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Greater Sage-Grouse (*Centrocercus urophasianus*) hen survival: effects of raptors, anthropogenic and landscape features, and hen behavior

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Abstract: Survival of breeding-age hens has been identified as the demographic rate with the greatest potential to influence population growth of Greater Sage-Grouse (*Centrocercus urophasianus* (Bonaparte, 1827); hereafter "Sage-Grouse"). During 2008–2011, we collected summer survival data from 427 Sage-Grouse hens in southern Wyoming, USA. We assessed the effects of raptor densities, anthropogenic features, landscape features, and Sage-Grouse hen behavior on Sage-Grouse hen survival. Survival of Sage-Grouse hens was positively associated with the proportion of big sagebrush (genus *Artemisia* L.) habitat within 0.27 km radius and road density and negatively associated with power-line density, proximity to forested habitat, and topographic ruggedness index within 0.27 km radius ($\mathrm{TRI}_{0.27}$). Raptor densities did not have individual effects on Sage-Grouse survival; however, an interaction between site-specific exposure to Golden Eagle (*Aquila chrysaetos* (L., 1758)) density (GOEA) and $\mathrm{TRI}_{0.27}$ indicated that negative effects of GOEA and $\mathrm{TRI}_{0.27}$ were dampened in areas with both high $\mathrm{TRI}_{0.27}$ and high GOEA. Survival of nonreproductive hens was greater than brooding or nesting hens. Hens that stayed in intermediate-size flocks and yearling hens had higher survival than hens in small or large flocks and hens >2 years old. Results indicated that risk of death for Sage-Grouse hens was greater relative to potential raptor perches but not anthropogenic and landscape variables that could provide food subsidies for predators.

Key words: Anthropogenic development, antipredation strategy, *Centrocercus urophasianus*, Greater Sage-Grouse, habitat, parental investment, survival.

Résumé : Il a été établi que la survie des femelles en âge de se reproduire constituait le taux démographique le plus susceptible d'influencer la croissance des populations de tétras des armoises (*Centrocercus urophasianus* (Bonaparte, 1827); ci-après « tétras »). De 2008 à 2011, nous avons recueilli des données sur la survie de 427 femelles de tétras dans le sud du Wyoming (États-Unis d'Amérique). Nous avons évalué les effets de la densité d'oiseaux de proie, d'éléments d'origine humaine, d'éléments du paysage et du comportement des tétras femelles sur la survie de ces dernières. La survie était positivement associée à la proportion de l'habitat d'armoises (genre *Artemisia* L.) dans un rayon de 0,27 km et à la densité des routes et négativement associée à la densité des lignes de transport électrique, la proximité d'habitats forestiers et l'indice d'irrégularité du relief dans un rayon de 0,27 km ($\mathrm{TRI}_{0,27}$). Si la densité d'oiseaux de proie n'avait pas d'effet individuel sur la survie des tétras, une interaction entre l'exposition propre au site à la densité d'aigles royaux (*Aquila chrysaetos* (L., 1758)) (GOEA) et le $\mathrm{TRI}_{0,27}$ indiquait que les effets négatifs de la GOEA et du $\mathrm{TRI}_{0,27}$ étaient atténués dans les zones présentant un $\mathrm{TRI}_{0,27}$ et une GOEA élevés. La survie des femelles non reproductrices était plus grande que celle des femelles couveuses ou nicheuses. Les femelles qui restaient dans des bandes de taille intermédiaire et les femelles de l'année avaient un meilleur taux de survie que les femelles dans des bandes plus petites ou plus grandes ou âgées de plus de 2 ans. Les résultats indiquent que le risque de mortalité pour les femelles de tétras était plus élevé en ce qui concerne les perchoirs possibles d'oiseaux de proie, mais non les variables humaines ou du paysage qui pourraient offrir des sources de nutriments pour les prédateurs. [Traduit par la Rédaction]

Mots-clés : aménagement humain, stratégie anti-prédation, *Centrocercus urophasianus*, tétras des armoises, habitat, investissement parental, survie.

Introduction

Survival of breeding-age birds in direct relation to predator communities has not been a main research focus for Greater Sage-Grouse (*Centrocercus urophasianus* (Bonaparte, 1827); hereafter "Sage-Grouse"). Sage-Grouse are a species of conservation concern because their distribution and abundance in western North America have declined over the last century (Gregg et al. 1994; Johnsgard 2002; Connelly et al. 2004). Survival related to predator communities was not likely to have negatively affected population status during pre-European settlement because Sage-Grouse coevolved with the predator communities present in sagebrush ecosystems (Schroeder et al. 1999, Schroeder and Baydack 2001). There are currently no predators that specialize on Sage-Grouse during any life-history stage (egg, chick, or adult; Connelly et al. 2011). Thus, Hagen (2011) indicated that predators may only be negatively affecting Sage-Grouse populations in fragmented habitats and areas with human-subsidized predator populations. However, these areas of habitat fragmentation and areas with human-subsidized predator populations have drastically increased in the recent past (Leu et al. 2008). For example, red fox (*Vulpes vulpes* (L., 1758)) and raccoon (*Procyon lotor* (L., 1758)) have increased

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in abundance in Sage-Grouse habitat, especially near human activities (Connelly et al. 2000*b*; Hagen 2011, Baxter et al. 2013). In addition, Golden Eagles (*Aquila chrysaetos* (L., 1758)) and Buteonine Hawks (genus *Buteo* Lacépède, 1799) use anthropogenic structures as perches and nesting structure (Lammers and Collopy 2007; Prather and Messmer 2010; Slater and Smith 2010). Presence of anthropogenic structures in sagebrush habitat may result in decreased survival of Sage-Grouse.

Sage-Grouse hen survival had the greatest potential to influence population growth in a range-wide sensitivity analysis (Taylor et al. 2012), and a population of Sage-Grouse in northern Colorado, USA, was most sensitive to adult and juvenile Sage-Grouse survival (Johnson and Braun 1999). This should not be surprising, because Sage-Grouse are relatively long-lived gallinaceous birds with low productivity (Connelly et al. 2000*b*, 2011; Holloran et al. 2005). Sage-Grouse hens typically have high annual survival (16%–78%; Holloran 2005; Connelly et al. 2011; Sedinger et al. 2011; Baxter et al. 2013; Blomberg et al. 2013*b*), with the breeding season having the lowest seasonal survival rate for Sage-Grouse hens (Baxter et al. 2013; Blomberg et al. 2013*b*). Research designed to evaluate potential factors affecting summer survival of Sage-Grouse in relation to predators and habitat quality will help guide management practices. Furthermore, low productivity of Sage-Grouse in combination with increased predation rates in fragmented habitats has the potential to decrease or extirpate local Sage-Grouse populations.

Increasing levels of human development in sagebrush habitat have brought a range of new stresses to sagebrush-obligate bird species, including Sage-Grouse, from habitat loss and fragmentation to increased predation (Connelly et al. 2004; Doherty et al. 2010; Gilbert and Chalfoun 2011; Kirol 2012). For example, Brewer's Sparrow (*Spizella breweri* Cassin, 1856), Sagebrush Sparrow (*Amphispiza nevadensis* (Ridgway, 1874)), and Vesper Sparrow (*Pooecetes gramineus* (Gmelin, 1789)) abundance was lower in areas with greater density of oil and gas infrastructure (Gilbert and Chalfoun 2011). Potentially additive impacts of human development on Sage-Grouse survival include increased hunting efficiency of raptors (perches), number of nesting structures available to raptors, and carrying capacity of generalist predators. Sources of perch and nesting structure for raptors include oil and gas structures, residential houses, communication towers, power lines, trees, and rugged terrain. Our research was focused on evaluating the effects of habitat quality and structure (both anthropogenic and environmental) related to potential negative effects of raptor predation.

Although raptors have been reported to prey on Sage-Grouse (Blomberg et al. 2013*a*), raptor densities have not been directly correlated to Sage-Grouse survival rates or population growth. Golden Eagles have been suggested as a major Sage-Grouse predator (Connelly et al. 2000*a*; Mezquida et al. 2006, Blomberg et al. 2013*a*); however, no Sage-Grouse study has directly related site-specific densities of raptors to Sage-Grouse hen survival. We recorded raptor densities associated with Sage-Grouse nesting and brood-rearing areas from 2008 to 2011 to determine if raptors impacted Sage-Grouse hen survival during the summer. We hypothesized that Sage-Grouse hen survival would be reduced in areas and years with more raptors, specifically, Golden Eagles, Buteonine Hawks, and Northern Harriers (*Circus cyaneus* (L., 1766); hereafter "Harrier"). In addition, we hypothesized that this effect would be intensified in areas with greater density or closer to potential perches, such as oil and gas structures, power lines, houses, trees, and rougher topography, whereas Sage-Grouse survival would be greater in areas with greater proportions of intact big sagebrush (genus *Artemisia* L.). To test these hypotheses, we assessed Sage-Grouse hen survival in relation to Sage-Grouse exposure to raptors, potential raptor perches, and proximity to areas associated with natural or human-provided food subsidies. As secondary objectives, we evaluated differences between yearling and adult Sage-Grouse hen survival, and the effect of Sage-Grouse hen behavior (parental investment, weekly movement, and flock size) on survival. We hypothesized that lower parental investment, shorter weekly movements, and medium-sized or large flocks would be associated with higher hen survival.

Materials and methods

Study area

Our study was conducted in southwest and south-central Wyoming, USA. We chose 12 circular study sites, each 16 or 24 km in diameter (eight study sites of 16 km diameter and four study sites of 24 km diameter). Study sites in southwest Wyoming were 16 km diameter and approximately centered around leks where hens were captured, because Holloran and Anderson (2005) found 93% of Sage-Grouse nested within 8.5 km of leks in Wyoming. Study sites in south-central Wyoming were 24 km in diameter, because Sage-Grouse were captured at several nearby leks over a larger area. Five study sites were located in Lincoln County, two in Sweetwater County, two in Uinta County, and three in Carbon County. Elevation of study sites ranged from 1925 to 2550 m. A majority of the land within all of the study sites was federally owned and administered by the Bureau of Land Management with a small percentage of private lands. Domestic sheep and cattle grazing were the dominant land uses in the study sites. All study sites had anthropogenic development, which consisted mostly of unimproved four-wheel drive roads. Conventional natural gas, coal-bed methane natural gas, and (or) conventional oil extraction activities were present in six (50%) of the study sites; well density within study sites averaged 0.12 ± 0.22 (mean ± SD) wells/km^2 (range = 0.0–0.64 wells/km^2).

The landscape at all study sites was dominated by sagebrush; Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) and mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle) were the most common. Black sagebrush (*Artemisia nova* A. Nelson) and little sagebrush (*Artemisia arbuscula* Nutt.) were found on exposed ridges. Other common shrub species in the study sites included alderleaf mountain mahogany (*Cercocarpus montanus* Raf.), antelope bitterbrush (*Purshia tridentata* (Pursh) DC.), chokecherry (*Prunus virginiana* L.), common snowberry (*Symphoricarpos albus* (L.) S.F. Blake), greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.), rabbitbrush (genus *Chrysothamnus* Nutt.), goldenbush (genus *Ericameria* Nutt.), Saskatoon serviceberry (*Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roem.), and spiny hopsage (*Grayia spinosa* (Hook.) Moq.). Isolated stands of juniper (genus *Juniperus* L.) and quaking aspen (*Populus tremuloides* Michx.) were found at the higher elevations on north-facing hillsides.

Sage-Grouse capture and monitoring

From 2008 to 2011, we monitored Sage-Grouse hen survival during late spring and summer (May through August). Hens were captured, radio-collared, and released in April of each year. We captured hens at night using ATVs, spotlights, and hoop-nets (Giesen et al. 1982; Wakkinen et al. 1992; Connelly et al. 2003) and fitted them with 17.5 or 22 g (<1.5% body mass) necklace radio collars (model RI-2D, Holohil Systems Ltd., Carp, Ontario, Canada, or model A4060, Advanced Telemetry Systems Inc., Isanti, Minnesota, USA). Collars were equipped with motion sensors (pulse rate of transmitter increased after 8 h without bird movement), which allowed us to detect deaths from a distance. We aged Sage-Grouse hens at the time of capture as yearlings or ≥2 years of age by examining outer primaries feathers (Patterson 1952). Institutional Animal Care and Use Committees from the University of Wyoming (protocol No. 03032009) and Utah State University (protocol No. 1357) approved protocols to capture, handle, and mark female Sage-Grouse in southern Wyoming.

We visually located hens weekly with VHF receivers (model R-1000, Communications Specialists, Orange, California, USA), and located and monitored nests with three-way Yagi antennas

(Communications Specialists, Orange, California, USA). To assess the effects of parental investment on survival, we classified Sage-Grouse hen status as nesting, brooding, or nonreproductive each week (hen status was a surrogate for differences in parental investment). Potential nests were identified with binoculars from approximately 15 m by circling a radio-marked hen until she was visually spotted under a shrub. Nests were verified by triangulating the hen under the same shrub from ≥50 m away or thoroughly searching the area of the potential nest when the hen was absent. After 1 July, we continued to visually locate brooding hens weekly, whereas nonreproductive hens were visually located at least biweekly. We identified brood hens by either visually detecting chicks or observing hen behavior that indicated the presence of a brood (e.g., hesitation to flush, feigning injury, or clucking). We classified a Sage-Grouse hen as a brood hen if there was evidence of at least one chick with that hen. A nonreproductive hen was a hen that never nested, her nest failed, or her brood failed. We reclassified a brooding hen as nonreproductive when we did not detect evidence of a brood during two consecutive telemetry visits. The reproductive status of an individual Sage-Grouse hen was reassessed every time a hen was visually located. We documented Sage-Grouse hen survival with telemetry equipment from a distance when a visual location was not possible, and telemetry signal from a distance was used as often as possible to identify date of death; thus, a live or dead signal for most Sage-Grouse was obtained >1 per week.

Sage-Grouse behavior variables

We used visual Sage-Grouse locations to record minimum flock size and minimum weekly movements. Both of these metrics were collected as indicators of exposure to predation. The minimum flock size each week was recorded as the number of adult Sage-Grouse near (within approximately 50 m^2) a radio-collared hen including the radio-collared hen. We considered this count a minimum flock size, because there were probably individuals that were not detected during each count. We assumed that any detection bias was random and equally likely to have occurred at all Sage-Grouse locations, which made the count of flock size relative. Flock size was averaged across all visits for each individual hen during a summer, because we did not know the flock size at a hen's time of death. Mean flock size was assumed to be related to a hen's preferential flock size, with higher mean values describing a hen's tendency to flock in larger groups. We calculated movement distances between a Sage-Grouse's sequential locations using Geospatial Modeling Environment version 0.7.1.0 (Spatial Ecology LLC, Marshfield, Wisconsin, USA) and ArcMap version 10.0 (ESRI (Environmental Systems Research Institute) Inc., Redlands, California, USA). We standardized movement distance between sequential visits to minimum weekly movement distances by dividing each distance between telemetry locations by the number of days that had elapsed between telemetry locations, we then averaged all weekly movement distances for each Sage-Grouse. This produced a minimum distance, because exact Sage-Grouse movements between telemetry locations were unknown.

Raptor variables

From 1 May to 1 August of each year, we conducted point-count surveys at random locations to calculate mean annual densities of raptors at the study-site level. We followed the point-count protocol described in Dinkins et al. (2012) and Dinkins (2013). All raptor variables were calculated from the raw count data within program DISTANCE estimated effective detection radii (EDR) as specified in Dinkins et al. (2012) and Dinkins (2013). Study-site-level density of Golden Eagles, Buteonine Hawks, and Harriers were individually calculated within 1000, 450, and 350 m, respectively, of each random point-count location within a study site (for further details see Dinkins et al. 2012 and Dinkins 2013).

We had noted through observation that relative annual changes in raptor densities within many study sites seemed to have positive or negative effects on survival of Sage-Grouse. We attributed this phenomenon to the possibility of raptors being more or less effective predators of Sage-Grouse depending on the study site owing to the overall characteristics of a particular study site (combination of individual raptor behavior, topographic roughness, large-scale cover, anthropogenic development, etc.). In addition to study-site-level raptor densities, we calculated site-specific exposure to raptor densities—from random point-count locations—as the increase or decrease in study-site-level raptor density (annual density) relative to the raptor density in a particular study site at the beginning of the study (2008). Thus, site-specific exposure to raptor density was 0 for all study sites in 2008. These variables were intended to look at relative change in risk of predation within each study site (i.e., does site-specific increase or decrease of raptor densities affect survival of Sage-Grouse). Thus, site-specific exposures to raptor densities were not quantifying the effect of the exact density of raptors on survival of Sage-Grouse among all study sites. Rather, they were assessing site-specific change in exposure to raptors.

Anthropogenic and landscape feature variables

We calculated Sage-Grouse proximity to anthropogenic features that could be used as perch or nest sites by raptors or could provide food subsidies with ArcMap version 10.0. Anthropogenic structures that were >2 m in height were considered available for perching or nesting by raptors. We quantified the distance from Sage-Grouse locations to the nearest oil and gas structure (energy well, compressor station, transfer station, refinery, or other energy-extraction-related buildings), major road, all road types, communication tower, house, and power line for each Sage-Grouse location. Major roads included paved, improved gravel roads, and railroads, whereas all road types included major roads and all unimproved four-wheel-drive roads. Most (>95%) oil and gas structures were energy wells. In addition to proximity variables, we calculated the density of oil and gas structures (no./km), major roads (km/km^2), all road type (km/km^2), houses (no./km), and power lines (km/km^2). Density variables were calculated within four radii from Sage-Grouse locations (0.27, 0.54, 1, and 3 km radii). Ongoing energy development was occurring in half of our study sites, which required us to assess the dates that energy-related structures and roads were added or removed from the landscape.

In distance and density calculations, we only included oil and gas structures and roads that were physically on the ground when each Sage-Grouse was located. We obtained information on oil and gas structures, including date construction started on the structure and date when wells were plugged and abandoned (date structure was removed), from the Wyoming Oil and Gas Conservation Commission (WOGCC 2012). We verified the spatial location and existence of older structures with color aerial satellite imagery from summer 2006 and August 2009 obtained from the National Agriculture Imagery Program (NAIP; U.S. Department of Agriculture (USDA) 2010). Aerial imagery from NAIP is produced by the USDA on a 3 year rotation; thus, we used WOGCC data and on the ground GPS units to map energy development that occurred after August 2009. However, energy development reported to WOGCC after August 2009 had better reporting of location, spud date, and plug abandon date.

We used 2009 NAIP imagery to digitize the location of major roads, all road types, communication towers, and houses within a 5 km buffer around study sites; roads constructed between August 2009 and September 2011 were mapped on the ground with GPS units. All transmission and distribution power lines within a 5 km buffer around the study sites were mapped on the ground with GPS units; telephone lines not associated with a power line were included in the power-line mapping.

Similar to anthropogenic features, landscape features could be used as perches or nest structure by raptors, or could be areas with higher productivity that attract predators. Thus, we used ArcMap version 10.0 to calculate the distance from every Sage-Grouse location to forested (deciduous and conifer stands) and riparian habitats. In addition to distance variables, we calculated the proportion of forested, riparian, and big sagebrush habitats around Sage-Grouse locations. Forested (stands of trees), riparian, and big sagebrush habitats were identified with Northwest ReGAP landcover data from 2011 (Lennartz 2007) and verified with NAIP imagery from 2009. Topography with greater surface roughness has the potential to create topographic structures (e.g., hilltops, knolls, and cliff edges) that provide vantage points similar to perches. For every Sage-Grouse location, we used ArcMap version 10.0 to extract topographic ruggedness index (TRI) values generated by Hanser et al. (2011) for the Wyoming Basins Ecoregion. Riley et al. (1999) created TRI to describe the roughness of landscapes and the index is quantified as the difference in elevation among adjacent pixels of a digital elevation map; the index is then averaged over a user defined area. Forested, riparian, and big sagebrush habitats and TRI variables were developed using a moving window analysis at 0.27, 0.54, 1, and 3 km radii (0.23, 0.92, 3.14, and 28.26 km^2 scales, respectively).

Statistical analysis

We analyzed Sage-Grouse hen survival with the Anderson–Gill formulation of the Cox proportional hazard (Cox PH) model using function “coxph” in package SURVIVAL version 2.36-14 in R version 2.14.2 (R Core Team 2009). Cox PH models are robust semiparametric models that are commonly used to analyze time-to-event data (Cox 1972), such as survival obtained from telemetry. The risk of death (hazard ratio: $h(t|x_t)$) is a function of the nonparametric baseline hazard ($h_0(t)$) and the parametric covariates (x values) affecting survival (Hosmer and Lemeshow 2000), with the Cox PH equation expressed as

$$h(t|x_t) = h_0(t) \times \exp(\beta_1 x_{i1} + \beta_2 x_{i2} + \beta_k x_{ik})$$

Coefficient values were expressed as hazard of death; thus, positive values would be associated with greater risk of death and lower survival.

Data can be left-censored for individuals entering the study at different times and right-censored for individuals that did not die during the study. In Cox PH models, fixed (time-independent) and time-dependent covariates can be fit to assess their effect on survival (Hosmer and Lemeshow 2000). The baseline hazard is allowed to vary with time in Cox PH and time-dependent variables are included by constructing time intervals between visits for each unique individual (Therneau and Grambsch 2000). However, covariates in Cox PH models are assumed to have proportional hazard of death over time (proportional hazard assumption; Hosmer and Lemeshow 2000). Thus, we used function “cox.zph” in package SURVIVAL in R (Therneau and Grambsch 2000) to test the proportional hazard assumption for each covariate in all models. In addition, we generated leverage plots and calculated df$_\beta$ and variance inflation factors (VIF) to evaluate if any observations were influential or multicollinearity was present; no observations were omitted as a result of high influence. We prevented multicollinearity by not including any two variables that covaried in any Cox PH model ($r > 0.65$) as determined with a Pearson’s correlation matrix; thus, we eliminated one covarying variable from further analysis by retaining the variable that made the most biological sense.

We constructed weekly time intervals for each individual Sage-Grouse hen by calculating the day that corresponded to halfway between each time that we located a Sage-Grouse. The time scale for constructing time intervals was defined as $t = 0$ on 1 May each year. Unless date of death could be more accurately assessed by evidence from a carcass, date of death was estimated as the time equal to halfway between the last date the hen was known to be alive and the date death was detected. We did not include survival data collected directly after radio-collaring, because survival may have been affected by trapping stress or the bird adjusting to the collar (Winterstein et al. 2001); this excluded four birds from analyses. There were approximately 118 days of exposure time for each Sage-Grouse per summer (i.e., summer survival was assessed from $t = 0$ to $t = 118$, which corresponded from 1 May to 26 August, respectively).

Study-site-level raptor densities or site-specific exposure to densities of raptors were defined as fixed variables by year, because raptor variables were quantified as annual densities (across an entire summer) at the study-site level. Anthropogenic and landscape features were incorporated as time-dependent variables (allowed to change each week), because the effect of these variables on survival was likely different depending on the bird’s location relative to these features, which changed as the bird moved through its environment over time. Reproductive status of Sage-Grouse (hen status) was incorporated as a time-dependent variable with the status reassessed each week. When a hen died, the status from the previous visual observation was attributed to the last survival interval, which was consistent with assigning death to halfway between the last date the hen was known to be alive and the date death was detected. Changes in status from nesting or brooding to nonreproductive were not likely to have bias because Sage-Grouse hens have low rates of nest and brood abandonment. In addition, we did not extend a nesting status with a death past approximately 25 days, which is a shorter timeframe than the 28 day incubation period of Sage-Grouse. There may have been instances where a nesting hen died before we detected her on a nest. These quickly depredated nests were likely to be the most vulnerable nests to depredation. For this reason, we classified our hen status variable as (*i*) potential nester (hens not observed on a nest during the nesting season until 21 days before the last hatched nest—first 1.5 months of the nesting season), (*ii*) late nonreproductive (all birds not on a nest or with a brood after 15 June), (*iii*) known to be nesting, and (*iv*) known to be brood-rearing. The potential nester status corresponded to Sage-Grouse that either did not initiate a nest or lost a nest quickly. Most Sage-Grouse hens initiate nests (Connelly et al. 2011; Taylor et al. 2012); thus, our potential nester status represented general nesting season survival with a combination of deaths while incubating, potentially initiating a nest, or nonreproductively active.

Modeling of Sage-Grouse survival was conducted with an information–theoretic approach (Anderson 2008). We compared Cox PH models with Akaike’s information criterion corrected for small sample sizes (AIC$_c$) and Akaike weights (w_i) (Burnham and Anderson 2002) with function “aictab” in package AICCMODAVG version 1.25 in R. We employed sequential AIC$_c$ modeling of covariate sets, which was suggested by Arnold (2010) as an appropriate approach for identifying and ranking the most parsimonious models. Noninformative covariates (85% confidence intervals (CI) of parameter estimates overlapped 0) were eliminated within each covariate set before comparing top AIC$_c$-selected models among covariate sets (Arnold 2010). Four covariate sets were evaluated sequentially: (1) raptor variables, (2) anthropogenic features, (3) landscape features, and (4) Sage-Grouse behavior. Cox PH models with raptor variables were compared as single variable models for each raptor species individually with AIC$_c$ to choose which type (study-site level or site-specific exposure density) of raptor variable fit the data best; thus, the raptor variable type with the lowest AIC$_c$ was used in all further modeling. We evaluated the effect of a Sage-Grouse’s age (AGE) on survival within the Sage-Grouse behavior covariate set. We included raptor variables × anthropogenic structure variables and raptor variables × landscape feature variables as pairwise interactions within anthropogenic and landscape feature covariate sets. Pairwise interactions with raptor variables were included to assess whether negative effects of raptor variables were intensified in areas closer to potential perches or nest structure or in areas closer to natural or human-provided food subsidies. We compared individual Cox PH models of density, proportion, and TRI variables measured at 0.27, 0.54, 1, and 3 km radii with AIC$_c$ to choose the best spatial scale for each density, proportion, and TRI variable to be used in the anthropogenic and landscape feature covariate sets. The best scale for each density, proportion, and TRI variable was used in all further modeling. As the final modeling step, we compared all top AIC$_c$-selected models from every covariate set among each other and as additive models with combinations of all four covariate sets.

The effects of Sage-Grouse behavior on survival in relation to raptors and anthropogenic and landscape features had to be analyzed as two separate Cox PH analysis steps. The sequential modeling procedure described above was applied to both Cox PH analyses. In "analysis 1" (parental investment analysis), we evaluated parental investment (hen status) with raptors and anthropogenic and landscape features by using all Sage-Grouse locations (nesting, brooding, and roosting locations). However, we excluded potential antipredation behaviors (mean weekly movement and mean flock size) from "analysis 1" model building, because all variables that potentially described an antipredation behavior were constant for two of three of the parental investment categories (nesting and brooding). In "analysis 2" (antipredation strategy analysis), we used nonreproductive locations to evaluate the effects of weekly movements and mean flock size with raptors and anthropogenic and landscape features on Sage-Grouse survival. Mean flock size was compared as a linear and quadratic variable in the Sage-Grouse behavior covariate set to assess the possibility of an optimal flock size (flock size where survival was the greatest). In "analysis 2", we included an interaction between mean flock size and AGE to assess if yearling Sage-Grouse in larger flocks had higher survival.

Although we could not test for spatial autocorrelation in Cox PH analyses, raptor densities derived from distance sampling techniques are robust to lack of independence of observation locations because distance sampling is set up to be a snapshot in time (Thomas et al. 2010). Our raptor sampling was designed to count the greatest proportion of raptors within a study site each week while not counting the same raptor more than once per week as suggested by Ralph et al. (1995) and Thomas et al. (2010). Conducting all point counts within a study site in 1 day reduced the possibility of double-counting individual raptors during that week's visit. Counting the same individual raptor during different weeks, regardless of the particular point-count location, was properly scaled by accounting for survey effort. Replication of point counts by sampling multiple weeks was done to increase the proportion of raptors detected as suggested by Thomas et al. (2010). Furthermore, raptor variables were averaged by study site and year; thus, the lowest unit of measurement was raptor density by study site. Time-dependent variables for Cox PH analyses were not subject to spatial autocorrelation, because Cox PH treats each time interval as a separate observation (Hosmer and Lemeshow 2000).

Results

During 2008–2011, we captured 427 Sage-Grouse hens that were included in our Cox PH analyses because they were available to monitor (i.e., they did not go missing or die within 2 weeks of radio-collaring). There were 132, 162, 156, and 165 Sage-Grouse hens in 2008, 2009, 2010, and 2011, respectively; thus, 50, 76, and 69 Sage-Grouse hens survived into subsequent years 2009, 2010, and 2011, respectively. From 1 May to 31 August, we found 88 Sage-Grouse hen deaths (22 nesting, 19 brooding, and 47 nonreproductive Sage-Grouse), which yielded estimated summer (May–August) mean survival of 0.83 (SE = 0.3; 95% CI = 0.77 to 0.89) and nesting season (May–June) mean survival of 0.86 (SE = 0.04; 95% CI = 0.78 to 0.95). There were 3523 weekly time intervals for analyzing survival (402 nesting, 817 brooding, and 2304 nonreproductive locations). We monitored 380 nesting Sage-Grouse and 162 brooding Sage-Grouse.

The distance to houses and forested habitat were highly correlated ($r = 0.73$) and distance to forested habitat fit the data better than distance to houses; thus, we included distance to forested habitat in models instead of distance to houses. The proportional hazards assumption was not violated for any model. All predictor variables had VIF ≤ 2, which indicated that the variances of coefficient values were not drastically increased by the inclusion of any predictor variable; thus, collinearity was not a problem (Hair et al. 1995).

To evaluate the effect of raptor densities on Sage-Grouse survival, we conducted 2948 point-count surveys during 2008–2011 at 660 random point-count locations. We counted 252 Golden Eagles, 138 Buteonine Hawks, and 57 Harriers within species-specific EDRs (Dinkins et al. 2012; Dinkins 2013). Neither study-site level nor site-specific exposure to Golden Eagle, Buteonine Hawk, and Harrier densities had individual effects on Sage-Grouse summer survival (all main effects of raptor densities had 85% CIs that overlapped 0). Mean study-site-level Golden Eagle, Buteonine Hawk, and Harrier densities at Sage-Grouse death locations were 2.22 per 100 km^2 (SE = 0.03 per 100 km^2), 7.66 per 100 km^2 (SE = 0.90 per 100 km^2), and 6.41 per 100 km^2 (SE = 0.74 per 100 km^2), respectively, compared with 1.91 per 100 km^2 (SE = 0.05 per 100 km^2), 7.02 per 100 km^2 (SE = 0.14 per 100 km^2), and 6.59 per 100 km^2 (SE = 0.13 per 100 km^2), respectively, at live Sage-Grouse locations. Variables describing site-specific exposure to raptor densities fit the data better than study-site-level densities of raptors; thus, we used site-specific exposure to raptor densities in interactive models.

We found that models with anthropogenic, landscape, and Sage-Grouse behavior variables described summer Sage-Grouse survival best for both parental investment and antipredation analyses. In the parental investment analysis, we found that the top AIC$_c$-selected Cox PH model included AGE, Sage-Grouse hen status (potential nester, nesting, brooding, or nonreproductive), density of all road types at the 0.54 km scale (road density$_{0.54}$), power-line density at the 1 km scale (power-line density$_{1.0}$), distance to forested habitat, proportion of big sagebrush at the 0.27 km scale (sagebrush$_{0.27}$), and site-specific exposure to golden eagles × TRI at the 0.27 km radius (TRI$_{0.27}$), which had $w_i = 0.94$ (Table 1). The top AIC$_c$-ranked antipredation strategy analysis included mean flock size, quadratic effect of flock size, AGE, AGE × mean flock size, gravel-road density at the 0.27 km scale (gravel-road density$_{0.27}$), power-line density$_{1.0}$, distance to forested habitat, sagebrush$_{0.27}$, and site-specific exposure to Golden Eagles × TRI$_{0.27}$, which had $w_i = 0.89$ (Table 1).

Higher survival of Sage-Grouse hens was associated with greater road density$_{0.54}$ or gravel-road density$_{0.27}$ in the parental investment analysis and antipredator strategy analysis, respectively, while lower survival was associated with greater power-line density$_{1.0}$ (Tables 2, 3; Figs. 1, 2). Distance to forested habitat, sagebrush$_{0.27,}$ and power-line density$_{1.0}$ were relatively imprecise predictors (parameters were informative in modeling, but estimates had overlapping 95% CI) for the parental investment analysis, whereas distance to forested habitat and gravel-road density$_{0.27}$ were imprecise predictors in the antipredator strategy analysis (Tables 2, 3). Locations where Sage-Grouse died had a mean of 1.42 km/km^2 (SE = 0.14 km/km^2) road density$_{0.54}$, 0.11 km/km^2 (SE = 0.05 km/km^2) gravel-road density$_{0.27}$, and 0.05 km/km^2 (SE = 0.02 km/km^2) power-line density$_{1.0}$, whereas locations of live Sage-Grouse had 1.94 km/km^2 (SE = 0.02 km/km^2) road density$_{0.54}$, 0.35 km/km^2 (SE = 0.01 km/km^2) gravel-road density$_{0.27}$, and 0.02 km/km^2 (SE = 0.00 km/km^2) power-line density$_{1.0}$. Survival of Sage-Grouse hens

Table 1. Model comparison of Cox proportional hazard (Cox PH) models from the parental investment and antipredator strategy analyses.

Models*	k	AIC$_c$	ΔAIC$_c$	w_i	Deviance
Parental investment					
AGE, status, GOEA × TRI$_{0.27}$, forest distance, sagebrush$_{0.27}$, road density$_{0.54}$, power-line density$_{1.0}$	11	1043.27	0.00	0.94	1021.20
AGE, status, GOEA × TRI$_{0.27}$, forest distance, sagebrush$_{0.27}$	9		5.57	0.06	1030.78
AGE, status, road density$_{0.54}$, power-line density$_{1.0}$	6		10.99	0.00	1042.24
GOEA × TRI$_{0.27}$, forest distance, sagebrush$_{0.27}$, road density$_{0.54}$, power-line density$_{1.0}$	7		16.69	0.00	1045.94
GOEA × TRI$_{0.27}$, forest distance, sagebrush$_{0.27}$	5		20.07	0.00	1053.32
AGE, status	4		21.16	0.00	1056.42
Road density$_{0.54}$, power-line density$_{1.0}$	2		27.94	0.00	1067.22
Null	0		36.64	0.00	1079.90
Antipredation strategy					
Flock^2, flock × AGE, GOEA × TRI$_{0.27}$, forest distance, sagebrush$_{0.27}$, gravel-road density$_{0.27}$, power-line density$_{1.0}$	11	486.70	0.00	0.89	464.58
Flock^2, flock × AGE, GOEA × TRI$_{0.27}$, forest distance, sagebrush$_{0.27}$	9		4.14	0.11	472.76
Flock^2, flock × AGE, gravel-road density$_{0.27}$, power-line density$_{1.0}$	6		16.09	0.00	490.74
GOEA × TRI$_{0.27}$, forest distance, sagebrush$_{0.27}$, gravel-road density$_{0.27}$, power-line density$_{1.0}$	7		20.02	0.00	492.68
Flock^2, flock × AGE	4		23.53	0.00	502.22
GOEA × TRI$_{0.27}$, forest distance, sagebrush$_{0.27}$	5		24.84	0.00	501.52
Fully saturated	25		28.11	0.00	464.24
Gravel-road density$_{0.27}$, power-line density$_{1.0}$	2		38.87	0.00	521.56
Null	0		48.27	0.00	534.96

Note: Models assessed the effects of four covariate sets including spatially standardized densities of raptors, anthropogenic features, landscape features, and Greater Sage-Grouse (*Centrocercus urophasianus*) behavior on Sage-Grouse hen survival. Models were compared with Akaike's information criterion adjusted for small sample sizes (AIC$_c$) and Akaike weights (w_i). Data were collected from eight study sites (each 16 km diameter) and four study sites (each 24 km diameter) in southern Wyoming, USA. A total of 427 Sage-Grouse hens were monitored during 2008–2011. Variables included in the final Cox PH model selection were Sage-Grouse age (AGE), Sage-Grouse parental investment status (status), mean flock size (flock), quadratic of mean flock size (flock^2), density of any road type within 0.54 km radius (road density$_{0.54}$), gravel-road density within 0.27 km radius (gravel-road density$_{0.27}$), power-line density within 1.0 km radius (power-line density$_{1.0}$), site-specific exposure to Golden Eagle (*Aquila chrysaetos*) density (GOEA), topographic ruggedness index within 0.27 km radius (TRI$_{0.27}$), distance to forested habitat, and proportion of big sagebrush (*Artemisia* spp.) within 0.27 km radius (sagebrush$_{0.27}$).

*Models with interaction terms included all individual variables within the interactions.

Table 2. Parameter estimates of Greater Sage-Grouse (*Centrocercus urophasianus*) survival from the top Akaike's information criterion adjusted for small sample sizes (AIC$_c$) selected Cox proportional hazard (Cox PH) model with *P* values and 95% confidence intervals (CI).

					95% CI	
Variable	Estimate	SE	Z	*P*	Lower	Upper
AGE	−0.71	0.30	−2.42	0.02	−1.29	−0.14*
Status potential nester†	1.79	0.50	3.58	<0.00	0.81	2.77*
Status nesting‡	1.50	0.47	3.20	<0.00	0.58	2.43*
Status brooding§	0.90	0.33	2.72	0.01	0.25	1.55*
GOEA	0.14	0.09	1.65	0.10	−0.03	0.31
TRI$_{0.27}$	0.01	0.01	0.51	0.60	−0.01	0.03
GOEA × TRI$_{0.27}$	−0.01	0.00	−2.74	0.01	−0.02	−0.00*
Forest distance	−0.07	0.05	−1.50	0.13	−0.17	0.02
Sagebrush$_{0.27}$	−0.83	0.58	−1.43	0.15	−1.96	0.30
Road-density$_{0.54}$	−0.22	0.09	−2.62	0.01	−0.39	−0.06*
Power-line density$_{1.0}$	0.89	0.60	1.50	0.13	−0.28	2.05

Note: Data for parental investment analysis using a Cox PH model were collected from eight study sites (each 16 km diameter) and four study sites (each 24 km diameter) in southern Wyoming, USA, during 2008–2011. A total of 427 Sage-Grouse hens were monitored during 2008–2011. Variables included in the top AIC$_c$-selected Cox PH model were Sage-Grouse age (AGE), Sage-Grouse parental investment status (status), density of any road type within 0.54 km radius (road density$_{0.54}$), power-line density within 1.0 km radius (power-line density$_{1.0}$), site-specific exposure to Golden Eagle density (GOEA), topographic ruggedness index within 0.27 km radius (TRI$_{0.27}$), distance to forested habitat, and proportion of big sagebrush (*Artemisia* spp.) within 0.27 km radius (sagebrush$_{0.27}$).

*A 95% CI that does not include zero.

†Sage-Gouse survival comparing potential nester to nonreproductive hens.

‡Sage-Grouse survival comparing nesting to nonreproductive hens.

§Sage-Grouse survival comparing brooding to nonreproductive hens.

Table 3. Parameter estimates of Greater Sage-Grouse (*Centrocercus urophasianus*) survival from the top two Akaike's information criterion adjusted for small sample sizes (AIC$_c$) selected Cox proportional hazard (Cox PH) models for antipredation strategy analysis with *P* values and 95% confidence intervals (CI).

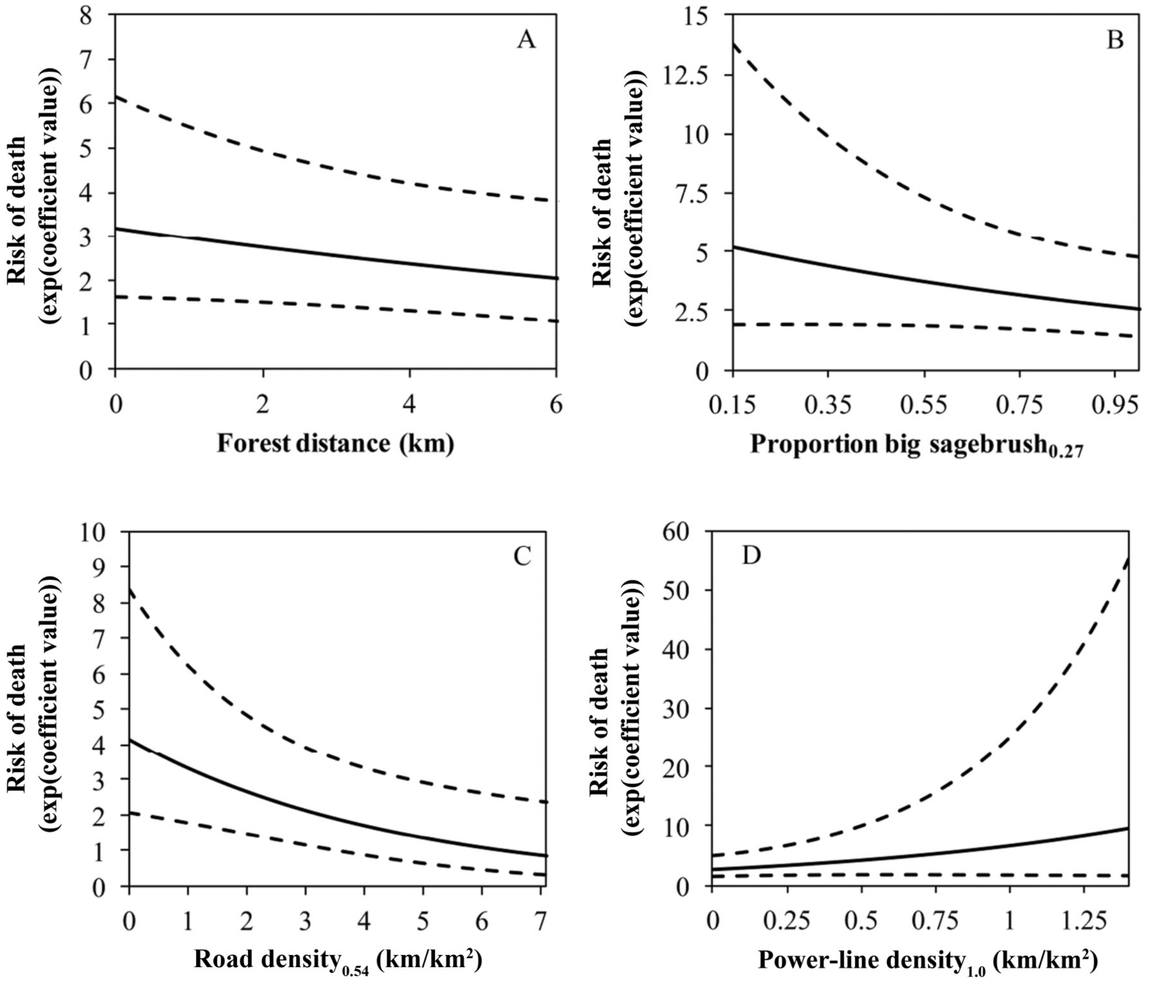
					95% CI	
Variable	Estimate	SE	Z	*P*	Lower	Upper
Flock	−0.55	0.18	−3.09	<0.01	−0.90	−0.20*
Flock^2	0.03	0.01	2.77	0.01	0.01	0.05*
AGE	0.73	0.77	0.94	0.35	−0.79	2.25
Flock × AGE	−0.64	0.45	−1.43	0.15	−1.51	0.24
GOEA	0.12	0.11	1.12	0.26	−0.09	0.32
TRI$_{0.27}$	0.01	0.01	0.98	0.33	−0.01	0.04
GOEA × TRI$_{0.27}$	−0.01	0.00	−1.87	0.06	−0.01	0.00
Forest distance	−0.16	0.08	−1.89	0.06	−0.32	0.01
Sagebrush$_{0.27}$	−2.23	0.85	−2.63	0.01	−3.89	−0.57*
Gravel-road density$_{0.27}$	−0.51	0.35	−1.49	0.14	−1.19	0.16
Power-line density$_{1.0}$	1.44	0.55	2.61	0.01	0.36	2.52*

Note: Data were collected from eight study sites (each 16 km diameter) and four study sites (each 24 km diameter) in southern Wyoming, USA, during 2008–2011. A total of 427 Sage-Grouse hens were monitored during 2008–2011. Variables included in the top two AIC$_c$-selected Cox PH models were Sage-Grouse age (AGE), mean flock size (flock), quadratic of mean flock size (flock^2), gravel-road density within 0.27 km radius (gravel-road density$_{0.27}$), power-line density within 1.0 km radius (power-line density$_{1.0}$), sitespecific exposure to Golden Eagle density (GOEA), topographic ruggedness index within 0.27 km radius (TRI$_{0.27}$), distance to forested habitat, and proportion of big sagebrush (*Artemisia* spp.) within 0.27 km radius (sagebrush$_{0.27}$).

*A 95% confidence interval that does not include zero.

was positively associated with locations farther away from forested habitat and greater sagebrush$_{0.27}$ (Tables 2, 3; Figs. 1, 2). Death locations of Sage-Grouse were a mean of 2.00 km (SE = 0.26 km) away from forested habitat compared with 2.87 km (SE = 0.05 km) for locations of live Sage-Grouse. Mean proportion of sagebrush$_{0.27}$ at locations where Sage-Grouse died was 0.79 (SE = 0.02) compared with 0.84 (SE = 0.00) at locations where Sage-Grouse were seen alive. Our results from anthropogenic and landscape variables indicated that risk of death for Sage-Grouse hens was greater relative to potential perches (power-line density$_{1.0}$ and distance to forested habitat) but not relative to anthropogenic features that could provide food subsidies for predators.

Fig. 1. Predicted effects (solid lines) with 95% confidence intervals (broken lines) from the parental investment analysis of (A) distance to forested habitat (deciduous and conifer), (B) proportion of big sagebrush (genus *Artemisia*) within 0.27 km, (C) density of all road types within 0.54 km, and (D) power-line density within 1 km on Greater Sage-Grouse (*Centrocercus urophasianus*) hen survival. Predicted effects displayed as the risk of death with the *y*-axis units plotted as exp(coefficient values). All other parameters were held at their mean values. Data from 427 Sage-Grouse hens were collected from eight study sites (each 16 km diameter) and four study sites (each 24 km diameter) in southern Wyoming, USA, during 2008–2011.



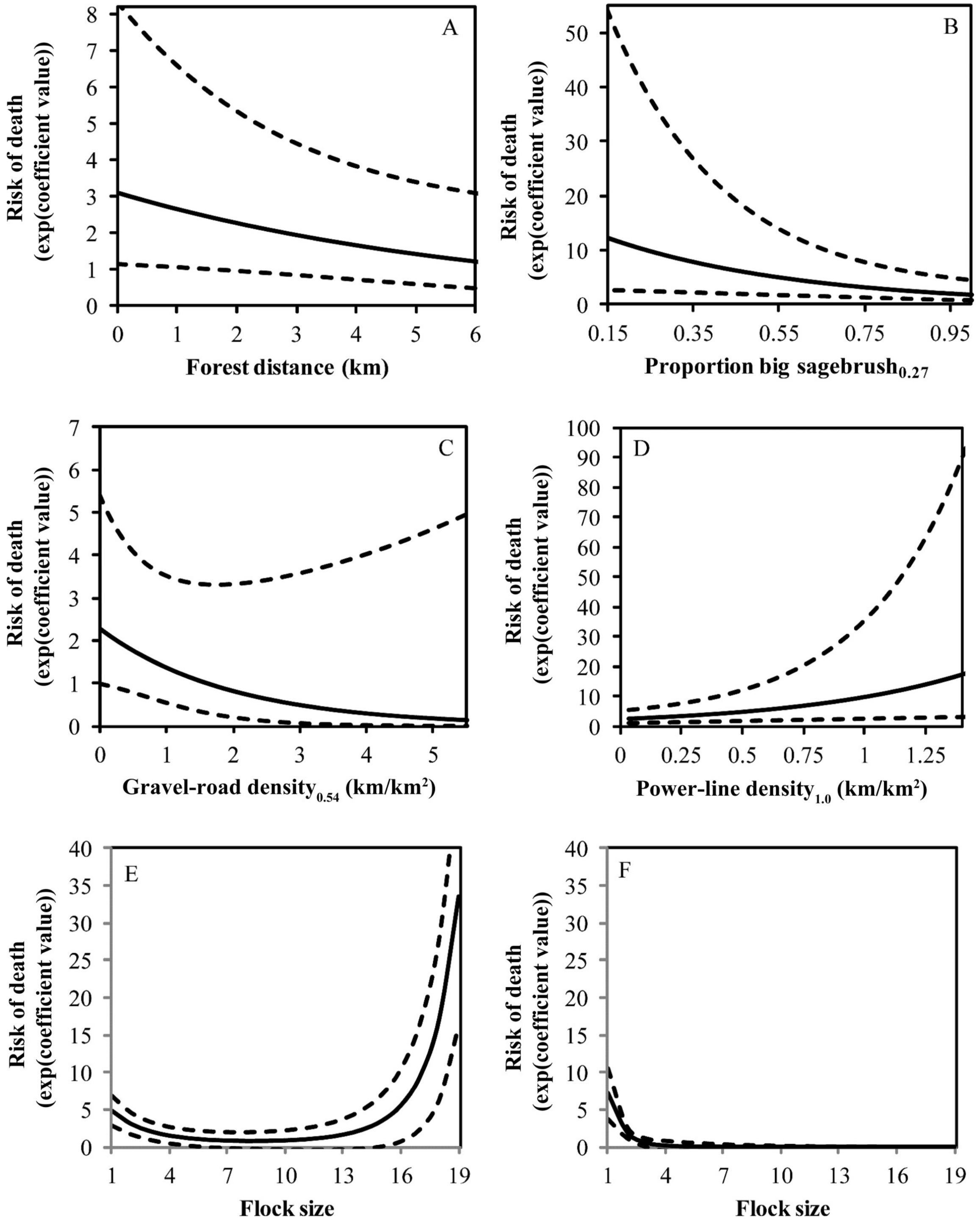
Even though raptor density variables did not independently describe Sage-Grouse survival, we found that the interaction between site-specific exposure to Golden Eagle density and $TRI_{0.27}$ was explanative of Sage-Grouse summer survival for both parental and antipredator strategy analyses (Tables 2, 3). Site-specific exposure to Golden Eagle density was negatively associated with Sage-Grouse summer survival only when taking $TRI_{0.27}$ into context. When site-specific exposure to Golden Eagle density was relatively high and Sage-Grouse were in areas with more rugged terrain, we found that the negative effects of site-specific exposure to Golden Eagle density and $TRI_{0.27}$ were dampened (Fig. 3). Higher $TRI_{0.27}$ values were correlated with lower Sage-Grouse summer survival when site-specific exposure to Golden Eagle density was low, and greater site-specific exposure to Golden Eagle density was associated with lower Sage-Grouse survival in flatter areas (Tables 2, 3; Fig. 3).

For variables describing the effect of Sage-Grouse behavior on Sage-Grouse summer survival, odds ratios indicated that potential nester, nesting, and brooding hen statuses, respectively, were 5.97 (95% CI = 2.24 to 15.91), 4.50 (95% CI = 1.79 to 11.31), and 2.46 (95% CI = 1.29 to 4.71) times more likely to die compared with the nonreproductive Sage-Grouse hen status in the parental investment analysis (Table 2). In the antipredation strategy analysis, we found that nonreproductive adults that flocked in intermediate numbers had higher survival (Table 3; Fig. 2E); thus, Sage-Grouse hens in small flocks (by themselves or another hen) and large flocks had lower summer survival. Top AIC_c-ranked Cox PH models for both parental investment and antipredator analyses included AGE. However, yearling Sage-Grouse hens had higher survival (parameter estimate = –0.71; SE = 0.30; 95% CI = –1.29 to –0.14) in the parental investment analysis and no difference in the main effect of AGE for the antipredator analysis (parameter estimate = 0.73; SE = 0.77; 95% CI = –0.79 to 2.25). In the antipredation strategy analysis, we also found the AGE × mean flock size interaction was marginally informative, which indicated yearlings that, on average, chose to flock in greater numbers had greater survival compared with adults (i.e., when a yearling hen was in a flock of >3 birds; Table 3; Fig. 2F).

Discussion

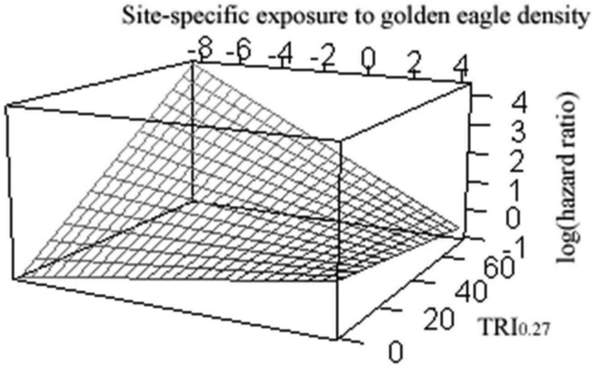
Anthropogenic variables had mixed effects on survival of Sage-Grouse hens, whereas effects of landscape variables aligned with expectations. Breeding season survival of Sage-Grouse hens was positively associated with the proportion of big sagebrush and road density and negatively associated with power-line density,

Fig. 2. Predicted effects (solid lines) with 95% confidence intervals (broken lines) from the antipredation strategy analysis of (A) distance to forested habitat (deciduous and conifer), (B) proportion of big sagebrush (genus *Artemisia*) within 0.27 km, (C) gravel-road density within 0.54 km, (D) power-line density within 1 km, and (E) mean flock size of adult Greater Sage-Grouse (*Centrocercus urophasianus*) hens, and (F) mean flock size of yearling Sage-Grouse hens on hen survival. The top Akaike's information criterion adjusted for small sample size (AIC_c) selected model included a quadratic of mean flock size and an interaction between flock size and Sage-Grouse age (adult or yearling). Predicted effects displayed as risk of death with the *y*-axis units plotted as exp(coefficient values). Data from 427 Sage-Grouse hens were collected from eight study sites (each 16 km diameter) and four study sites (each 24 km diameter) in southern Wyoming, USA, during 2008–2011.



close proximity to forested habitat, topographic ruggedness, and site-specific exposure to Golden Eagle density (only in flatter habitat). The positive effect of greater proportions of big sagebrush on Sage-Grouse survival indicated areas with more contiguous sagebrush were better for Sage-Grouse survival. Greater sagebrush cover was connected to chick survival of Sage-Grouse in Oregon, USA (Gregg and Crawford 2009); Sage-Grouse hen survival was higher with greater variability in shrub height (Kirol 2012); and proportion of intact sagebrush habitat has been widely recognized as the most important component to long-term viability of

Fig. 3. Interactive effect of site-specific exposure to Golden Eagle (*Aquila chrysaetos*) density and topographic ruggedness index at 0.27 km radius ($TRI_{0.27}$) on Greater Sage-Grouse (*Centrocercus urophasianus*) hen survival (as a hazard ratio depicting risk of death) from the antipredation strategy analysis. All other parameters were held at their mean values. Data from 427 Sage-Grouse hens were collected from eight study sites (each 16 km diameter) and four study sites (each 24 km diameter) in southern Wyoming, USA, during 2008–2011.



Sage-Grouse populations (Aldridge et al. 2008; Connelly et al. 2011). Likewise, Brewer's Sparrows, Sage-Grouse, Sagebrush Sparrows, and Sage Thrashers (*Oreoscoptes montanus* (Townsend, 1837)) are highly dependent on sagebrush-dominated habitat (Knick et al. 2005). Abundance and occupancy of Brewer's Sparrows, Green-tailed Towhees (*Pipilo chlorurus* (Audubon, 1839)), and Sage Thrashers were positively related to greater sagebrush cover within 100 m or proportion of sagebrush within 1 km in Oregon (Noson et al. 2006).

It was possible that distance variables associated with time intervals when deaths occurred were biased because of a predator moving a Sage-Grouse carcass. However, we did not find summer deaths with evidence of drastic predator movements (>1 km) and Sage-Grouse carcasses were typically found close to the last location where the Sage-Grouse was known to be alive. For example, Sage-Grouse killed while nesting were found, on average, 0.38 km from their nests (an area that hens likely used during foraging bouts), and only 2 out of 22 (9%) were found >1 km away from their nest.

Previous research has shown that most Sage-Grouse deaths in the spring and summer can be attributed to predation (Connelly et al. 2011; Blomberg et al. 2013*a*), but other possible sources of death include collisions with vehicles, fences, and power lines (Braun 1998; Connelly et al. 2000*a*, 2004; Beck et al. 2006; Blomberg et al. 2013*a*) and the West Nile virus (Naugle et al. 2004; Walker et al. 2007; Walker and Naugle 2011). We did not find evidence of any Sage-Grouse colliding with a fence or power line (no carcasses near fences or under power lines). West Nile virus was not likely to have killed many birds in this study, because West Nile virus was not known to be prominent in our study sites during this study (Walker and Naugle 2011). In addition, deaths from West Nile virus usually occur from July to mid-September (Walker et al. 2007; Walker and Naugle 2011), and we only found 17 out of the 88 deaths after 5 July. Sage-Grouse survival has been documented to be lowest from March to June and relatively higher after July (Connelly et al. 2011; Walker and Naugle 2011; Blomberg et al. 2013*b*); thus, the timing of deaths in our study coincided with typical Sage-Grouse summer survival.

Terrain roughness has been negatively correlated with summer survival of adult female Sage-Grouse in south-central Wyoming (Kirol 2012). Similarly, we found moderate support for lower Sage-Grouse survival when Sage-Grouse were exposed to high values of $TRI_{0.27}$ when site-specific exposure to Golden Eagle density was low. Golden Eagles in sagebrush habitat selected areas with more rock outcrops and cliffs in southern Idaho (Marzluff et al. 1997). Thus, we hypothesized that rugged terrain would be riskier habitat for Sage-Grouse and high raptor densities would intensify this effect because hilltops, knolls, and cliff edges associated with rugged terrain would act as perch or nesting structure for raptors. Contrary to our hypothesis, we found that the negative effects of $TRI_{0.27}$ and site-specific exposure to Golden Eagle density were dampened by the combination of greater rugged terrain and high site-specific exposure to Golden Eagle density (Fig. 3). Two potential explanations for this finding include (1) rugged topography may provide some refugia from visual predators (e.g., Golden Eagles), because topographic features such as slight depressions may decrease the effective distance that a raptor can detect a Sage-Grouse on the ground and (2) greater abundance of Golden Eagles in rugged topography (risky habitat) may competitively exclude other predators. Golden Eagles and coyotes (*Canis latrans* Say, 1823) are known to be the top predators in sagebrush ecosystems (Mezquida et al. 2006; Hagen 2011) and the presence of Golden Eagles may reduce the hunting efficiency of mammalian predators via indirect interactions among predators (Mezquida et al. 2006); however, this is an untested hypothesis. Dinkins (2013) found that nesting and brooding Sage-Grouse from this study selected locations with lower topographic ruggedness compared with the landscape at random, which has been verified by other Sage-Grouse research (Doherty et al. 2010; Dzialak et al. 2011, Hanser et al. 2011; Kirol 2012); thus, Sage-Grouse avoid extremely rugged terrain. The moderately rugged topography (relative to the landscape) where Sage-Grouse had higher mortality rates may have been correlated to greater risk of predation from olfactory predators (mammalian predators), which have been known to hunt in areas such as drainage bottoms (Conover 2007). Clearly, interactive effects among raptors and habitat attributes need more study to assess potential mechanisms, and our potential explanations are largely speculative.

Other landscape features such as forested and riparian habitats have the potential to pose a higher risk of predation for Sage-Grouse (Aldridge and Boyce 2007; Casazza et al. 2011; Baruch-Mordo et al. 2013), and Sage-Grouse avoidance of forested habitat, especially pinyon (genus *Pinus* L.) – juniper, has been documented (Atamian et al. 2010; Doherty et al. 2010; Casazza et al. 2011). Sagebrush-obligate songbirds (Brewer's Sparrow, Sagebrush Sparrow, and Sage Thrasher) have lower abundance in areas with pinyon–juniper encroachment (Knick et al. 2005; Noson et al. 2006), and nest survival of Brewer's Sparrows was lower in areas with greater tree density (Welstead 2002). Low levels of juniper encroachment were connected to greater inactivity at leks in eastern Oregon, which represent a population-level negative effect of forested habitat on Sage-Grouse (Baruch-Mordo et al. 2013), but there has been little research looking at the impact of proximity to forested habitat on Sage-Grouse survival. The proportion of pinyon–juniper woodland in the home range of a Sage-Grouse was not connected to fall survival in Nevada, USA (Sedinger et al. 2011). In contrast, our results suggested that proximity to forested habitat was negatively related to breeding season and summer survival of Sage-Grouse hens. Although distances to forested habitat and rural houses were highly correlated, distance to forested habitat predicted survival better than distance to rural houses.

Several studies have demonstrated that Sage-Grouse avoid habitat with man-made features, such as oil and gas infrastructure (Aldridge and Boyce 2007; Holloran 2005; Doherty et al. 2008; Kirol 2012; Dinkins 2013), power lines (Hanser et al. 2011; Dinkins 2013), and roads (Holloran 2005; Aldridge and Boyce 2007; Dzialak et al. 2011; Dinkins 2013), which are potential perches or nest structure for raptors or provide reliable food subsidies. Annual survival of adult female Sage-Grouse was lower in a natural gas field (Holloran 2005), greater surface disturbance was negatively correlated with brood survival (Kirol 2012), and collisions with vehicles are known to cause Sage-Grouse deaths (Braun 1998). Thus, we hypothesized that Sage-Grouse survival would be lower near anthropogenic features and that this effect would be amplified when there were also high densities of raptors. Greater density of power lines represented riskier habitat, but we did not find support for interactive effects of raptors and any anthropogenic features. Opposite of our expectation, hen survival was higher with greater density of roads. Similarly, proximity to anthropogenic edge, including roads, has been found to be positively correlated with adult female survival (Kirol 2012), which Kirol (2012) suggested may be related to roads disproportionately located in less rugged topography (i.e., flatter locations with higher Sage-Grouse survival).

Behaviors associated with parental investment and antipredation strategies have the potential to influence survival rates of animals. Increased experience, quantified as age, should also be positively correlated with survival. Yet, there has been mixed results with higher yearling survival compared with adults in Colorado (Zablan et al. 2003) and Wyoming (Holloran 2005), no age-related effects on survival in Montana, USA (Moynahan et al. 2006), or Utah (Baxter et al. 2013), and higher survival of adults ≥2 years of age compared with yearlings in Nevada (Blomberg et al. 2013*a*). Yearling Sage-Grouse hens have been documented to initiate nests and renest less often than adult hens (Connelly et al. 1993; Holloran 2005; Moynahan et al. 2007). We found similar results with 56% and 60% apparent nest initiation for yearling and adult hens, respectively, and 11 out of 14 renesting events were from adult hens. Adult Sage-Grouse hens have higher nest success compared with yearlings, which indicates that adults are more likely to have a brood (Connelly et al. 2011). We found broods with 19% and 30% of yearling and adult Sage-Grouse hens, respectively, and we found Sage-Grouse hens that were nesting or brooding had lower survival than hens outside of the nesting season without a brood (Table 2). Thus, yearling Sage-Grouse hens may have had higher survival, because they were less likely to be incubating or tending a brood.

Similar to our results, reproductive effort (both nesting and raising chicks) imparted costs on future survival of Sage-Grouse in Nevada (Blomberg et al. 2013*b*). Although the cost of reproductive effort on future survival is similar, we examined the probability that a Sage-Grouse would die during the nesting season or while caring for chicks. In contrast to Blomberg et al. (2013*b*) and our hen status results, Moynahan et al. (2006) and Baxter et al. (2013) found Sage-Grouse that initiated a nest in Montana and Utah, respectively, had higher survival than non-nesting hens. They attributed their findings to better physical condition of nesters versus non-nesters, increased visibility of non-nesting hens, or both. The apparent inconsistency with these studies and our results most likely arises from differences in analyses. Moynahan et al. (2006) and Baxter et al. (2013) compared survival (annual or monthly) of hens that had initiated a nest within a summer versus hens that did not initiate a nest within a summer, which did not allow them to compare survival of hens on a nest versus hens not on a nest during the nesting season. Neither of these studies were capable of including nests where the hen died before an observer detected the hen nesting, which may have biased their sample of nests to proportionally more hatched nests (possibly less susceptible to predation); thus, confounding their nesting hen survival results. On the other hand, we allowed the nesting status (nesting, brooding, or nonreproductive) of each hen to change weekly with a time-dependent Cox PH variable; thus, we assigned each death to a time-dependent breeding status.

Our results from the antipredation strategy analysis suggested that survival was greater for nonreproductive hens that stayed in intermediate size flocks (Fig. 2E). We did not find higher survival of yearlings versus adults when comparing survival of only nonreproductive hens (i.e., the main effect of AGE was not significant; Table 3), and yearling hen survival was connected to mean flock size (interaction AGE × mean flock size; Tables 1, 3). In fact, survival of yearling Sage-Grouse hens was lower than adults when yearlings were in flocks of less than three grouse, on average (Fig. 2F). However, the interaction between AGE and mean flock size indicated that yearlings that chose to stay in larger groups had higher survival, although this interaction was an imprecise predictor (95% CI overlapped 0; Tables 1). Medium-sized flocks may have had higher survival compared with small or large flocks, because small and large flocks could represent increased risk of predation. Small flocks could decrease the benefits of sentinel behavior (i.e., Sage-Grouse detecting a predator) and the dilution effect, whereas large flocks could increase a predator's probability of detecting a flock of Sage-Grouse and thereby increasing exposure to predation. The dilution effect predicts that an individual in a larger flock will have a lower probability of being eaten. Intermediate flock sizes would allow individual Sage-Grouse to benefit from the dilution effect and sentinel behavior, while having a lower probability of a predator detecting the flock compared with larger flocks. We found support for an optimally sized flock of 3–14 birds for nonreproductive Sage-Grouse (Fig. 2E).

Raptors including Golden Eagles, Buteonine Hawks, and Harriers have been identified as significant threats to Sage-Grouse survival (Schroeder et al. 1999; Schroeder and Baydack 2001). However, we did not find any independent negative effects of raptor densities on Sage-Grouse survival, even in conjunction with anthropogenic features. This may be attributed to Sage-Grouse avoiding raptors and anthropogenic features; negative effects of high raptor densities may also have been masked by other spatiotemporal processes such as weather. Dinkins et al. (2012) found that nesting and brooding Sage-Grouse avoided raptors, and many researchers have found Sage-Grouse also avoid risky habitats (Aldridge and Boyce 2007; Doherty et al. 2008, 2010; Dzialak et al. 2011; Hanser et al. 2011; Kirol 2012). There was moderate support for a negative association with Golden Eagles in flatter habitats. This interaction also illustrated a dynamic interaction where areas with rugged topography—which has been associated with lower Sage-Grouse survival—could have higher Sage-Grouse survival when there was relatively greater site-specific Golden Eagle density.

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