

Influences of wolves and high-elevation dispersion on reproductive success of pronghorn (*Antilocapra americana*)

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Mitigation of predation risk promotes high-elevation dispersion prior to birthing in many ungulate populations. Coyotes (*Canis latrans*) account for nearly 80% of pronghorn (*Antilocapra americana*) fawn mortality in Yellowstone National Park, but reintroduced gray wolves (*Canis lupus*) and factors associated with mountainous terrain can strongly influence space use by predators during summer and are likely to underlie significant spatial variation in survival rates of pronghorn fawns. We used generalized logit models paneled by maternal identity to assess the relative and interactive influences of summer wolf density, winter snow depth, and terrain slope on survival of pronghorn fawns in Yellowstone during 1999–2001 and 2004–2006. In this partially migratory population only migrant pronghorn accessed areas where wolves were numerous and winter snow depths were high. Survival of migrant fawns was higher in areas that experienced deep winter snow and had steeper slope. The influence of wolves on fawn survival was positive only in areas of low winter snowfall where coyotes were abundant, supporting predictions of a coyote-mediated effect of wolves and winter snowfall on pronghorn reproductive success. Our results suggest that deep winter snow, coupled with constraints on mobility imposed by reproduction in populations of social carnivores, can lead to the formation of high-elevation refugia for migrant ungulates. This research offers novel insights into the indirect effects of wolf restoration and climatic factors on the Yellowstone predator–prey complex and a conceptual framework for examining the ecological effects in other mountain communities of restoration of, and seasonal space use by, large carnivores. DOI: 10.1644/09-MAMM-A-057.1.

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Risk of predation is a major determinant of habitat selection by ungulates (Kie 1999), and parturient females are particularly sensitive to giving birth in areas where predation on neonates may be high (Barten et al. 2001; Berger 1991b; Bongi et al. 2008; Ciuti et al. 2006; Festa-Bianchet 1988; Kohlmann et al. 1996; Rachlow and Bowyer 1998). Prior to birthing, females in many mountain-dwelling populations attempt to reduce predation risk to themselves and neonates by dispersing into relatively vacant, high-elevation habitat where predators are few. For example, moose (*Alces alces*) in some areas shift to higher elevations prior to birthing to avoid riparian areas where predation rates by grizzly bears (*Ursus arctos*) and gray wolves (*Canis lupus*) are high (Langley and Pletscher 1994; Poole et al. 2007; Wilton and Garner 1991). Female woodland caribou (*Rangifer tarandus*) in other areas

disperse from moose-rich lowland habitat into high-elevation, often forage-poor sites for calving (Barten et al. 2001; Bergerud et al. 1984; Bergerud and Elliott 1998; Bergerud and Page 1987; Gustine et al. 2006; James et al. 2004; Johnson et al. 2002; Seip 1992). In Yellowstone National Park some elk (*Cervus elaphus*) may have shifted into higher-elevation summer ranges for birthing in response to wolf reintroduction and denning in low-lying areas (Mao et al. 2005; Thurston 2002). Females in these and other populations appear to capitalize on reproductive constraints within predator social groups and seasonal fluctuations in alternate prey abundance, which concentrate predators at low elevations during the



ungulate birthing season (Bergerud et al. 1984; Haroldson et al. 2002; McLellan and Hovey 2001; Schaller 1972, 1998; Thurston 2002).

The northern range of Yellowstone National Park is characterized by substantial habitat and topographical heterogeneity and supports an isolated population of partially migratory pronghorn (*Antilocapra americana*). Coyotes (*Canis latrans*) account for nearly 80% of total predation on pronghorn fawns in Yellowstone (Barnowe-Meyer et al. 2009) with approximately 66% of total mortality occurring within 2 weeks of birth (Barnowe-Meyer 2009). Patterns of space use by coyotes during spring and early summer are likely to structure juvenile survival significantly across areas selected by migrant and nonmigrant pronghorn in Yellowstone. However, the factors influencing the distribution of coyote territories across landscapes (2nd-order selection—Johnson 1980) are poorly understood. Adult coyotes generally do not migrate seasonally in mountainous areas (Bowen 1982; Gantz and Knowlton 2005; Shivik et al. 1997; Van Etten 2006; Weaver 1979), and deep winter snow often restricts coyotes to establishing territories in low-lying areas where prey are readily available (Crabtree and Varley 1995; Gese et al. 1996a). In addition, coyotes typically select against steep terrain (Arjo and Pletscher 2004; Moorcroft et al. 2006; Van Etten 2006). Pronghorn rarely inhabit mountainous areas or steep terrain (Yoakum 2004) except during brief migratory periods in certain populations (Sawyer and Lindzey 2000; Trainer et al. 1983). However, some Yellowstone pronghorn disperse to high-elevation areas prior to birthing (Barnowe-Meyer et al. 2009). Snow- and terrain-induced constraints on 2nd-order habitat selection by coyotes may lead to potentially significant differences in spring predation rates between low- and high-elevation areas of Yellowstone National Park.

The reintroduction of wolves to Yellowstone in 1995 (Bangs and Fritts 1996) was predicted to have numerous impacts on local ungulate populations (Boyce 1993; Buskirk 1999; Singer and Mack 1999). One prediction was that coyote numbers would be reduced by the larger wolves and that this mesopredator suppression (Soulé et al. 1988) might indirectly benefit the Yellowstone pronghorn population (Berger 1991a). Wolves are generally intolerant of coyotes (Ballard et al. 2003), and recent work elsewhere suggests that, where both occur, wolf and coyote densities are inversely related due to interference competition (Berger and Gese 2007). The extent to which this occurs on Yellowstone's northern range has not been assessed. Wolf predation on adult and juvenile Yellowstone pronghorn is rare based on mortality and diet studies (Barnowe-Meyer et al. 2009; Stahler et al. 2006), despite a peak in year-round wolf density of 50 individuals/1,000 km² on Yellowstone's northern range in 2002 (Smith et al. 2003). However, opportunistic wolf predation on pronghorn is likely to increase with wolf density, and wolves might reduce pronghorn fecundity indirectly by forcing females into areas of suboptimal habitat (Creel et al. 2007). Wolves maintain large territories relative to coyotes and are less restricted to

low-lying areas during the summer months (Thurston 2002), expanding their potential influence across both low- and high-elevation areas.

Our objective was to assess support for 3 predictions involving spatial heterogeneity in survival of pronghorn fawns during spring and early summer. We predicted that fawn survival in Yellowstone would be higher in areas with deep winter snows and steep terrain due to their impacts on 2nd-order coyote habitat selection and in areas of high summer wolf densities due to competitive exclusion of the more numerous coyote. Based on the reproductive success of individual pronghorn females over 6 years of study, we used generalized estimating equations for correlated data, information-theoretic criteria, and model averaging to assess the relative and absolute influence of these factors on spatial variation in predation risk to pronghorn fawns.

MATERIALS AND METHODS

Study area.—Yellowstone pronghorn inhabit various open portions (~330 km²) of the approximately 1,500-km² northern range in and near Yellowstone National Park, Montana and Wyoming (Fig. 1). These areas range in elevation from 1,500 to approximately 3,000 m. Pronghorn activity during winter is restricted to the arid and windswept basin surrounding Gardiner, Montana, on the northwestern portion of the northern range, an area of approximately 30 km². The habitat in this area is generally open grassland and shrub-steppe dominated by fringed sage (*Artemisia frigida*), big sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus* spp.), bluebunch wheatgrass (*Pseudoroegneria spicata*), Idaho fescue (*Festuca idahoensis*), prairie junegrass (*Koeleria macrantha*), prickly pear cactus (*Opuntia polyacantha*), Sandberg bluegrass (*Poa secunda*), and greasewood (*Sarcobatus vermiculatus*—Boccardori et al. 2008).

Beginning in April of each year portions of the Yellowstone pronghorn herd migrate to various meadow complexes and high-elevation ridges within the park (White et al. 2007). Vegetation in these areas is a mixture of grassland, shrub-steppe, and forest types with minor areas of riparian habitat. Dominant nonforest plant species in these areas include big sagebrush, rabbitbrush, bluebunch wheatgrass, Idaho fescue, and Sandberg bluegrass. Migrating individuals return to the winter range by October of each year. Nonmigrant individuals occupy the winter range year-round for foraging, birthing, and the rearing of young (White et al. 2007). Yellowstone pronghorn share portions of their winter and summer ranges with numerous potential predator species, including badgers (*Taxidea taxus*), bobcats (*Lynx rufus*), coyotes, cougars (*Puma concolor*), golden eagles (*Aquila chrysaetos*), gray wolves, grizzly bears, black bears (*Ursus americanus*), red foxes (*Vulpes vulpes*), and wolverines (*Gulo gulo*).

Pronghorn birthing and survival.—All capture and monitoring efforts were conducted in compliance with guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). We monitored 44 global positioning system-

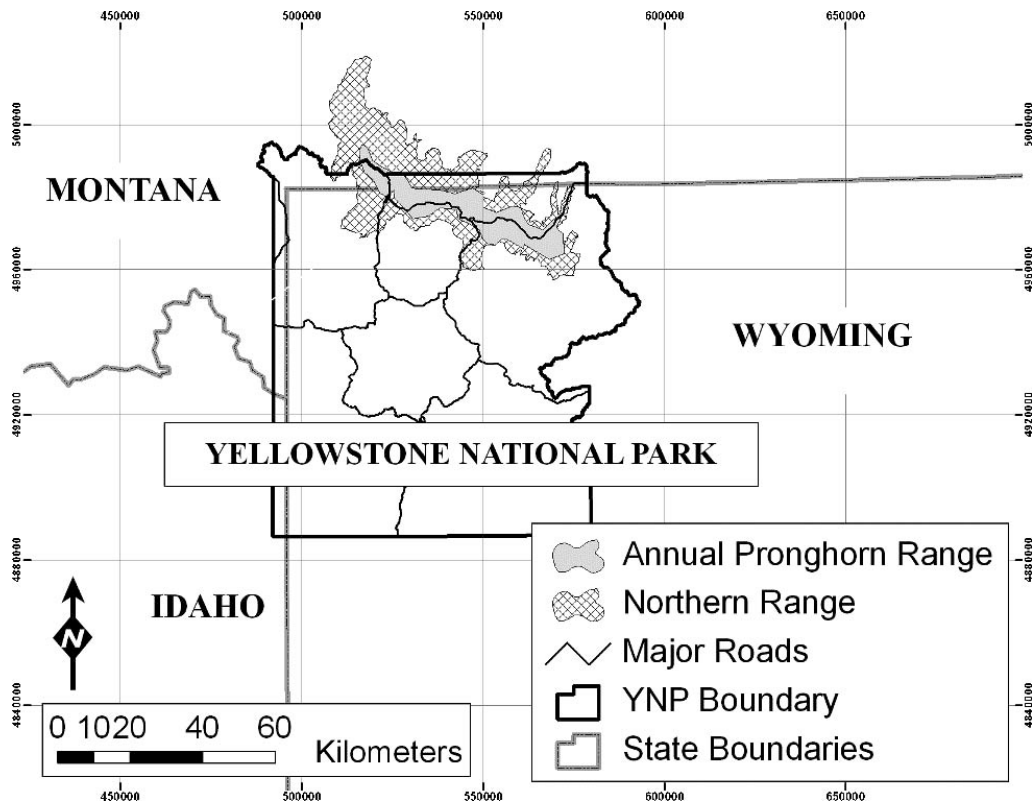


FIG. 1.—Study area and approximate range of pronghorn within and adjacent to Yellowstone National Park, Idaho, Montana, and Wyoming.

(Telonics, Mesa, Arizona) and very high frequency-collared (Lotek Wireless, Ontario, Canada) adult female pronghorn approximately twice weekly during the spring, summer, and early fall of 1999 ($n = 19$), 2000 ($n = 17$), 2001 ($n = 18$), 2004 ($n = 11$), 2005 ($n = 24$), and 2006 ($n = 20$), with many individuals monitored across consecutive years. Animals were located using standard radiotelemetry methods (White et al. 2007). We observed animals from the ground to record locations and reproductive status (pregnant, birthing, or lactating). We identified approximate birth sites for previously pregnant females using ground-based observations of females in labor, with placental material or other physical indications of parturition present, accompanied by fawns <3 days old, or exhibiting behavioral characteristics of a doe with hidden fawns (Byers 1997). We recorded survival to 1 September of fawns born to collared females based on fawn presence and suckling, the female's behavior (Byers 1997), and the size of her udder. Because of our inability to determine the number of fawns (single or twins) born to each female in some years, we defined the dichotomous response variable, Fawn Survival, for each female that birthed in each year as $FS_{(0 \text{ fawns surviving})} = 0$ and $FS_{(1 \text{ or } 2 \text{ fawns surviving})} = 1$. We assessed evidence for differences in Fawn Survival between migrants and nonmigrants using a t -test in SPSS Statistics 17.0 (SPSS Inc., Chicago, Illinois).

Habitat factors.—We assessed terrain slope using 30-m nontransformed slope data (Yellowstone Spatial Analysis Center, <http://www.nps.gov/yell/naturescience/spatialanalysiscenter.htm>; accessed 1 July 2004). We quantified winter snow depth

using a 100-m snow data model incorporating slope, aspect, elevation, habitat types, geothermal effects, and data from 28 fixed weather stations within and surrounding Yellowstone National Park (Wockner et al. 2002). We derived monthly average snow water-equivalent estimates (water content of a column of snow) across the study area from December through February, the period of coyote territory establishment (Crabtree and Varley 1995), preceding each fawning season during our study. We hypothesized that the maximum monthly snow water-equivalent value during this 3-month period would dictate coyote territory establishment each year. We retained February snow water-equivalent values for analyses (the maximum monthly average value observed at the weather station at Buffalo Ranch in the Lamar Valley in all years) and converted these values to snow depth (cm) using multipliers specific to our study area (Fig. 2, bottom—Farnes et al. 1999; Murray and Boutin 1991). We derived slope and snow depth values in areas subsequently selected by female pronghorn using conditional point sampling within 500 m of birth sites and female locations, up to 2 weeks postpartum, in ArcGIS 9.2 (ESRI, Redlands, California) using Hawth's Analysis Tools 3.27 ($n = 500$ samples per point—Beyer 2004). For analyses, we transformed snow depth using a zero-skewness natural-log transformation via the LNSKEW command in Stata 9.2 (StataCorp LP, College Station, Texas).

Where winter snow depths are high some pronghorn females in Yellowstone may be more likely to encounter areas of reduced visibility where predation risk to adults is increased (Barnowe-Meyer et al. 2009; Goldsmith 1990). We

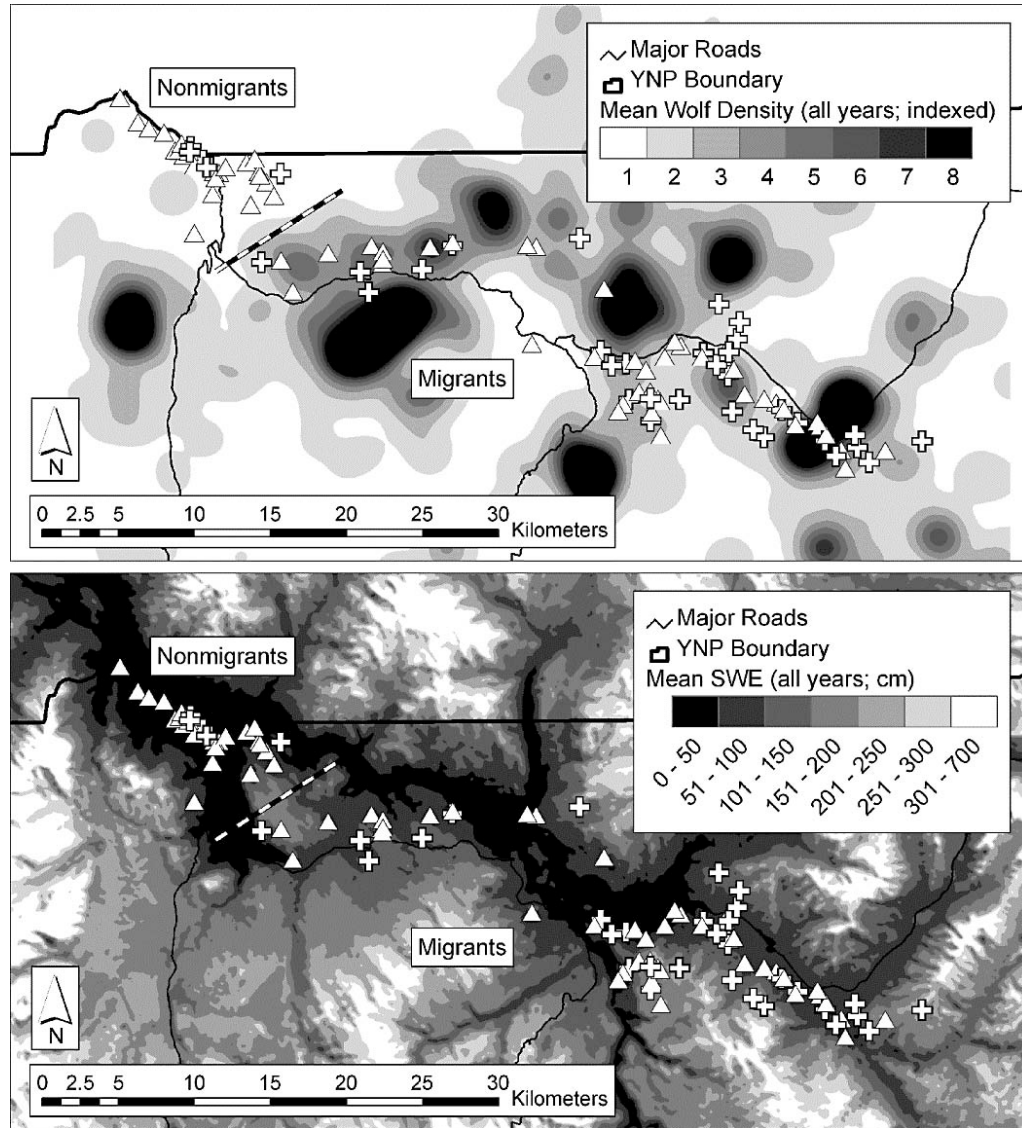


FIG. 2.—Distribution of birth sites ($n = 109$) of 44 instrumented female pronghorn, 1999–2001 and 2004–2006, along the northern boundary of Yellowstone National Park. Birth sites are indicated as triangles where the variable Fawn Survival = 0 and as crosses where Fawn Survival = 1. Sites are shown with mean wolf density (top) and mean February snow water-equivalent (SWE) values (bottom) across study years. The division between nonmigrant and migrant areas is indicated as a dashed line (White et al. 2007).

calculated an index of visibility as the average proportion of area visible surrounding females during parturition and up to 2 weeks postpartum in each year. We used ETM+ satellite imagery to classify vegetation hierarchically across Yellowstone's northern range on a 30-m-pixel basis (Savage 2005). We selected a simplified classification scheme to reflect hypothesized differences in sightability, predator detection rates, and vigilance by pronghorn in 4 generalized habitat classes (Goldsmith 1990): sparse vegetation, grasslands, shrublands, and forest. To quantify visual occlusion due to vegetation we assigned approximate mean vegetation height values to habitat types based on field experience and species composition (Despain 1990): 0 cm (sparse vegetation), 30 cm (grasslands), 70 cm (shrublands), and 15 m (forest). We used these data to assess average terrain visibility using the Viewshed function of Spatial Analyst extension of ArcGIS

9.2. Calculations were based on a 10-m digital elevation model (Yellowstone Spatial Analysis Center, <http://www.nps.gov/yell/naturescience/spatialanalysiscenter.htm>; accessed 1 July 2004) adjusted to incorporate vegetation height at each pixel. We randomly seeded 25 points within 500 m of each radiocollared-female location at the birth site and during the first 2 weeks following parturition. We vertically offset observation points to approximate average pronghorn shoulder height (1 m) while accounting for the height of vegetation above ground level at each point. We limited sighting distances to 500 m to approximate reasonable detection and reaction distances and to reduce computational complexity. Average terrain visibility for each female in each year was transformed using an arcsin/square-root transformation (Zar 1999).

Wolf density.—We derived wolf densities from aerial point locations of radiocollared wolves during 1 May to 31 August

TABLE 1.—Summary of covariate values for areas used by nonmigrant and migrant female pronghorn in Yellowstone National Park, 1999–2001 and 2004–2006 (pooled years), in the 2 weeks following parturition.

Variable	Nonmigrants				Migrants				Mann–Whitney <i>U</i> (2-tailed exact <i>P</i>)
	\bar{X}	<i>SE</i>	<i>n</i>	Range	\bar{X}	<i>SE</i>	<i>n</i>	Range	
Winter snow depth (cm)	7.86	1.08	34	2.75–27.07	26.25	1.57	75	7.72–59.16	174 (<0.001)
Wolf density (indexed)	0.03	0.01	34	0.0–0.40	1.58	0.24	75	0.0–10.21	120 (<0.001)
Slope (degrees)	24.73	1.88	34	4.24–50.07	22.86	1.35	75	2.56–44.24	1,176 (0.520)
Visibility (%)	37.2	0.02	34	19–60	32.5	0.01	74	9–65	935 (0.032)

1999–2001 and 2004–2006. This time period encompassed both wolf denning and rendezvous activity (Packard 2003) and was sampled to ensure sufficient data for density calculations. All packs were known, with 3–7 wolves monitored in each pack by the National Park Service (Smith et al. 2007). We pooled points from multiple individuals within packs due to spatial association of pack members on the same day, then subsampled each pack once daily ($n \approx 15$ points pack⁻¹ year⁻¹). We calculated fixed-kernel utilization distributions for each pack in each year using Hawth's Analysis Tools 3.27 in ArcGIS 9.2. We selected a smoothing parameter of 1,500 m to reflect the approximate extent of space use by packs in the study area (Kauffman et al. 2007). We weighted values of each utilization distribution by the number of adults per pack within years and summed these across the study area for each year. We derived wolf density values using conditional point sampling within 500 m of birth sites and female locations, up to 2 weeks postpartum, in ArcGIS 9.2 using Hawth's Analysis Tools 3.27 ($n = 500$ samples per point). For analyses, we transformed wolf density using a zero-skewness natural-log transformation via LNSKEW command of Stata 9.2.

Statistical analyses.—In Yellowstone, migrant and nonmigrant pronghorn occupy areas of differing habitat types (Despain 1990) and faunal communities (Barnowe-Meyer et al. 2009). To avoid biasing our results by pooling data from individuals inhabiting areas of substantially dissimilar conditions, we split our pronghorn reproductive data into migrant and nonmigrant sets and assessed predictions for each group. We assessed evidence for differences in winter snow depth, slope, terrain visibility, and wolf density between migrants and nonmigrants using Mann–Whitney tests in SPSS Statistics 17.0. We assessed evidence for trends in elevation, slope, terrain visibility, and wolf density by winter snow depth in migrant areas using nonparametric tests of association in SPSS Statistics 17.0.

We constructed 16 models of migrant and 8 models of nonmigrant fawn survival to assess the individual, combined, and interactive linear influences of the derived variables Snow, Slope, Visibility, and Wolves. Sparse nonzero values of wolf density on the winter range prevented the inclusion of Wolves in nonmigrant models. We did not include the variables Snow and Slope within individual models due to collinearity; instead, we assessed Snow and Slope in competing models to determine which more accurately accounted for variation in fawn survival.

We fit generalized estimating equations for repeated-measures binomial response data using the quasi-likelihood under the independence model criterion (QIC) procedure in Stata 9.2 (Cui and Qian 2007). We selected a repeated-measures model structure to account for differences in maternal condition and behavior maintained across years. We treated Fawn Survival (0/1) as the dependent variable and paneled models by maternal identity ($n = 44$) with an independent correlation structure (Cui and Qian 2007). We used Huber–White sandwich estimators of variance to derive valid *SEs*. We assessed relative support in the data for competing models using an information criterion suited to the quasi-likelihood approach used by generalized estimating equations QIC (Pan 2001). The procedures of model selection and multimodel inference were otherwise identical to those used in Akaike information criterion (AIC)–based analyses. We used relative variable importance values (Burnham and Anderson 2002) to compare the predictive power of variables across models in our candidate sets. We also used model averaging to generate a robust foundation for inference based upon all, rather than the single most, strongly supported models in our suites ($\Delta\text{QIC} < 2.0$ from QIC_{\min} —Burnham and Anderson 2002). We calculated odds ratios with confidence intervals (*CI*s) for variables averaged across the best-supported models to assess the strength of the various factors and their directions of effect on fawn survival for migrants and nonmigrants.

RESULTS

Pronghorn birth sites during 1999–2001 and 2004–2006 ($n = 109$) were distributed widely across Yellowstone's northern range, from 1,585-m elevation near the northern park boundary in the Gardiner basin in the west to 2,560 m on the slopes of Mt. Norris in the east (Fig. 2). Birthing and fawn-hiding sites were documented in all major habitat types, including grasslands, sagebrush-steppe, broken coniferous forests, mixed talus slopes, and subalpine meadows. Fawn Survival was significantly higher in migrant ($\bar{X} = 0.41 \pm 0.06$ *SE*) than in nonmigrant ($\bar{X} = 0.18 \pm 0.07$) areas (unequal variances $t_{80.5} = -2.703$, $P = 0.008$). Areas selected by migrants and nonmigrants from 1999 to 2001 and 2004 to 2006 differed markedly by wolf density (Fig. 2, top), winter snow depth (Fig. 2, bottom), and visibility but not by terrain slope (Table 1). Areas of high winter snow depth selected by

TABLE 2.—Model selection results for a priori models of Fawn Survival (0/1) for nonmigrant and migrant female pronghorn in Yellowstone National Park, 1999–2001 and 2004–2006 (pooled years). Table contains information criterion score (QIC), deviation of information criterion from the lowest corresponding value within the suite (Δ QIC), model likelihood (L_i), and model weight (ω_i).

Model structure	QIC	Δ QIC	L_i	ω_i
Nonmigrant suite				
Constant	33.887	0.000	1.000	0.2647
Snow	35.046	1.159	0.560	0.1483
Visibility	35.118	1.231	0.540	0.1431
Slope	35.529	1.642	0.440	0.1165
Snow + Visibility	35.691	1.804	0.406	0.1074
Slope + Visibility	35.837	1.950	0.377	0.0999
Snow + Visibility + Snow \times Visibility	35.868	1.981	0.371	0.0983
Slope + Visibility + Slope \times Visibility	38.875	4.988	0.083	0.0219
Migrant suite				
Snow	100.888	0.000	1.000	0.1955
Snow + Visibility	101.580	0.692	0.708	0.1383
Snow + Wolves + Visibility	101.967	1.079	0.583	0.1140
Snow + Wolves + Visibility + Snow \times Wolves	102.144	1.256	0.534	0.1043
Slope + Visibility	102.968	2.080	0.353	0.0691
Slope + Wolves + Visibility + Slope \times Wolves	103.249	2.361	0.307	0.0600
Slope	103.422	2.534	0.282	0.0551
Constant	103.607	2.719	0.257	0.0502
Slope + Wolves + Visibility	103.985	3.097	0.213	0.0416
Snow + Visibility + Snow \times Visibility	104.511	3.623	0.163	0.0319
Visibility	104.678	3.790	0.150	0.0294
Slope + Visibility + Slope \times Visibility	104.827	3.939	0.140	0.0273
Wolves	104.872	3.984	0.136	0.0267
Snow + Wolves + Visibility + Snow \times Visibility	105.121	4.233	0.120	0.0235
Wolves + Visibility	105.749	4.861	0.088	0.0172
Slope + Wolves + Visibility + Slope \times Visibility	105.907	5.019	0.081	0.0159

migrants were characterized by mixed coniferous forest and meadow habitat, higher elevation (Kendall's $\tau = 0.559$, $n = 75$, 1-tailed $P < 0.001$), steeper slope ($\tau = 0.199$, $n = 75$, 1-tailed $P = 0.006$), and more limited terrain visibility ($\tau = -0.158$, $n = 74$, 1-tailed $P = 0.023$) than were areas of low winter snow depth selected by migrants.

Model-selection criteria indicated equivalent support for most a priori models of nonmigrant Fawn Survival (Table 2). Relative importance values were 0.354 for Snow and 0.238 for Slope (Visibility was included in most models as a covariate and, as a result, had an inflated relative importance value). The model-averaged odds ratios and *CI* estimates for Snow, Slope, and Visibility indicated a highly variable effect of each covariate on Fawn Survival (Table 3).

The migrant Fawn Survival suite of models produced relative importance values of 0.608 for Snow, 0.403 for Wolves, and 0.269 for Slope (Table 2). The model-averaged odds ratio and *CI* estimate for Snow indicated a strong positive effect of deep winter snow on Fawn Survival (Table 3). Results for Slope indicated a moderate positive effect of terrain slope on Fawn Survival. Results for Wolves suggested an equivocal or weakly positive overall effect of wolf density on Fawn Survival. Results for Visibility indicated an equivocal and highly variable effect of terrain exposure on Fawn Survival.

For migrants, 1 model containing an interaction of the variables Snow \times Wolves was strongly supported (Δ QIC =

1.256). We assessed the interaction by binning the variables Snow and Wolves into tertiles and deriving estimated values of Fawn Survival at various combinations of the new categorical predictors. In migrant areas where winter snow depth was within the lowest tertile (i.e., at low elevations) mean Fawn Survival was positively associated with wolf density (from 0.00 [0.00 *SE*] at low-wolf sites to 0.42 [0.20 *SE*] at high-wolf sites). In migrant areas where winter snow depth was within the highest tertile (i.e., at high elevations) mean Fawn Survival was unassociated with wolf density (0.70 [0.15 *SE*] at low-wolf sites and 0.70 [0.14 *SE*] at high-wolf

TABLE 3.—Model-averaged odds ratio estimates for variables included in strongly supported models (Δ QIC ≤ 2.0) of Fawn Survival (0/1) for nonmigrant and migrant female pronghorn in Yellowstone National Park, 1999–2001 and 2004–2006.

Parameter	Odds ratio estimate	95% <i>CI</i>
Nonmigrants		
Snow	0.810	0.480–1.367
Slope	0.897	0.280–2.873
Visibility	1.207	0.457–3.189
Migrants		
Snow	2.081	1.074–4.031
Slope	1.614	1.017–2.562
Wolves	1.260	0.886–1.790
Visibility	1.102	0.001–4.344
Snow \times Wolves	0.414	0.125–1.366

sites). Across wolf densities predicted Fawn Survival averaged 0.25 (95% CI = 0.07–0.47) in low-snow migrant areas and 0.70 (95% CI = 0.36–0.91) in high-snow migrant areas. Across snow depths predicted Fawn Survival averaged 0.47 (95% CI = 0.23–0.61) in low-wolf migrant areas and 0.59 (95% CI = 0.27–0.86) in high-wolf migrant areas.

DISCUSSION

As predicted, both winter snow depth and terrain slope positively influenced the survival of pronghorn fawns in Yellowstone. Of the 2, winter snow depth more strongly accounted for variation in survival of pronghorn fawns by elevation. Steep terrain was associated with improved fawn survival in migrant but not nonmigrant areas, although steep areas were used by pronghorn of both groups. Relative variable importance values ranked winter snow depth ahead of terrain slope for both migrants and nonmigrants. Neither the direct nor interactive influence of terrain visibility improved the power of terrain slope or winter snow depth to predict fawn survival in either group.

The impetus for dispersion by some female pronghorn into high-elevation areas was not assessed as part of this study. However, by restricting habitat selection by coyotes during the winter, deep winter snow is likely to promote the formation of refugia from coyote predation at higher elevations during the spring and early summer. Coyote pair-bonding and territory establishment occur from December through February in Yellowstone (Crabtree and Varley 1995; Gehman et al. 1997), and these territories are generally maintained throughout the year (Camenzind 1978; Gantz and Knowlton 2005; Gese et al. 1996a; Shivik et al. 1997; Van Etten 2006; Weaver 1979). During the winter deep snow limits the availability of small mammals to coyotes (Gese et al. 1996a, 1996b) and concentrates ungulate use and carcass subsidies from wolves in open, low-lying habitat where kill rates by wolves are high (Crabtree and Sheldon 1999a; Kauffman et al. 2007; Switalski 2003; Van Etten 2006; Wilmers et al. 2003). Subsequent spring and early summer movements by coyote pack members are constrained by the demands of territory maintenance and the location of the den (Camenzind 1978; Crabtree and Sheldon 1999b; Gantz and Knowlton 2005; Moorcroft et al. 2006). Transient (nonterritorial) coyotes may use high-elevation areas during summer (Crabtree and Varley 1995; Gantz and Knowlton 2005), but these constitute only 10–20% of the total coyote population in northern Yellowstone (Crabtree and Sheldon 1999b). Following the establishment of territories in low-lying areas, the majority of coyotes on Yellowstone's northern range appear to remain at low elevation despite substantial, yet temporary, habitat vacancy away from the valley floors.

Overall, the survival of fawns born to migrant pronghorn was weakly or not at all associated with wolf density. However, wolf density appeared to interact with winter snow depth such that fawn survival was positively influenced by wolf density in low-lying but not high-elevation migrant areas.

This result is difficult to explain except in terms of the impact of winter snow depth on the distribution of coyotes and further supports our hypothesis that winter conditions structure summer predation risk to pronghorn fawns in Yellowstone. Wolf pack territories and local densities varied considerably during the study period (Smith 2005), reducing the possibility that spatially coincident factors, such as forage or alternate prey availability, influenced this result.

The mechanism by which wolves improve fawn survival at low elevation is not fully understood. High wolf activity adjacent to wolf dens and rendezvous sites during spring and summer may create areas of intense interspecific conflict and coyote exclusion (Berger and Gese 2007). Berger et al. (2008) suggested that improved fawn survival in areas of high wolf activity in Grand Teton National Park, Wyoming, resulted from competition between wolves and transient coyotes (Berger and Gese 2007). We separately assessed the effects of wolves where territorial coyotes were present and absent and found indications that fawn predation by transient coyotes may be minimal even in the absence of wolves. Equivalent fawn survival rates at high elevations where wolves were present and absent further suggests that opportunistic wolf predation on fawns can, in some areas, equal or surpass predation by transient coyotes where both occur. Our results indicate that wolf competition with territorial coyotes most strongly dictates the net effect of wolf presence on pronghorn fawn survival in Yellowstone. At low elevations where territorial coyotes are numerous, wolf-coyote competition improves overall fawn survival rates and appears to facilitate limited pronghorn recruitment within Yellowstone's otherwise risky low-lying migrant areas. High-resolution spatial and behavioral data are needed to assess the extent to which wolves exclude coyotes, both territorial and transient, from key areas during the spring and summer months. Like dispersion to high elevation, the use of areas of high wolf activity by female pronghorn may be an active response to fewer total predators in these areas, lower perceived risk from coyotes due to the solitary status of transients (Berger and Gese 2007), other observable, qualitative changes in coyote behavior when wolves are present (Switalski 2003), or a result of simple isolating movements (Byers 1997) and birth-site fidelity (Wiseman et al. 2006).

We were unable to assess coyote abundance and space use directly in portions of our study area used by pronghorn, despite intensive monitoring. Coyote research activities during our study occurred in several low-lying areas of the park adjacent to major roads (Crabtree and Sheldon 1999b). These areas are used commonly by pronghorn, but during fawning, numerous female pronghorn occupied more remote areas in which coyote capture was not permitted by the National Park Service. Highly informative models of space use by coyotes exist for some areas of Yellowstone's northern range (Moorcroft et al. 2006), but these require detailed behavioral data not easily obtained in more remote areas of the park. Sample size limitations in areas of intense coyote monitoring did not allow for fawn survival analyses restricted to these

areas. Additional data are needed to assess fully the social and ecological factors governing the risk of predation posed by coyotes across Yellowstone's northern range.

Our results are the 1st to document high-elevation dispersion prior to parturition in pronghorn, a species rarely associated with montane habitat, and to link such behavior to improved reproductive success. Our results further suggest that deep winter snow, coupled with constraints on the mobility of coyotes, can lead to the formation of high-elevation refugia for pronghorn fawns. Reproductive constraints are known to limit the ability of predators to follow migrant ungulates on the Serengeti and Tibetan plateaus (Fryxell and Sinclair 1988; Schaller 1998). In mountainous regions winter snowfall likely concentrates predators during periods of territory and social group formation, thereby indirectly dictating the summer distribution of predators even before their reproductive period.

Examination of our data demonstrates that wolves influence pronghorn fawn survival by excluding coyotes from areas of intense wolf use, but that this effect is only pronounced in low-lying areas where territorial coyotes are otherwise numerous. These results tentatively confirm early predictions that wolf reintroduction to Yellowstone would impact ungulate populations indirectly by altering the habitat use and behavior of mesopredators (Berger 1991a; Buskirk 1999; Singer and Mack 1999). Despite a lack of detailed pronghorn and coyote demographic data before and immediately after wolf reintroduction in 1995, our results suggest that wolf reintroduction has been of net benefit to the Yellowstone pronghorn population. This is further supported by the higher overall rate of fawn survival in relatively wolf-rich migrant areas compared to areas inhabited solely by nonmigrants and an increase in the proportion of migrants from pre-1995 to the current study period (from 20% to 70%—White et al. 2007).

More broadly, these results indicate that winter conditions and predator space use may interact dramatically, with important consequences for migrant ungulate populations. Researchers working with isolated or at-risk mountain populations should attempt to account for the strong structuring influence of winter conditions on the year-round distribution of important predator species. Unfortunately, few studies have attempted to assess this influence. We recommend detailed study of the nature and severity of predator competition in Yellowstone, the realized consequences of such competition and winter conditions on space use by mesopredators in mountainous areas, and the extent to which these interactions influence overall predation risk to juvenile ungulates.

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