0.23, w_i = 0.14). This model predicted that spring migrations occurred 1.6 days later for every 1-m increase in SWE (β_{SWE} = 1.6, 95% CI = 0.7–2.5) and 5 days earlier for every 10 units increase in NDVI (β_{NDVI} = −5.3, 95% CI = −10.8–0.2).

We estimated utilization distributions for the spring migratory routes of 53 elk fitted with GPS collars. Data from 3 elk with GPS collars collecting locations at 5-h intervals

TABLE 2.—Model selection results for models that had weight for explaining variation in the timing of spring migrations by northern Yellowstone elk in Yellowstone National Park and nearby areas of Montana during 2001, 2002, 2007, and 2008. SWE = snow water equivalent; NDVI = normalized difference vegetation index.

Covariates	AIC$_c$	ΔAIC$_c$	w_i
SWE + Outside Park	485.70	0.00	0.26
SWE + NDVI	486.90	1.20	0.14
SWE + NDVI + Outside Park	487.99	2.29	0.08
Outside Park + Age + SWE	488.03	2.33	0.08
Outside Park + Pregnant + SWE	488.09	2.39	0.08
SWE + Elevation	488.17	2.47	0.08
SWE	488.25	2.55	0.07
Elevation + Wolf Density	488.86	3.16	0.05
Outside Park + Wolf Density	489.06	3.36	0.05
SWE + NDVI + Elevation	489.07	3.37	0.05

were censored because <5 GPS locations were collected during the migratory period. For elk captured outside of YNP and fitted with GPS collars programmed to record locations at 30-min intervals, the Brownian-motion variance of individual migration routes was 667 ± 50 m^2 (mean $\pm$ SE, $n = 37$ migrations). For elk captured inside of YNP and fitted with GPS collars programmed to record locations every 5 h, the Brownian-motion variance of individual migration routes was $4,721 \pm 1,597$ m^2 ($n = 16$ migrations). The population-level migration routes, which represented a probabilistic measure of where spring migrations occurred, included stopover sites, where elk spent most of their time presumably feeding or resting, and movement corridors through which elk moved more quickly (Fig. 2). The utilization distributions calculated from 30-min GPS data defined more precise migratory pathways (Fig. 2A) than utilization distributions calculated from 5-h GPS data (Fig. 2B).

Northern Yellowstone elk migrated 10–140 km (straight-line distance) to 12 primary summer areas (Table 3). Fifty (96%) of the 52 radiocollared elk monitored for 2–4 summers returned to the same area each year, generally using the same route to and from their summer range. The general migration routes and use areas for elk in our study (Fig. 2; Table 3) were similar to those reported for this population before wolf restoration (Craighead et al. 1972; Shoesmith 1979; Skinner 1925; Vore 1990). Radiocollared elk that spent winters in the upper-elevation Lamar River valley tended to migrate to summer ranges in the eastern (51%), northern (31%), and central (14%) portions of YNP (Table 4). Conversely, elk that spent winters in the lower-elevation Yellowstone River valley tended to migrate to the western (56%) portion of YNP, although migration by this herd was more dispersed through the entire park. The proportion of elk that spent the summer in the eastern portion of the park apparently decreased, but the proportion in the west increased, between 1963–1966 and 1984–1987 (prewolf reintroduction) and remained higher through 2000–2003 and 2007–2008 (post–wolf reintroduction; Table 3).

Few radiocollared elk ($n = 140$ monitored) died during summer ($n = 5$) or migration in spring and autumn ($n = 3$), but 22 elk died in winter, during March 2000 through February 2004 and March 2007 through February 2009. All 8 elk harvested by hunters north of YNP during winter spent their summers in the northwestern portion of the park and winters in the lower-elevation Yellowstone River valley. Seven of 9 elk killed by wolves during winter spent their summers in the eastern and northern portions of YNP and winters at relatively high elevations northeast of the confluence of the Lamar and

FIG. 2.—Estimated population-level migration routes and relative amounts of use for northern Yellowstone elk in Yellowstone National Park (delineated by bold line) and nearby areas of southwestern Montana. Panel A shows migration routes for elk that spent winter in the portion of the winter range located outside the park. The area shaded in solid gray delineates the winter range for elk. Panel B shows migration routes for elk wintering in all portions of the winter range, both inside and outside the park. The high-use areas (upper 25% quartile, lighter gray) represent stopover sites and the lower-use areas (lower quartiles, darker gray) represent movement corridors where animals spent relatively less time during migration. The

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utilization distributions calculated from 30-min global positioning system (GPS) data ($n = 37$ elk) defined more-precise migratory pathways than utilization distributions calculated from 5-h GPS data ($n = 16$ elk) because the Brownian-motion variance of individual migration routes was 6–7 times lower for the 30-min location interval.

TABLE 3.—Principal summer areas used by northern Yellowstone elk marked with individualized neck collars during 1963–1966 (Craighead et al. 1972) and fitted with telemetry collars during 1984–1987 (Vore 1990) and 2000–2003 and 2007–2008 (this study) in and near Yellowstone National Park, Montana and Wyoming.

Summer areas	1963–1966		1984–1987		2000–2003		2007–2008	
	No. elk	% elk	No. elk	% elk	No. elk	% elk	No. elk	% elk
East portion of Yellowstone National Park		77		30		35		40
Northeast (Saddle Mountain to Cut-Off Mountain)	7	1	3	11	9	10	6	16
Mirror Plateau, Specimen Ridge, and Pelican Valley	543	70	4	15	18	20	5	13
East of Yellowstone Lake (Mt. Chittenden to Mt. Stevenson)	24	3	1	4	4	4	3	8
Southeast (Two Ocean Plateau; Chicken and Big Game ridges)	20	3	0	0	1	1	1	3
West portion of Yellowstone National Park		8		52		36		44
Northwest (Joseph Peak to Mt. Holmes)	66	8	10	37	17	19	7	18
Mammoth, Bunsen Peak, Blacktail Deer Plateau, Mt. Everts	0	0	4	15	6	7	2	5
Madison (Cougar Creek to Shoshone Lake)	0	0	0	0	3	3	2	5
West of Yellowstone Lake (Bridge Bay and West Thumb)	0	0	0	0	0	0	3	8
Southwest (Pitchstone Plateau, Lewis Lake, Snake River)	0	0	0	0	6	7	3	8
Central portion of Yellowstone National Park		8		0		10		8
Canyon (Mt. Washburn, Solfatara Plateau, Hayden Valley)	61	8	0	0	9	10	3	8
North of Yellowstone National Park		8		19		20		8
Buffalo Plateau	59	8	1	4	18	20	2	5
Dome Mountain–Dailey Lake	0	0	4	15	0	0	1	3
Total	780		27		91		38	

Yellowstone rivers (i.e., Hellroaring Creek to Little Buffalo Creek).

In contrast to spring migration, initiation of autumn migration was relatively consistent across years; however, duration differed among elk moving to winter ranges inside versus outside of YNP. Mean date of the start of autumn migration was 22 October in 2001 ($SD = 16$ days, $n = 9$), 11 October in 2002 ($SD = 19$ days, $n = 7$), 12 October in 2007 ($SD = 11$ days, $n = 11$), and 23 October in 2008 ($SD =$ 20 days, $n = 25$). Elevation of summer ranges averaged 2,585 m ($SD = 187$ m, range 2,206–3,091 m). For elk migrating to winter ranges inside YNP, the autumn migration averaged 7 days ($SE = 2.4$ days). For elk migrating to winter ranges outside YNP, the autumn migration averaged 43 days ($SE = 4.7$ days). The maximum number of wolves potentially using individual elk summer areas ranged from 0 west of Yellowstone Lake and in the southwestern portion of YNP to 57 in the Mirror Plateau–Pelican Valley area. The SWE values

TABLE 4.—Proportion of northern Yellowstone elk that spent winters in the Lamar River and Yellowstone River valleys and spent summers in and near various portions of Yellowstone National Park, Montana and Wyoming, during 2000–2003 and 2007–2008.

Summer areas	Winter river valleys			
	Lamar River		Yellowstone River	
	No. elk	% elk	No. elk	% elk
East portion of Yellowstone National Park		51		27
Northeast (Saddle Mountain to Cut-Off Mountain)	4	11	7	11
Mirror Plateau, Specimen Ridge, and Pelican Valley	13	37	5	8
East of Yellowstone Lake (Mt. Chittenden to Mt. Stevenson)	1	3	3	5
Southeast (Two Ocean Plateau; Chicken and Big Game ridges)	0	0	2	3
West portion of Yellowstone National Park		3		56
Northwest (Joseph Peak to Mt. Holmes)	0	0	17	26
Mammoth, Bunsen Peak, Blacktail Deer Plateau, Mt. Everts	0	0	6	9
Madison (Cougar Creek to Shoshone Lake)	0	0	3	5
West of Yellowstone Lake (Bridge Bay and West Thumb)	0	0	3	5
Southwest (Pitchstone Plateau, Lewis Lake, Snake River)	1	3	7	11
Central portion of Yellowstone National Park		14		9
Canyon (Mt. Washburn, Solfatara Plateau, Hayden Valley)	5	14	6	9
North of Yellowstone National Park		31		10
Buffalo Plateau	11	31	5	8
Dome Mountain–Dailey Lake	0	0	1	2
Total	35		65	

at the initiation of autumn migration averaged 1.8 cm ($SD = 1.7$ cm, range 0–7.9 cm). Sixty-three percent (33 of 52) of individuals initiated autumn migrations within 72 h of a storm event.

We found little support for our predictions that previous winter severity, autumn snow pack, elevation, distance to winter range, number of wolves, or age affected the timing of autumn migrations. The most-supported model explaining variation in the timing of autumn migrations included the covariate distance to winter range and predicted that animals traveling farther to winter range departed summer ranges later ($AIC_c = 455.06$, $w_i = 0.27$). However, this model explained little of the variance in timing of autumn migration ($R^2_{adj} = 0.05$). Models containing the covariates previous winter severity and previous winter severity plus autumn snow pack also received some support from the data ($\Delta AIC_c = 1.7$, $w_i = 0.11$, $\Delta AIC_c = 1.8$, $w_i = 0.11$), but these models each explained little of the variance in timing of autumn migrations ($R^2_{adj} = 0.04$, and $R^2_{adj} = 0.01$).

DISCUSSION

The timing of spring migrations varied annually and appeared to be most strongly related to the severity and duration of the previous winter. Elk delayed spring migration after winters with high snow pack but migrated earlier in years with lower snow pack and earlier vegetation green-up. We also documented that elk spending winter outside YNP initiated spring migrations an average of 13 days earlier than elk inside the park. The portion of the winter range north of YNP receives less snow and has earlier green-up of nutritious forage for elk just prior to their spring migration. Thus, elk at lower elevations likely are able to begin tracking the retreat of snow pack and phenology of vegetation green-up earlier than elk spending winter at higher elevations.

The timing of spring migration and duration of elk occupancy on winter range north of the park has possible implications for the risk of transmission of brucellosis (*Brucella abortus*) to cattle adjacent to YNP. Wild, free-ranging bison (*Bison bison*) and elk in the greater Yellowstone area persist as the last reservoir of brucellosis in the United States (Cheville et al. 1998). Transmission from elk to cattle can occur when susceptible cattle contact infected fetuses or birth fluids (Cheville et al. 1998) that result from late-term elk abortions or birthing events, which occur from about 1 February through 30 June. The risk of brucellosis transmission between elk or from elk to cattle should increase as the numbers and density of elk increase and the degree of mingling increases between infectious and susceptible animals (Greater Yellowstone Interagency Brucellosis Committee 1997).

The timing of autumn migrations varied annually and appeared to have little correlation with elevation, wolf numbers, timing of spring migration, distance to winter range, or winter range destination. Although elk traveling to winter ranges inside and outside YNP departed from summer ranges at similar times, elk traveling to winter ranges outside of the

park delayed arrivals to winter range, likely to avoid hunting risk. This system, with elk spending summer in areas with no hunting risk and winter in areas of variable risk, contrasts with the nearby Madison Valley system, where elk spend summer in areas of variable risk (some in YNP and some in areas that allow hunting) and winter primarily on private lands that limit or restrict hunting. In the Madison Valley elk that spent summer in areas with hunting risk initiated autumn migrations earlier than animals that spent summer in protected areas (Grigg 2007). Together, these results suggest that migratory ungulates display a flexible strategy aimed at reducing hunting risk by varying either the timing of autumn migrations or timing of arrivals onto winter range, similar to findings of other studies near YNP and elsewhere (Burcham et al. 1999; Millspaugh et al. 2000; Proffitt et al. 2009; Vieira et al. 2003).

The northern Yellowstone elk population expanded its winter range north of YNP and into the Paradise Valley of Montana during the late 1970s in response to increasing elk abundance, changes in the structure and timing of harvests, and protection of winter ranges outside the park (Coughenour and Singer 1996; Lemke et al. 1998). The number of northern Yellowstone elk using this area each winter increased substantially after the extensive fires in YNP during summer 1988 and varied thereafter around approximately 3,000 elk (Cross et al. 2009b). This range expansion resulted in spatial overlap and mingling of elk and cattle in the Gardiner Basin and Paradise Valley of Montana during the potential abortion period from February through April (Cunningham et al. 2009). Thus, if elk abundance increases in the herd segment that spends winter in the Yellowstone River valley, this could facilitate disease transmission if these elk aggregate in large numbers on winter ranges occupied by cattle (Cross et al. 2009a; Hamlin and Cunningham 2008). Also, our results suggest that risk of transmission of brucellosis from elk to cattle is higher following winters of increased snow pack when elk initiate spring migrations later, and consequently, some elk spend a greater proportion of the brucellosis risk period in areas where mingling with cattle can occur.

Our population-level Brownian bridge movement model identified a network of migratory corridors connecting the northern Yellowstone elk winter and summer ranges. Elk wintering in different elevation sectors of the winter range used common migratory routes, with many of the individuals wintering in lower-elevation sectors migrating through the higher-elevation sectors of the winter range before moving onto summer ranges. Identification of these migratory corridors is important for conservation planning, and although much of the area is protected by YNP, development north of the park or expansion of visitor services within the park could occur. Estimation of population-level routes provides a foundation for prioritizing the population-level importance of various routes, allowing managers to target protections on certain routes most frequently used by the sampled population. Further, the population-level Brownian bridge movement model will facilitate the detection of any future quantitative changes in elk migration patterns.

Radiocollared adult female elk showed fidelity to travel routes and returned to specific areas of the summer and winter ranges in successive years. Elk that spent winter in the upper-elevation portions of the winter range (Lamar River valley) tended to migrate to summer ranges in the eastern two-thirds of YNP, and elk that spent winter at lower elevations in the park along the Yellowstone River valley generally migrated to summer ranges in the western portion of the park. However, other elk showed flexibility from year to year, especially on winter range because elk occasionally moved to lower elevations as winters progressed and snow pack increased. Also, elk that wintered north of YNP toward the southern Paradise Valley in Montana migrated to summer ranges throughout the park. These findings lend some support to the proposals by Craighead et al. (1972) and Hamlin (2006) that there are 2 herd segments (Lamar River valley and Yellowstone River valley) in the northern Yellowstone population, with additional elk varying their migration strategies in response to weather conditions.

Mortality of radiocollared females was low during summer and migration, regardless of migration distance and area. However, all radiocollared elk that were harvested by hunters north of YNP during 2000–2003 spent their summers in the northwestern part of the park and winters in the lower-elevation Yellowstone River valley. No radiocollared elk that spent winter in the Lamar River valley and summer in the eastern two-thirds of the park were harvested during our study. This disproportionate harvest of adult female elk that spent winter in the Yellowstone River valley occurred because these elk were more likely to use low-elevation winter range outside YNP. Exploitative selection due to human harvest could reduce the proportion of elk in this herd segment, especially during severe snow-pack conditions when elk increase migration to lower-elevation ranges outside YNP (White and Garrott 2005). The Montana Department of Fish, Wildlife, and Parks decreased the allowable harvest of antlerless elk from 1,102 permits in 2005 to 100 per season during 2006–2009 to minimize antlerless harvest as a significant factor decreasing elk survival (Lemke 2008).

We did not detect higher predation risk for elk during migration, in contrast to other recent studies from the Canadian Rockies and elsewhere (Hebblewhite and Merrill 2007), likely because migration distanced elk from the most-concentrated area of wolf activity in YNP (i.e., northern winter range). Migration also diluted individual risk for northern Yellowstone elk because they mixed with elk from 6 or 7 other discrete herds that winter outside YNP but occupy portions of it during summer. As a result, northern Yellowstone elk have not grossly modified their migration timing, routes, or use areas after wolf restoration. However, elk that spent winter in upper-elevation sectors of the northern winter range were killed by wolves at a higher rate than elk that spent winter at lower elevations. This disproportionate predation on adult female elk occurred because wolf densities and risk of predation to elk were high in middle- and upper-elevation sectors compared to lower elevations in and outside of YNP

(Kauffman et al. 2007; Smith 2005). The attrition of adult females and their calves from higher-elevation sectors of the winter range has decreased the number of elk that spend winter in the Lamar River valley (Hamlin 2006) and migrate to summer areas in and near the eastern and northern portions of the park. It is possible that density-dependent predation by wolves on elk on different segments of the winter range also could contribute to future changes in elk migration tendencies and patterns.

Most analyses of the northern Yellowstone elk population have treated it as 1 randomly mixing, homogeneous unit (Hamlin 2006). However, our findings suggest that demographic assessments of this population should consider separate herd segments because they have different movement patterns and are exposed to different levels and sources of mortality (e.g., hunting and predators). Temporal comparisons of northern Yellowstone elk distributions since the 1960s suggest that a higher proportion of the population now spends winter in the lower-elevation Yellowstone River valley (in and outside of YNP), and they spend summer in the western portion of the park following range expansion northwest of the park along the Yellowstone River valley that occurred during 1980–1985 (Coughenour and Singer 1996; Hamlin 2006; Lemke et al. 1998). This trend could be intensified in future years by the elimination of the antlerless harvest (i.e., higher adult female survival) outside YNP and by higher recruitment (2–3 times greater) in the lower-elevation portions of the Yellowstone River valley compared to the higher-elevation Lamar River valley due to lower predator densities (Barber-Meyer et al. 2008). Migratory habits of elk appear to be passed between generations of northern Yellowstone elk based on the movement patterns of elk marked as calves and monitored as yearlings (Barber-Meyer et al. 2008).

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