

Changes in Elk Distribution and Group Sizes after Wolf Restoration

P. J. WHITE¹

National Park Service, P.O. Box 168, Yellowstone National Park, Mammoth, Wyoming 82190

KELLY M. PROFFITT AND THOMAS O. LEMKE

Montana Fish, Wildlife, and Parks, 1400 South 19th Street, Bozeman 59718

ABSTRACT.—Changes in ungulate distribution can alter competitive interactions, plant communities, risks of zoonotic disease transmission, and availability of animals for harvest. We used annual aerial survey data for northern Yellowstone elk in Montana and Wyoming, USA to evaluate factors influencing distribution and group sizes during 1987–2009 in four sectors of elk winter range corresponding to river watersheds with different minimum elevations and snowpacks. Our best logistic regression model suggested the proportion of elk occupying the upper elevation sector decreased following wolf restoration and increased snowpack. The proportion of elk occupying the lower elevation sector increased following wolf restoration and as snowpack increased at higher elevations. Linear regression suggested group sizes increased in the lower elevation sector after wolves were restored. Concurrent demographic and movement studies suggest these changes resulted primarily from the attrition of elk from high snow areas in Yellowstone National Park due to predation, and increased survival and recruitment of elk in lower snow areas outside the Park in Montana following a substantial reduction in hunter harvest. Fitness trade-offs between foraging conditions and the risks of predation (or harvest) as constrained by snow vary considerably among elk populations in the Yellowstone ecosystem.

INTRODUCTION

Understanding elk (*Cervus elaphus*) responses to changes in climate, land use, and predation risk is necessary because such responses may have significant ecological consequences, including changes in prey distributions, effects on plant communities, and changes in risks of disease transmission. Temperatures in the greater Yellowstone ecosystem have shown a pronounced warming over the past 50 y and contributed to decreased snow levels and increased drought (Wilmers and Getz, 2005). Elk may be sensitive to these changes in forage availability and quality resulting from changes in climate. For example, warmer temperatures could decrease winter snow, accelerate snow melt, and cause vegetation growth to occur earlier in the season at higher elevations (Walther *et al.*, 2002; Wilmers and Getz, 2005). These changes could influence the condition and abundance of elk, their migration patterns and distribution, the degree to which they transmit diseases, and the extent and outcome of competitive interactions (Walther *et al.*, 2002).

In addition, elk responses to predation risk may include changes in vigilance, grouping patterns, habitat selection, or distributions (Gude *et al.*, 2006; Gower *et al.*, 2009a, b, c; Proffitt *et al.*, 2009). Several studies in the greater Yellowstone ecosystem have noted that elk are less likely to occupy areas with deeper snow or other conditions that increase predation risk in the presence of wolves (*Canis lupus*; Mao *et al.*, 2005; White *et al.*, 2009). Also, social ungulates regularly form larger groups in more open areas that contain more abundant,

¹ Corresponding author: Telephone: (307) 344-2442; FAX: (307) 344-2211; e-mail: pj_white@nps.gov

high-quality forage than closed habitat types (Jarman, 1974; Hirth, 1977; Clutton-Brock *et al.*, 1982). Mao *et al.* (2005) found group sizes of elk were larger in areas of higher wolf density, which may have enhanced their probability of detecting predators or escaping attack by being one of many prey with less chance of selection by a predator (Pulliam, 1973; Pulliam and Caraco, 1984).

The northern Yellowstone elk population spends winter on approximately 1530 km² of grasslands and shrub steppes along the northern boundary of Yellowstone National Park (Park) and nearby areas of southwest Montana (Fig. 1, Houston, 1982; Lemke *et al.*, 1998). These elk migrate seasonally, moving from higher-elevation summer ranges throughout the Park to the winter range in the northern portion of the Park and nearby areas of southwest Montana (Craighead *et al.*, 1972; White *et al.*, 2010). The population expanded its winter range north of the Park and into Paradise Valley, Montana, during the 1970s and 1980s in response to increasing elk abundance, changes in structure and timing of hunter harvests, and protection of winter ranges outside the Park (Coughenour and Singer, 1996; Lemke *et al.*, 1998).

Wolves were restored to this ecosystem during 1995–1997 and their abundance and distribution rapidly increased (Smith, 2005). Estimates of elk numbers on northern Yellowstone winter range decreased from 13,654–25,453 during 1987–1994 to 12,420 in winter 2003 (*i.e.*, Dec. 2002 through Apr. 2003) and 9675 in winter 2009 (Eberhardt *et al.*, 2007). This decrease was due to predation by wolves and other large carnivores (*e.g.*, bears *Ursus arctos*, *U. americanus*), concurrent hunter harvests of antlerless elk, and drought effects on maternal condition and recruitment (Vucetich *et al.*, 2005; White and Garrott, 2005; Barber-Meyer *et al.*, 2008). To our knowledge, previous research investigating factors influencing spatial distribution and grouping tendencies of elk in northern Yellowstone are limited (Houston, 1982; Barmore, 2003). Thus, our objective was to use aerial survey data from 1987–2009 to evaluate the distribution and grouping patterns of northern Yellowstone elk on their winter range.

METHODS

The winter range for northern Yellowstone elk consisted primarily of foothills and valley bottoms along the Gardner, Lamar, and Yellowstone river watersheds (Houston, 1982; Lemke *et al.*, 1998). The climate was characterized by short cool summers and long cold winters. Mean annual precipitation varied from 25–35 cm as elevation increased from 1500 m in river drainages to 3400 m on mountains. Average snow-water equivalents (*i.e.*, amounts of water in snow) ranged from 2–30 cm along this elevation gradient (Farnes *et al.*, 1999). Vegetation was primarily steppe or shrub steppe (primarily Idaho fescue *Festuca idahoensis*, blue-bunch wheatgrass *Pseudoroegneria spicata*, and big sagebrush *Artemisia tridentata*) with stands of montane forest (primarily lodgepole pine *Pinus contorta* and Douglas fir *Pseudotsuga menziesii*) at higher elevations and woody riparian communities (primarily aspen *Populus tremuloides* and willow *Salix sp.*) in the valleys. Extreme drought during summer 1988 contributed to fires that burned about 27% (11,427 ha of grasslands, 15,580 ha of forest) of the winter range for northern Yellowstone elk inside the Park and adjacent to the Park boundary (Singer *et al.*, 1989). Severe to extreme drought conditions also prevailed on the northern range during 1999–2006 (National Climatic Data Center, <<http://www.ncdc.noaa.gov/>>).

The Northern Yellowstone Cooperative Wildlife Working Group used 3–4 Super Cub airplanes to conduct annual winter (Nov.–Mar.) counts of northern Yellowstone elk during 1987–2009. Annual counts typically were completed during a single morning. Each plane

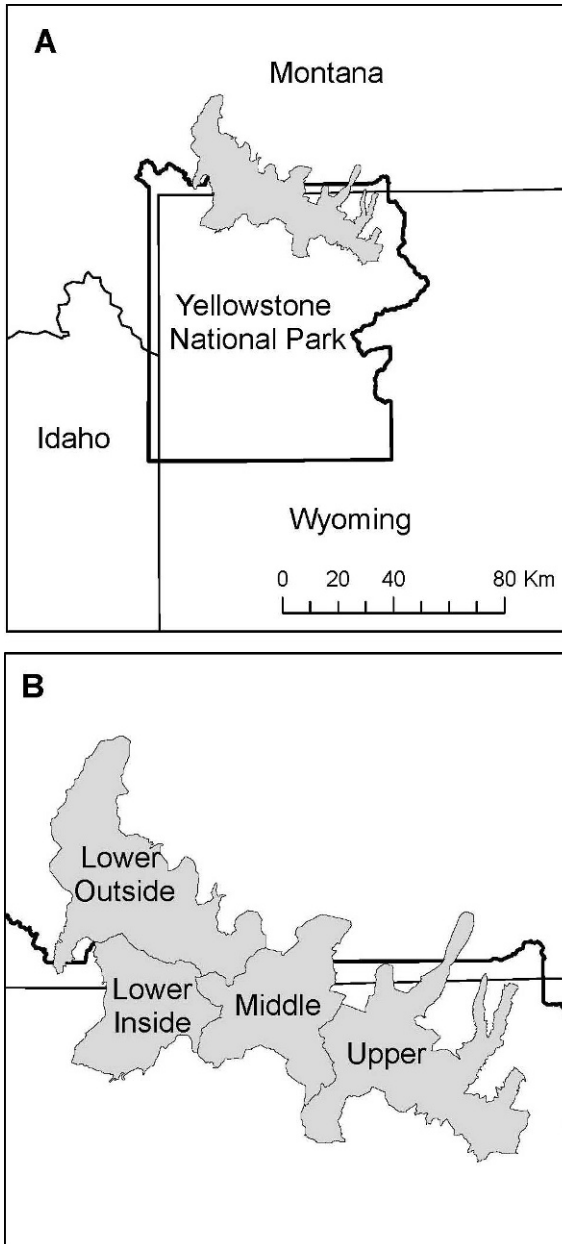


FIG. 1.—Northern Yellowstone elk winter range located in northern portion of Yellowstone National Park, Wyoming and southwest Montana (Panel A). Winter range was divided into four sectors: the high-elevation upper sector, mid-elevation middle sector, lower-elevation sector inside the Park, and lower-elevation sector outside the Park (Panel B). The upper, middle, and lower inside sectors primarily are located within the Park, whereas the lower sector outside the Park primarily is located on public and private lands in southwest Montana

TABLE 1.—Response variables and covariates for analyses of potential factors influencing group distribution and sizes of northern Yellowstone elk on their winter range in the northern portion of Yellowstone National Park and southwest Montana during winters 1987–2009. Period = 0 refers to aerial elk surveys during Dec. and Jan. and Period = 1 refers to surveys during Feb. through Apr.

Winter	Period	Estimated elk numbers	Snow water equivalent (m)	No. of hunters
2009	1	9675	5.8	140
2008	1	8570	8.3	107
2007	0	9241	1.7	138
2006	1	8849	15.6	140
2005	0	12861	1.9	826
2004	0	11138	1.4	1107
2003	0	12420	1.1	1545
2002	0	15926	1.7	1953
2000	0	19315	2.1	2255
1998	0	15785	4.2	2136
1994	0	25453	3.3	1222
1993	0	23693	1.2	1952
1992	1	19702	15.8	1816
1991	1	13654	6.3	1704
1990	0	20550	5.9	690
1989	1	14961	20.5	2486
1988	0	25368	1.7	967
1987	0	23343	1.2	1448

covered a segment of the northern winter range (both inside and outside the Park), which was divided into four count sectors that corresponded to river watersheds with different minimum elevations and snowpacks (Coughenour and Singer, 1996). Elk locations were classified as being in either the upper, middle, lower inside, or lower outside sector of the winter range (Fig. 1). The upper sector included portions of the Lamar River watershed, where elevation ranged from 1890–2590 m and winter snow depths averaged 0.6–0.7 m. The middle sector included the portion of the Yellowstone River watershed from the confluence of the Lamar and Yellowstone rivers near Tower Junction through the Blacktail Deer Plateau, where elevation ranged from 1890–2375 m and snow depths averaged 0.5 m. The lower sector inside the Park included the Gardner River watershed between Gardners Hole and Mt. Everts near Mammoth Hot Springs and north to Reese Creek at the northern Park boundary near Gardiner, Montana, where elevation ranged from 1615–2315 m and snow depths were <0.3 m. The lower sector outside the Park included mostly Forest Service and private lands in the Yellowstone River watershed north of the Park boundary where elevation ranged from 1615–2590 m and snow depths were <0.3 m. No counts were conducted during winters 1995–1997 or 1999 and 2001. Location and size of individual elk groups were recorded during five winter surveys from 1988–1992 and during six winter surveys in 2003 and 2005–2009. Data from other years were excluded from analyses because elk group sizes were not available for individual sectors.

Elk distribution.—We investigated the potential effects of various combinations of continuous covariates describing hunting pressure and severity of snowpack, and categorical covariates describing the timing of aerial surveys [*i.e.*, early (Dec.–Jan.) or late (Feb.–Apr.) winter] and wolf restoration [*i.e.*, pre-wolf (1987–1995) vs. post-wolf periods (1996–2009)], on elk distribution across winter range sectors (Table 1).

Elk that spent winter outside the Park were exposed to archery and rifle hunts during Sept. through Feb., with approximately 500–4500 elk (mean ~ 1700 , $SD = 1025$) killed annually during 1987–2005, but only 200–500 elk (mean ~ 330 , $SD = 93$) killed during 2006–2009 after Montana Fish, Wildlife, and Parks reduced the number of antler-less permits for the Gardiner Late Elk Hunt by $>90\%$ from 1102 in 2005 to 104 during 2006–2009 owing to decreases in elk abundance and recruitment (Lemke, 2009). We used the number of elk hunters issued a permit each year during the Gardiner late elk hunt, which was highly biased towards harvesting females, as an index of hunting pressure.

Snow is a fundamental limiting factor for ungulates occupying high-elevation, montane environments because it influences energetic costs of foraging and locomotion. We used a validated snowpack simulation model to index snowpack severity by summing daily snow water equivalent (*i.e.*, amount of water in snow; SWE) values across all 28.5×28.5 m pixels within the Blacktail Deer Plateau (middle sector) and Lamar Valley (upper sector) areas used by elk during Oct. 1 through the date of the aerial elk survey in a given winter (Watson *et al.*, 2009).

We evaluated six generalized linear models (post-wolf period, hunting pressure, snowpack, snowpack + post-wolf period, snowpack + hunting pressure, post-wolf period + hunting pressure) to estimate coefficients representing the effects of covariates on the proportion of the elk population occupying the upper (or lower outside) sector of the winter range. We treated number of elk in the upper (or lower outside) sector and total number of elk as binomial count data. Explanatory variables were screened for collinearity and variables with Pearson's correlation coefficient >0.5 were not included in the same model. Late survey period and snowpack were closely correlated ($r = 0.80$). Thus, survey period was removed from all models and snowpack was used as a covariate to account for variations in the timing of surveys. We used Akaike's Information Criterion, adjusted for sample size (AIC_c), to compare models and Akaike weights (w_i) to address model selection uncertainty (Burnham and Anderson, 2002).

Elk group sizes.—We investigated effects of total elk abundance, wolf restoration, winter severity, timing of the elk survey date, vegetation type, and hunting pressure on variations in group size. We used a categorical covariate to contrast pre-wolf (1988–1992) and post-wolf (2003–2009) years of study. We defined hunting pressure for each group observation as a categorical covariate contrasting groups in the lower-outside-the-park sector during the Gardiner Late Elk hunt in Montana with group observations collected in other sectors during the hunt and in the lower-outside sector before and after the hunt. We used the 2001 National Land Cover Dataset (<http://www.mrlc.gov/>) to classify vegetation type at a resolution of 30 m, and consolidated vegetation types into four categories: forest, shrubland, grassland (which included pastureland), and other (*e.g.*, rock, developed, water).

Migratory movements in response to changes in density and climate have been reported for ungulate populations, including northern Yellowstone elk (White and Garrott, 2005). Thus, we estimated total elk abundance from airplane surveys by (1) dividing counts by average detection rates for “good” and “poor” survey conditions (estimated by Eberhardt *et al.*, 2007) and (2) adding pre-survey hunting removals for the sector outside the park to resulting post-hunting estimates. Elk selected slightly more open habitats in winter after wolf recovery than before but largely occupied the non-forested landscape (*i.e.*, open grassland and sagebrush), where detection rates were high on all sectors of winter range during both periods (Mao *et al.*, 2005).

We expected total elk population size, snowpack, and vegetation cover to influence elk group sizes and included these effects in each model (Proffitt *et al.*, 2009). We also expected

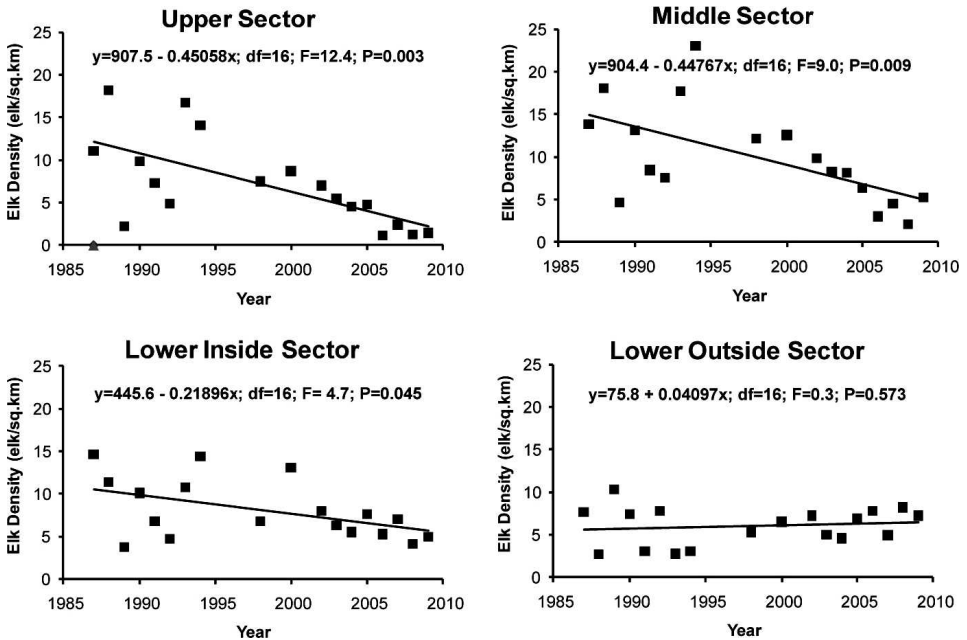


FIG. 2.—Density of elk per km^2 in upper, middle, lower elevation sectors inside Yellowstone National Park, and lower elevation sector outside the Park of the northern Yellowstone winter range during 1987–2009

group sizes to increase after wolf restoration in the middle and upper elevation sectors, where wolf densities were among the greatest reported (Fuller *et al.*, 2003; Smith, 2005; Gower *et al.*, 2009b). In addition, we expected group sizes to decrease in the lower elevation sector outside the Park during the hunting season (Gude *et al.*, 2006; Proffitt *et al.*, 2009). To evaluate causes of variation in \ln -transformed group sizes, we used AIC_c (Burnham and Anderson, 2002) to compare 15 *a priori* linear regression models.

RESULTS

Elk distribution.—During our study, densities of wintering elk declined in the upper, middle, and lower sectors of winter range inside the Park. In contrast, elk densities were relatively stable in the lower sector outside the Park (Fig. 2). Our best model explaining variations in elk group distributions across the northern winter range suggested the proportion of the population occupying the upper sector decreased following wolf restoration ($\hat{\beta} = -0.53$, 95% CI = $-0.51, -0.55$, $w_i = 1.00$, Fig. 3A) and with increasing snowpack ($\hat{\beta} = -0.057$, 95% CI = $-0.059, -0.055$). In contrast, our best model suggested the proportion of the elk population occupying the lower outside sector increased following wolf restoration ($\hat{\beta} = 0.82$, 95% CI = $0.80, 0.84$, $w_i = 1.00$, Figure 3B) and with increasing snowpack at higher elevations ($\hat{\beta} = 0.077$, 95% CI = $0.075, 0.079$).

Elk group sizes.—Mean group size varied by elevation sector and year (Fig. 4A), and was influenced by attributes such as vegetation, elevation sector, and snowpack. Our best model explaining variations in group size contained the covariates vegetation, snowpack, elevation sector of the winter range, study period (2003–2009), and hunting pressure (Table 2, $w_i =$

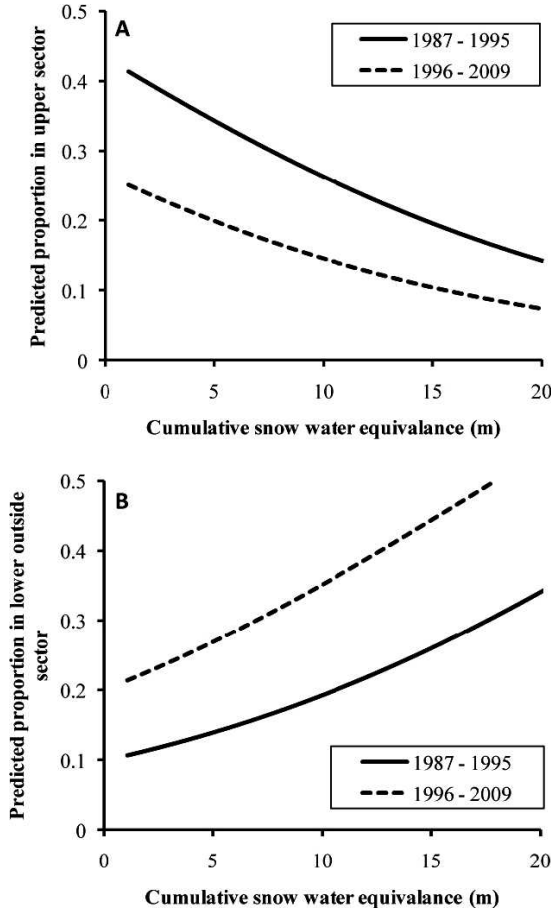


FIG. 3.—Predicted proportions of the total elk population in the upper (Panel A) and lower outside (Panel B) sectors of northern Yellowstone winter range prior to wolf restoration (1987–1995) and following wolf restoration (1996–2009) as cumulative winter snowpack varied

0.88) but explained minimal variation in group size ($R^2_{\text{adj}} = 0.07$). Group sizes increased as elk population size increased ($\hat{\beta} = 5.5 \times 10^{-5}$, 95% CI = 4.1×10^{-5} , 6.9×10^{-5}). Group sizes were similar in grassland, shrubland, and other habitat types but decreased in forested areas ($\hat{\beta} = -0.64$, 95% CI = -0.80 , -0.47). Group sizes decreased as snowpack increased in grassland, shrubland, and other habitats, but snowpack had little effect on group sizes in forested areas (Fig. 5).

There was an increase in group sizes in all habitats during 2003–2009 that was strongest in the lower elevation sector outside the Park and weakest in the upper sector. Group sizes in the lower outside sector decreased from 11.6 (95% CI = 9.7, 13.8) to 9.3 (95% CI = 8.0, 11.1) in grassland and 7.6 (95% CI = 6.5, 8.9) to 6.1 (95% CI = 5.3, 7.1) in forests during the hunting season, though the magnitude of effect was small (Fig. 5). Ninety-five percent of all groups observed during our study contained <100 elk. During the post-wolf period,

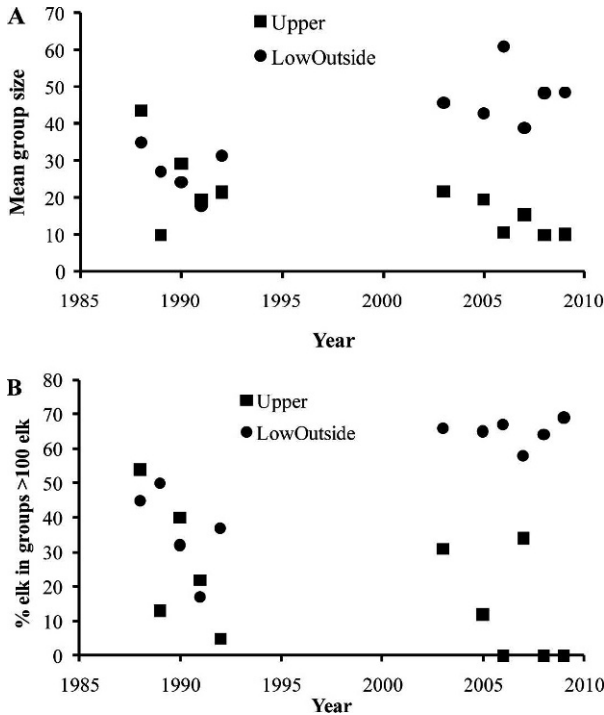


FIG. 4.—Comparisons of mean group size (Panel A) and proportion of elk in groups with ≥ 100 elk (Panel B) for northern Yellowstone elk occupying upper elevation sector of winter range in Yellowstone National Park and lower elevation sector outside the Park in nearby areas of Montana during 1988-2009

however, the proportion of elk in large groups increased in the lower sector outside the Park but decreased in the upper, middle, and lower sectors inside the Park (Fig. 4B).

DISCUSSION

The number of northern Yellowstone elk counted each winter has decreased by $>60\%$ (White and Garrott, 2005), primarily due to a decrease in the number of elk counted on middle to upper sectors inside the Park. Elk that spent winter in these sectors were not subject to hunting but were exposed to high predation risk from high densities of wolves during winter and bears during calving in spring (Smith, 2005; Kauffman *et al.*, 2007; Barber-Meyer *et al.*, 2008). Also, chronic summer-autumn nutritional limitations probably lowered pregnancy rates for lactating elk and contributed to lower recruitment (Cook *et al.*, 2004). Thus, the portion of the northern Yellowstone elk population that spent winter at lower elevations outside the park increased in recent years due, in part, to increased vulnerability of elk at higher elevations to wolf predation caused by deeper snowpacks and decreased recruitment to replace these animals. Also, elk tended to form larger groups, and proportionately more elk were in larger groups, outside the Park. These trends may be exacerbated in future years by continued attrition of adult elk and calves from higher elevation portions of the winter range, continued warming climate with a shorter peak growing season at higher elevations that contributes to summer-autumn nutritional

TABLE 2.—Model selection results for *a priori* models examining the effects of covariates on variation in northern Yellowstone elk group sizes. Covariates included vegetation type (Veg), snowpack (SWE), elevation sector of the winter range (Sector), wolf restoration (Wolf), elk population size (Elk), timing of elk survey (Late), and hunting pressure (Hunting). All models are presented along with the number of parameters (*k*), the ΔAIC_c value, and Akaike weight (w_i)

Covariates	<i>k</i>	ΔAIC_c	w_i
Elk + Veg + SWE*Veg + Wolf + Sector + Wolf*Sector + Hunting	18	0.00	0.88
Elk + Veg + SWE*Veg + Wolf + Sector + Wolf*Sector	17	3.85	0.12
Elk + Veg + SWE*Veg + Wolf + Sector + Late	15	25.23	0.00
Elk + Veg + SWE*Veg + Wolf + Sector + Hunting	15	33.17	0.00
Elk + Veg + SWE*Veg + Wolf + Sector	14	35.63	0.00
Elk + Veg + SWE*Veg + Hunting + Sector	14	50.86	0.00
Elk + Veg + SWE*Veg + Sector	13	56.03	0.00
Elk + Veg + SWE*Veg + Wolf + Hunting	12	77.58	0.00
Elk + Veg + SWE*Veg + Wolf + Late	12	82.17	0.00
Elk + Veg + SWE*Veg + Wolf	11	89.61	0.00
Elk + Veg + SWE*Veg + Hunting	11	99.88	0.00
Elk + Veg + SWE*Veg + Hunting + Late	12	101.87	0.00
Elk + Veg + SWE*Veg	10	108.87	0.00
Elk + Veg + SWE*Veg + Late	11	110.83	0.00
Elk + Veg + SWE	7	117.55	0.00

limitations and lower pregnancy rates in lactating elk (Cook *et al.*, 2004), higher survival of elk following the elimination of the antler-less harvest outside the park (Evans *et al.*, 2006; Hamlin *et al.*, 2009), and 2–3 times higher recruitment in the lower-elevation portions of the northern range compared to higher-elevation areas (Barber-Meyer *et al.*, 2008).

Craighead *et al.* (1972) and Hamlin (2006) suggested there was spatial structuring in the northern Yellowstone elk population on the winter range, with one herd segment occupying the Lamar River Valley at middle to upper elevations in the Park, another herd segment occupying the Yellowstone River Valley at middle to lower elevations in and outside the Park, and some elk moving across the northern range in response to variations in the weather (primarily snowpack). Even though the proportion of the northern Yellowstone elk population spending winter outside the Park increased after wolf restoration, the density of elk outside the Park did not significantly increase because there were fewer elk overall in the population. However, there were more large groups and higher mean group sizes outside the Park during 2003–2009, which could have implications for disease transmission. Larger group sizes of elk on lower elevation winter ranges may increase the risk of elk-elk or elk-livestock brucellosis transmission, or result in increasing crop damage issues in the southern portion of Paradise Valley (Cross *et al.*, 2010).

Decreases in elk abundance and group sizes on the middle and upper portions of the northern range also could contribute to a trophic cascade from wolves to elk to woody plants, provided other circumstances (*e.g.*, growing-degree days, water table levels, snowpack) are suitable. A trophic cascade occurs when the limiting effect of predation influences not only the prey but also lower trophic levels (Hairston *et al.*, 1960). Recent increases in the heights and growth rates of aspen (*Populus tremuloides*), cottonwoods (*Populus sp.*), willows (*Salix sp.*), and other woody plants in portions of Yellowstone National Park and nearby areas have been attributed to a behaviorally mediated (*i.e.*, altered elk behavior) trophic cascade (Ripple *et al.*, 2001; Beschta, 2003; Ripple and Beschta, 2004;

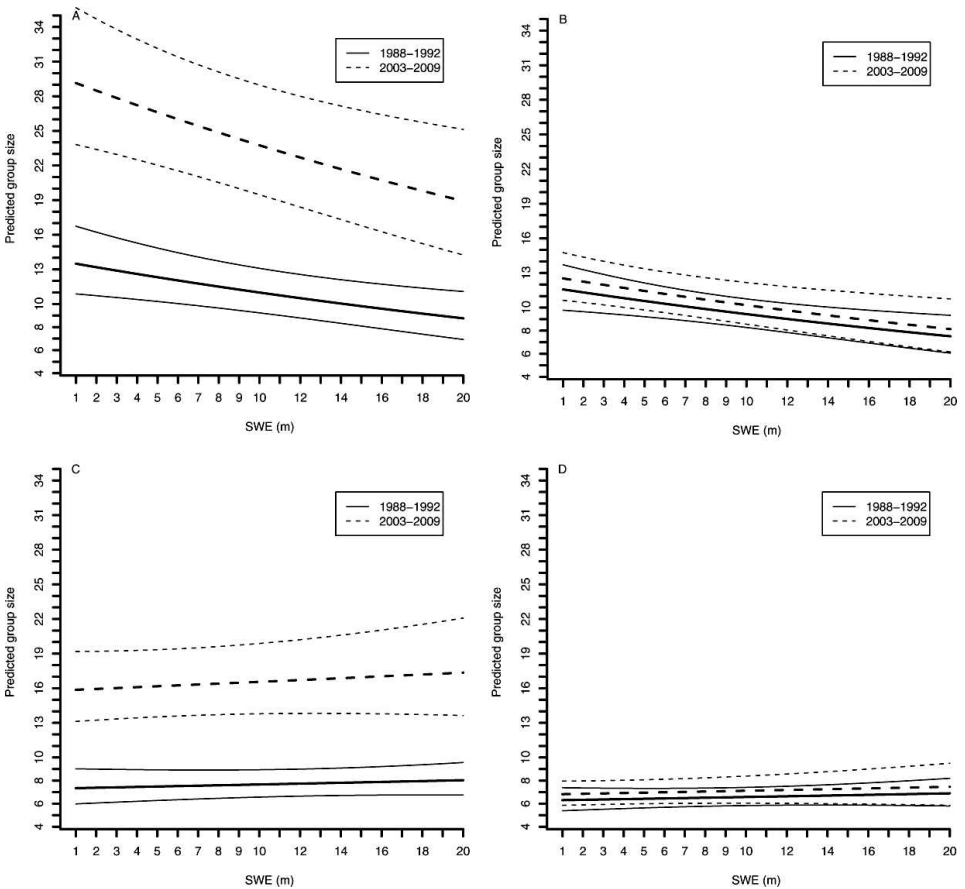


FIG. 5.—Predicted group size and 95% confidence intervals for elk groups in Yellowstone National Park located in open grassland areas in lower outside (Panel A) and upper (Panel B) sectors, and forested areas in lower outside (Panel C) and upper (Panel D) sectors, of northern Yellowstone winter range and varying snowpack during pre-wolf (1988–1992; solid lines) and post-wolf (2003–2009; dashed lines) periods

Beyer *et al.*, 2007). However, wolves also could produce trophic cascades by decreasing numbers of elk, thereby decreasing the intensity of herbivory on woody plants (*i.e.*, numerical mediated effect; White and Garrott, 2005).

A similar pattern of changes in the distribution and group sizes of elk in the Madison headwaters of Yellowstone occurred after wolf recovery (White *et al.*, 2009). Prior to wolf recolonization in 1997–1998, elk were distributed throughout the Firehole (40%), Gibbon (37%), and Madison (23%) river drainages. Following wolf recolonization, elk essentially were eliminated from the Gibbon drainage by 2004 and decreased 60% in the Firehole drainage by 2007. However, the proportion of elk in the Madison drainage increased to 84% by 2007. This shift in distribution primarily was due to wolf predation removing animals rather than elk redistributing among drainages (White *et al.*, 2009). Also, elk aggregated into somewhat larger groups in response to wolf predation risk, with lower mean annual kill

rates on larger groups (Becker *et al.*, 2009; Gower *et al.*, 2009b). However, there was a substantial increase in variations in group size as elk evidently attempted to balance the conflicting demands of minimizing predation risk and maximizing food acquisition (Gower *et al.*, 2009b). Slightly larger group sizes and more dynamic grouping behavior may be an effective strategy when other defensive tactics of elk, such as fleeing, do not work well in deep snow or thick vegetation that hinder efficient escape (Gower *et al.*, 2009b).

Predation risk is a function of where predators hunt and the landscape attributes, individual behaviors, and physiological stressors that render prey more or less susceptible to detection, attack, and predation (Mech and Peterson, 2003; Hebblewhite *et al.*, 2005). Wolves in Yellowstone are associated closely with elk and frequently course through winter ranges occupied by elk (Bergman *et al.*, 2006; Kauffman *et al.*, 2007). Thus, differences in predation risk among areas are not due to differences in detection or encounter probabilities but rather differences in vulnerability of elk once attacked (White *et al.*, 2009). Elk tended to avoid deeper snow areas, likely because snowpack is a significant factor affecting the vulnerability of ungulate prey (Mech and Peterson, 2003). Also, wolves selectively removed elk from areas with deeper snow (Mech *et al.*, 2001; Gower *et al.*, 2009c; White *et al.*, 2009). Thus, elk apparently minimized predation risk during winter by selecting portions of the landscape that increased their probability of escape if attacked, while still providing relatively high quality vegetation and snow characteristics that allowed access to forage (Mao *et al.*, 2005; Kauffman *et al.*, 2007; White *et al.*, 2009). Elk apparently obtained necessary food resources as there was no indication of any considerable change in foraging time or over-winter nutrition after wolves became established in the system (Cook *et al.*, 2004; Gower *et al.*, 2009a; White *et al.*, 2009).

Other studies in the greater Yellowstone ecosystem have detected different changes in elk distributions or group sizes in the presence of wolf predation risk. Gude *et al.* (2006) reported that wolves created a more dynamic distribution of elk in the lower Madison Valley located 40 km west of the Madison headwaters area. Elk in areas where wolves frequently hunted tended to move following wolf encounters in those areas. However, wolves had no detectable effect on the size of elk groups, which were strongly influenced by habitat type and hunting by humans (Gude *et al.*, 2006). Elk in the Gallatin Canyon area, Montana, outside the northwestern boundary of Yellowstone shifted habitats from grasslands to forests, formed smaller groups to reduce their level of predation risk, and sustained a decrease in diet quality (Creel *et al.*, 2005; Christianson and Creel, 2010). Thus, landscape disparities among areas may strongly influence the behavioral responses of elk to wolf presence and the degree to which these behaviors are manifested (Gower *et al.*, 2009b). As a result, fitness trade-offs between foraging conditions and the risk of predation (or harvest) as constrained by snow appear to vary considerably among elk populations in the greater Yellowstone ecosystem due to differences in land use, vegetation communities, large predator densities and management, local environmental conditions, elk migratory patterns, and human-related harvests (Garrott *et al.*, 2005; Hamlin *et al.*, 2009).

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