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Research Article

Cougar Survival and Source-Sink Structure on Greater Yellowstone's Northern Range

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ABSTRACT We studied survival and causes of mortality of radiocollared cougars (*Puma concolor*) on the Greater Yellowstone Northern Range (GYNR) prior to (1987–1994) and after wolf (*Canis lupus*) reintroduction (1998–2005) and evaluated temporal, spatial, and environmental factors that explain variation in adult, subadult, and kitten survival. Using Program MARK and multimodel inference, we modeled cougar survival based on demographic status, season, and landscape attributes. Our best models for adult and independent subadults indicated that females survived better than males and survival increased with age until cougars reached older ages. Lower elevations and increasing density of roads, particularly in areas open to cougar hunting north of Yellowstone National Park (YNP), increased mortality risks for cougars on the GYNR. Indices of ungulate biomass, cougar and wolf population size, winter severity, rainfall, and individual characteristics such as the presence of dependent young, age class, and use of Park or Wilderness were not important predictors of survival. Kitten survival increased with age, was lower during winter, increased with increasing minimum estimates of elk calf biomass, and increased with increasing density of adult male cougars. Using our best model, we mapped adult cougar survival on the GYNR landscape. Results of receiver operating characteristic (ROC) analysis indicated a good model fit for both female (area under the curve [AUC] = 0.81, 95%CI = 0.70–0.92, $n = 35$ locations) and male cougars (AUC = 0.84, 95%CI = 0.74–0.94, $n = 49$ locations) relative to hunter harvest locations in our study area. Using minimum estimates of survival necessary to sustain the study population, we developed a source-sink surface and we identify several measures that resource management agencies can take to enhance cougar population management based on a source-sink strategy. © 2011 The Wildlife Society.

KEY WORDS cougar, infanticide, elevation, Greater Yellowstone Northern Range, Program MARK, *Puma concolor*, road density, source-sink dynamics, survival, wolf.

Cougars (*Puma concolor*) are considered habitat generalists and their broad distribution is a testament to their ability to persist in a variety of habitats that provide adequate cover and prey (Cougar Management Guidelines Working Group [CMGWG] 2005). Nonetheless, habitat quality may vary spatially and temporally and affect cougar survival and production. Ultimately, survival of individuals and population resiliency may be strongly influenced by various factors including land use (i.e., roads, livestock, homes), management through hunting and depredation removal, and likely by competition with other carnivores (Murphy 1983, Torres et al. 1996, Creel et al. 2001, CMGWG 2005, Schwartz et al. 2010). Across western North America, large areas of contiguous habitat support cougar populations managed primarily through sport hunting within hunting districts, game management units (GMU), or data analysis units (DAU), except where harvest is prohibited, such as in California (California Wildlife Protection Act of 1990, CMGWG 2005). Management with sport hunting typically identifies areas where cougars are targeted for population reduction in hopes of increasing prey populations, reducing conflicts with humans, or for stable population growth while providing sport hunting opportunity (CMGWG 2005, Stoner et al. 2006). Within this management structure parks and wilderness are often assumed to function as refugia and

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source habitats for cougars, yet those areas may not always operate in such a manner (CMGWG 2005). The difficulties associated with monitoring cougar populations has challenged management at landscape scales and biologists' understanding of factors that explain variation in survival and other population characteristics of cougars (Stoner et al. 2006).

Cougars immigrate and emigrate via dispersal that strongly influences population dynamics and regional source-sink structures (Sweanor et al. 2000, Robinson et al. 2008). Furthermore, cougar movements within their large annual home ranges potentially overlap boundaries of state management units and refuges such that individuals might not reside exclusively in either source or sink habitats. Recently, the CMGWG (2005) suggested mapping habitat and landscape features and managing subpopulations of cougars using source and sink structure that may or may not conform to delineated boundaries of GMUs or DAUs. Such an approach acknowledges large movements of individual cougars and incorporates habitat heterogeneity: a local demographic surplus arises in good quality habitats (source), and a local demographic deficit (sink) occurs in habitats of poor quality or in high quality habitats that pose high risk of death (attractive sinks or ecological traps; Dias 1996, Delibes et al. 2001, Robinson et al. 2008). Thus, the source-sink model implies that some habitat patches may be more important to the long-term survival of a cougar population and alterations of the availability of source habitat could greatly affect production and survival in other nearby habitats (Pulliam and Danielson 1991). An understanding of source-sink dynamics requires not only identifying quality habitats but also identifying risks that influence production and survival in various habitats (see Schwartz et al. 2010).

Accurate characterization of local populations in different habitats as sources or sinks and their relative contributions to the larger population (i.e., metapopulation) at a landscape level is important in an increasingly fragmented world (Runge et al. 2006). In the Greater Yellowstone Ecosystem (GYE), rural residential development is increasing rapidly because of the area's natural amenities (Hansen et al. 2002). People attracted to lands surrounding reserves may impact natural buffers and alter ecological process within reserves (Hansen et al. 2002). Several authors have noted the combined effects of roads, hunters, and conflicts with humans along reserve boundaries, which have contributed significantly to the extinctions of large carnivores, particularly in small reserves (Woodroffe and Ginsberg 1998, Revilla et al. 2001, Sunquist and Sunquist 2001, Woodroffe 2001). Competition with wolves (*Canis lupus*) reintroduced in 1995 and 1996 may also influence and affect cougar behaviors, survival, movements, and habitat use in the GYE. Because wolves are pack animals, and tend to be dominant in direct interactions, wolf reestablishment may alter the behavior and population dynamics of cougars (Ruth 2004*a*,*b*). Wolves kill cougars and steal their kills, and cougars show avoidance of wolves (Ruth 2004*a*,*b*; Kortello et al. 2007). Thus, associated energetic costs from these interactions may affect cougar reproductive and survival rates. Whether wolf reestablishment influences vital rates of sympatric cougars has not been documented, yet is relevant to cougar management and conservation in many western states.

Although numerous authors have examined survival rates of hunted and non-hunted cougar populations, none have used probabilistic analyses to examine temporal, spatial, and environmental factors that explain variation in survival and constructed a map of survival at a landscape scale (Beier and Barrett 1993, Logan and Sweanor 2001, Lambert et al. 2006, Stoner et al. 2006, Robinson et al. 2008). We studied survival and mortality of radiocollared cougars on the Greater Yellowstone Northern Range (GYNR) prior to and after wolf-reintroduction. Our objectives were to: 1) estimate and use survival rates to assess the effect of wolf reintroduction on cougar survival on the GYNR, 2) identify individual, temporal (i.e., environmental), and spatial (i.e., landscape) factors that explain variation in adult, subadult, and kitten survival, and 3) use estimates of survival that incorporate landscape heterogeneity to construct a source-sink surface that allows managers to evaluate probability of cougar survival on the GYNR.

STUDY AREA

We conducted our study on the GYNR, Montana, and Wyoming, including the northern range and adjacent backcountry areas in Yellowstone National Park (YNP), the adjoining Absaroka-Beartooth Wilderness, and the Gardiner Basin north of YNP (3,779 km^2). Fifty-seven percent of the study area fell within the northern range of YNP with the remainder of the study area to the north of the YNP boundary. Elevations increase from west to east from 1,500 m to >2,400 m (Despain 1990, Cook et al. 2004). Vegetation was primarily grassland and sagebrush steppe at lower elevations, dominated by Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and big sagebrugh (*Artemesia tridentata*; Despain 1990). At higher elevations, conifer forest of Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) covered about 41% of the northern range (Houston 1982, Wright et al. 2006). Mean annual precipitation varied from 24 cm in the Gardiner basin to 35 cm in the upper Lamar River valley (Coughenour and Singer 1996) with average monthly temperatures ranging from -12° C to 13° C. Vegetation, climate, and geology of the area were described in detail by Houston (1982) and Despain (1990).

The GYNR was occupied year-round by cougars prior to and after wolf reintroduction in 1995–1996 (Murphy 1998). A cougar hunting season occurred in Montana outside the north boundary of YNP. Hunting season length was December through February during 1987–2000 and was extended to December through April in winter 2000–2001. Our study area overlapped Montana hunting unit 313 and the southern portion of unit 314. Hunter-killed cougars were sexed and age-estimated by Montana Department of Fish, Wildlife and Parks (MDFWP) Wildlife Laboratory (Aune and Schladweiler 1995). During 1988–2005, 55% of annual hunter harvest in these units occurred in the north portion of our study area and averaged 1.4 (range 0–2) adult females (≥3 yr old) and 0.6 (range 0–1) yearling–subadult females (1–2 yr old) per year. During the same time span, annual hunter harvest averaged 1.8 (range 0–3) adult males (≥3 yr old) and 0.9 (range 0–1) yearling–subadult males (1–2 yr old).

Wolves were protected under the Endangered Species Act, which allowed no hunting of wolves except for lethal removal following livestock depredation (Bangs and Fritts 1996). Grizzly bears (*Ursus arctos*), black bears (*U. americanus*), and coyotes (*C. latrans*) were sympatric with cougars and wolves on the GYNR.

Five ungulate species inhabited the northern range. Elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) were the most abundant ungulate prey for cougars and wolves (Murphy 1998). Minimum counts of elk and mule deer ranged between 9,400–19,000 and 1,600–2,500, respectively, prior to wolf reintroduction (1987–1994; Lemke et al. 1998, Murphy 1998). After wolf reintroduction (1998–2005), elk and deer numbered 8,300–14,500 and 1,600–2,300, respectively (Eberhardt et al. 2007, Cross 2009). Moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), and pronghorn (*Antilocapra americana*) were also documented as prey for cougars (Murphy 1998). Bison (*Bison bison*) numbered 2,000–4,000 but were not cougar prey (Murphy 1998). Wolves also preyed on moose, bison, and pronghorn (Smith et al. 2005, Smith and Bangs 2009).

METHODS

Cougar population characteristics were quantified pre-wolf (PW) reintroduction (1987–1994; Murphy 1998) and during wolf (DW) reestablishment (1998–2005) on the GYNR. We estimated population size and density of independent cougars during winter by surveying for cougar tracks in snow while traversing non-overlapping transects (approx. 1,500 km each winter during both PW and DW) and through intensive efforts to capture cougars ($\bar{x} = 228$ person-days/5 months winter during PW and 226 person days/4–5 months winter during DW) following Murphy (1998). Although cougars were constrained to winter range during months with snow, there was some movement across the study boundary. Thus, estimates represented the minimum number of cougars that used the study area.

Using trained hounds we captured and collared adult, independent subadult, and dependent kitten cougars (see individual covariates below) in and adjacent to YNP. Cougar capture and handling procedures followed Logan et al. (1986) and Quigley (2000) and were approved by the Hornocker Wildlife Institute/Wildlife Conservation Society Animal Care and Use Committee (no. 1998-YCW-502) and YNP (research permit no. YELL-SCI-0039). We backlogged cougars into the winter population and estimated proportion of adults marked each year using percent accuracy methods of Logan and Sweanor (2001). We radiomarked an estimated 77% of adult cougars by winter 1988–1989 during the PW study with 87–94% radiomarked in all subsequent years until the final year of study. We radiomarked an estimated 68% and 88% of adult cougars present in the DW study by winters 2000–2001 and 2001–2002, respectively, with 88–93% radiomarked in all subsequent years until the final year of study.

When possible, we ear tagged and radio-collared kittens at the den at 4.5–8.5 weeks of age following procedures described by Logan and Sweanor (2001). We generally captured kittens not marked during this time frame during the first winter after birth at 4–8 months of age. We radio-collared 57–78% of PW kittens and 60–70% of DW kittens prior to 3.5–4.8 months of age.

We estimated ages of cougars with unknown birthdays and >9 weeks of age by tooth development and wear, body weight, neck measurements, pelage characteristics, and gum-line recession (Ashman et al. 1983, Murphy 1998, Anderson and Lindzey 2000, Laundré et al. 2000). We fitted subadult collars with a biodegradable canvas spacer that ensured collar drop after dispersal and kitten collars were designed to expand to the neck size of adult cougars. All transmitters had a motion sensor that increased pulse rate if stationary for 4–6 hr, allowing for detection of mortalities and dropped collars. In addition to a Very High Frequency (VHF) mortality sensor, Global Positioning Satellite (GPS) collars we used during the DW study recorded the date and time the radio collar became stationary.

We located or monitored cougars for a mortality signal with radio telemetry every 1–5 days from the ground and every 7–14 days from an airplane. We investigated a site the day of or day following reception of the mortality signal unless another carnivore was present at the site, in which case we waited until the carnivore was no longer detected at the area. We determined causes of mortality through visual inspection of carcasses and through necropsies performed both in and out of the field. Necropsies were occasionally performed by a veterinarian in a laboratory. Pathology of tissue and blood samples was conducted by the Montana Veterinary Diagnostic Laboratory, Bozeman, Montana, USA or the Wyoming Game and Fish Laboratory, Laramie, Wyoming, USA.

We located cougars from close proximity (generally 100–300 m) and used tree cover and topography and assessed direction of air currents to avoid disturbing cougars as we took ≥3 compass bearings. Our telemetry error averaged 33 m (SD = 81) for 863 ground-based locations. Mortalities and dropped collars that were located aerially and investigated by site searches from the ground had average aerial telemetry error of 161.7 m (SD = 216.0, *n* = 41) in the PW study and 156.8 m (SD = 121.1, *n* = 21) in the DW study. Similar to Schwartz et al. (2010), pixel size accounted for telemetry error for some spatial layers. Although distance measurements were influenced by telemetry error, the overall magnitude should not have affected results (i.e., even with telemetry error, locations close to escape habitat would still have a small value compared to those that were distant).

Survival Analysis

We used Program MARK and the known fate data type to estimate mean survival and investigate the influence of covariates on survival (White and Burnham 1999, Haroldson et al. 2006). We converted radio-location records into monthly encounter histories for each cougar in each year monitored during both study phases (White and Burnham 1999). Because no cougars died as a result of capture, availability began at the date of capture and continued through the end of the year, a change in reproductive status (from non-maternal to maternal or vice versa) for females, a change in age class (from subadult to adult), or until the cougar died or was censored. We followed methods of Haroldson et al. (2006) and censored data from an individual beginning with the day after its last location if time between telemetry locations exceeded 60 days. The median number of days between successive locations was 6 days ($\bar{x} = 7.4$, SD $= 8.1$) across both study phases. We assigned cougars that died a death date based on the median day between the last location and the date we received the mortality signal. Excluding hunter-killed cougars, we estimated the average number of hours between the last location and date of death at 65.8 hr (SD = 86.2, range = 4–336).

We defined a study area boundary for the survival analysis based on the 95% fixed kernel home range (Hawth's Analysis Tools for ArcGIS®, www.spatialecology.com/htools/, accessed 15 Aug 2005) for the combined location set of all adults monitored in both phases. We did not include in the analysis independent subadults that dispersed beyond the study area because we monitored them infrequently and often obtained no locations until their death. Additionally, we removed adult or independent cougars that moved beyond the defined study area boundary permanently or for periods >60 days for those time frames they were outside the boundary.

We analyzed kitten survival separately from adult and independent subadult cougar survival. Because we assumed each kitten record to be an independent random sample, we used data bootstrap analyses to evaluate if the distribution of mortalities among litter sizes was random and estimated the overdispersion parameter ($\hat{c}$) following methods of Bishop et al. (2008). We used Program MARK to run the bootstrap analysis with 10,000 replicate datasets generated by resampling litter size (1, 2, 3, and 4) with replacement. We used our most parameterized model and the mean value of individual covariates in the bootstrap procedure. The bootstrap option generated a mean and standard deviation of 10,000 survival estimates and we compared standard deviations of the replicate estimates with the theoretical standard errors obtained from our original kitten survival estimates. The ratio of the empirical (i.e., bootstrap) variance to the theoretical variance provided the estimate of overdispersion, $\hat{c}$. Following Bishop et al. (2008), we considered $1.0 < \hat{c} \leq 1.2$ as weak evidence of overdispersion. We used $\hat{c}$ to adjust the quasi-likelihood estimate for kitten survival in Program MARK.

Covariate Selection

We developed separate a priori sets of individual and temporal covariates hypothesized to affect survival for the 2 distinct age groups of 1) adults and independent subadults and 2) dependent kittens. We selected covariates after discussions with carnivore experts and from published information on cougars (see Tables S1 and S2 available online at www.onlinelibrary.wiley.com) and other large carnivores in North America (grizzly bears: Haroldson et al. 2006; Schwartz et al. 2006, 2010; wolves: Mech et al. 1988, Mladenoff et al. 1995, Smith and Bangs 2009).

Individual covariates.—We assigned each cougar individual covariates including sex, age class, and age (Tables S1 and S2). We included a quadratic term, age plus age^2, in some models because, similar to grizzly bears, we expected cougar survival to increase with age and then decline at older ages (Johnson et al. 2004). After we attributed locations with individual covariates, we calculated the mean value of attributes for all telemetry locations for each cougar each year (seasonal or annual); mean values for binomial covariates represented the proportion of locations in the area of interest (Schwartz et al. 2010). We then used mean values as individual covariates in the Program MARK input file.

We identified cougars as resident adults when they bred or reached the average age of known breeders in the population and showed fidelity to a home area (Logan and Sweanor 2001). Independent subadult cougars were pre-breeding and pre-dispersal age cougars that were immigrants to the study area or individuals that separated from their mother but remained within the study area (Logan and Sweanor 2001). Kittens were dependent on and generally remained with their mother (Logan and Sweanor 2001) between an average (SD) of 12.8 (3.2; PW) months and 17.1 (3.2; DW) months of age unless they were orphaned. One male and 2 female kittens in the PW study were separated from their mother at approximately 9.6 to 10.8 months old and remained as independent subadults on the study area. As a consequence, we included them as independent, pre-dispersal subadults, which resulted in overlap in independent, pre-dispersal ages and dependent kitten ages between our 2 survival analyses. We classified kittens orphaned prior to 9 months of age as dependent and included them in the kitten survival analysis. We assigned adult female cougars an additional covariate to indicate absence (0) or presence (1) of dependent offspring.

Reproductive rates of animals frequently improve with age due to changes in experience at breeding or raising young (see Clutton-Brock 1988). To evaluate the effect of a mother's age, thus increased experience, on survival of dependent young, we attributed each kitten year with the mean age of their mother in years.

Female cougars can give birth to young in all months of the year (Anderson 1983), yet numerous studies report a peak in births, often referred to as a birth pulse (Murphy et al. 1999, Logan and Sweanor 2001). Logan and Sweanor (2001) hypothesized that kittens born during the birth pulse of July–September would have increased survival. Laundré and Hernández (2007) found a greater number of litters were born during July–September, yet those authors did not find support for the hypothesis. We evaluated the effect of kitten birth during 2 pulses appropriate for our data set: a primary birth peak of May–July (35 of 59 litters documented in PW and DW) and a secondary birth peak of September–October. We compared alternative models that included only the primary birth peak (Bpeak1) against those that included the primary through secondary birth peak (Bpeak2) of May–October (53 of 59 litters). We additionally evaluated whether Julian birth days of kittens would affect survival and predicted survival would be low earlier in the year, increase around peak birth months, and decline for births later in the year. Thus we included a quadratic term (Julbirth^2) in some models.

After reintroduction, the wolf population increased from 48 wolves/1,000 km^2 to a peak of 106 wolves/1,000 km^2 on the northern range of YNP between 1995 and 2003 (Smith et al. 2005, 2006). We evaluated the effect of increasing wolf density on cougar survival by comparing models with a temporal covariate of wolf density/1,000 km^2 per year with those that included an individual spatial covariate that indexed wolf density through intensity of wolf use. For each yearly season (e.g., winter 2001; winter: 1 Nov–30 Apr, snow free: 1 May–31 Oct) we generated 95% utilization distribution (UD) grids (30 × 30 m cell size) from the locations of all radio-collared wolves using Hawth's Analysis Tools with least-squares cross-validation bandwidth values. Regression analyses indicated that the number of radio collared wolves per pack was a good indicator of pack size over each year ($F = 131.83$, $P = 0.000$, $R^2 = 0.78$), thus high UD values occurred in areas with more wolves and reflected spatial variability in wolf use across the landscape. We then scaled each yearly seasonal UD by the number of wolves present to capture variability in the wolf population across seasons and years. We attributed cougar locations with the wolf use value for the matching date.

We evaluated the influence of landscape characteristics such as cover, elevation, and elk winter range on cougar survival (Tables S1 and S2). We calculated the average minimum distance (in meters) to either tree cover or areas of high topographic roughness, whichever was closest in any direction, as an index of escape terrain (index ranged from 0 to 100 with zero indicating flat and 100 indicating greatest heterogeneity in elevation; Ruth et al. 2003). We evaluated the impact of annual and seasonal elevation on cougar survival and attributed all telemetry locations with elevation (km) using 1:24,000-scale digital elevation models from the United States Geological Survey (USGS 2005).

In northern latitudes, cougars follow migrating elk to winter ranges of limited spatial extent, resulting in increased spatial overlap between predator and prey (Murphy 1998, Pierce et al. 1999). Increased access to prey on winter range could have positive influences on cougar survival. However, cougar and wolf overlap increases during winter as both carnivores seek access to prey on winter range (Ruth 2004*a*). Wolf detection of cougar-killed prey and movements of cougars away from high wolf activity may have energetic costs that reduce survival (Ruth 2004*b*, Kortello et al. 2007). The Northern Yellowstone winter range has long been defined by a static boundary based on winter distribution of elk (Houston 1982, Lemke et al. 1998). To investigate the effect of cougar use of elk winter range during winter, we attributed telemetry locations as in or out of elk winter range and then calculated the proportion of locations a cougar was in winter range for intervals entered in the survival analysis (Johnson et al. 2004).

Few if any cougar populations are untouched by human influences because few protected areas are big enough that cougars, with their large home ranges, are able to completely avoid humans (Beier et al. 2010). Based on findings for grizzly bears and hunted cougars, we hypothesized that measures of human disturbance help explain spatial heterogeneity of cougar survival (Table S1, Murphy 1983, Schwartz et al. 2010). For each cougar during each year, we calculated the proportion of telemetry locations inside YNP and the Absaroka-Beartooth Wilderness. Although hunting occurred in the Wilderness, few roads and deep snows during winter limited access and no cougars were removed from the Wilderness during the PW or DW studies (R. DeSimone, MDFWP, unpublished data).

Because the density of open and closed roads affect the probability that houndsmen will detect a cougar track and reach a treed cougar, road access increases the vulnerability of cougars to hunters during the cougar hunting season (Murphy 1983, Barnhurst 1986, Murphy 1998). We evaluated the impact of roads on cougar survival by comparing covariates of average annual and seasonal distance to roads (km), average annual total road density, and average total road density in hunt areas during the cougar hunting season. We calculated road density following Schwartz et al. (2010) using a thematic layer of motorized routes from the Cumulative Effects Model (CEM) database for the GYE created by the Interagency Grizzly Bear Study Team (IGBST; Schwartz et al. 2010). We based total motorized route density (TMRD) on all roads including those that were open, restricted (administrative access only), and closed to all motorized vehicular access. We attributed telemetry locations with annual and seasonal total road density at 2 scales using a 17 × 17-pixel (roaded 30-m cells/500 m^2, Trdann17) moving window and a 54 × 54-pixel (roaded 30-m cells/2.59 km^2, Trdann54) moving window (Table S2 available online at www.onlinelibrary.wiley.com). We used the estimated average length of road of 25.8 m per cell as found by Schwartz et al. (2010) and converted lengths to kilometers of road/km^2 when discussing road densities. Because all roads provide increased access for hunters during winter, we used TRMD to calculate the average density of roads for individual cougars in hunt areas (Hunttrd17 and Hunttrd54) during the cougar hunting season. Finally, we measured distance from each telemetry point to the nearest road (km).

To evaluate the influence of secure habitat on cougar survival (Tables S1 and S2), we attributed telemetry locations as in or outside of secure habitat and then calculated mean values for each cougar (annual and seasonal) as the proportion of locations in secure habitat. We compared this measure of security against the remoteness index from Merrill et al. (1999). We attributed locations with the remoteness index (0 to 1 floating decimal with 1 being most remote) and then calculated annual and seasonal mean values for each cougar. We compared the amount of secure habitat and remote habitat to alternative models that included road density.

Since 1970, the human population in the 21 counties surrounding the GYE has grown by >60% with the current form of development consisting of large lot rural subdivisions (Hernandez 2004, Schwartz et al. 2010). We used a map of home distribution on private lands across 20 counties surrounding the GYE from Hernandez (2004) and which was updated to include incorporated cities and town sites by Schwartz et al. (2010). We used attribute fields for total homes present in 1990 and 2000 to assign housing estimates to telemetry data from the PW and DW studies, respectively. We attributed each telemetry location with the total number of homes within a 2.59 km^2 cell.

Temporal covariates.—We included phase (PW or DW), density of cougars and wolves, biomass of prey, climactic factors, and season (winter or summer) as temporal covariates (Tables S1 and S2). We used minimum population counts based on radio-marked individuals and tracks of unmarked individuals as an index to minimum population size each winter. We estimated summer population size each year by assuming that a new independent subadult present during a winter (Nov–Apr) had immigrated into the study area during the previous summer. During the PW study 95% (21 of 22) of offspring dispersed from their natal area June–August. During the DW study 90% (27 of 30) of offspring dispersed from their natal area April–July and in September. This time also coincided with post-dispersal localization of cougars on the GYNR winter range prior to the onset of the next winter. We then added the number of new independent subadults detected to the minimum population index of the previous winter to calculate the minimum summer population size. We used minimum population size as an index of cougar population density by calculating a density (cougars/1,000 km^2) for the total winter and total summer area (95% fixed kernel) used by all adult radio-marked cougars within each study phase.

Sexually selective infanticide (SSI) theory (Hrdy 1979) suggests that increased removal of adult males can increase kitten mortality through SSI by immigrating males (Stringham 1980). Through their use of large, defended territories, resident males may provide a spatial umbrella of protection for maternal females against newly establishing males or intruding adult males that could be infanticidal (Seidensticker et al. 1973; Logan and Sweanor 2001, 2010). The opposite effect also has been postulated; because adult males kill kittens, a reduction in the number of adult males should reduce kitten mortality (Miller 1990). Our PW study coincided with reestablishment and increase of the GYNR cougar population and included territorial instability as immigrant males established territories and dominance; 3 established males shifted territories from inside YNP to the north outside YNP (K. Murphy, Yellowstone National Park, unpublished data). Therefore, there was uncertainty in adult territorial boundaries as new males vied to establish residency, some males shifted home ranges, and females also exhibited lower home range fidelity (T. K. Ruth, Selway Institute, unpublished data). In contrast, the early to mid-years of our DW study represented a time of greater home range stability, thus stable social relationships, of resident adult females and dominant adult males (T. K. Ruth, unpublished data). Consequently, we hypothesized that instability of adult males, whether through removal (hunting or management related) or during reestablishment and population recovery, can result in increased kitten mortality. We lacked adequate sample sizes to calculate fidelity indices for early and later years in our PW and DW studies. To avoid dropping years with missing data from our analyses, we tested the influence of stability of adult males on kitten survival by comparing alternative models using adult male density and average annual age of adult males as indices of stability.

Because cougars preyed primarily on elk, particularly elk calves (66% of elk killed PW, Murphy 1998; 53% of elk killed DW, Ruth 2004*b*), we compared covariates of total elk biomass, adult elk biomass, and calf elk biomass in several a priori survival models. We hypothesized that dependent kittens would have increased survival in years when calves were abundant versus years when adult females supporting kittens might have reduced access to vulnerable calves (low calf abundance). We obtained estimates of minimum numbers of elk and sex–age ratios of elk from annual airplane and helicopter-based winter counts and classification conducted on the Northern Range of YNP (Lemke et al. 1998, Eberhardt et al. 2007, Cross 2009). The spatial extent of sampling matched our study area during both the PW and DW studies. We calculated calf elk, adult elk, and total elk biomass by multiplying average live weights (Houston 1982) for each sex–age class by number of individuals and then summing and converting to metric tons (metric ton = 1,000 kg). We interpolated estimates from surrounding years for counts missing in 1993 and 1994 (Haroldson et al. 2006).

We included a winter severity index (WSI; Farnes et al. 1999) and cumulative summer rainfall, which are both climatic factors that influence distribution and condition of ungulates and which may directly and indirectly affect cougar survival (Table S1). Because elk may be limited by the nutritive quality of summer forage as well as winter severity, we included summer precipitation separately from WSI in our seasonal models (Merrill and Boyce 1991, Cook et al. 2004). Although we know of no studies relating precipitation and vulnerability of elk to predation or cougar survival, vulnerability of deer appeared linked to limited food availability and cougars exploited deer as they concentrated at water sources during an extended drought in a desert environment (Logan and Sweanor 2001). We used climate data collected at four climatological (CLIM) stations distributed across the GYNR at Gardiner, Montana and Mammoth, Tower Falls, and Lamar Valley, Wyoming and from remote snow monitoring equipment (SNOWTEL sites) in and around the park (Despain 1990, Farnes et al. 1999). By combining monthly precipitation and temperature records, an index of relative winter severity was produced by Farnes et al. (1999) to provide a measure of winter influences on ungulate species. Values above zero typically correlate with low winter mortality, higher reproduction and recruitment, and presumably, additional effort by predators to obtain prey that are in improved physical condition (Farnes et al. 1999). Values between −1.0 and −2.0 show some reduction in reproduction, but typically little mortality of older animals and yearlings occurs. Winter severity index values <-2.0 generally indicate significant mortality, low reproduction rates, weaker calves and lower birth weights, smaller or even negative herd recruitment rates (i.e., more animals die than enter the population), and increased predation. We averaged 3 WSI values from across the GYNR and attributed them to cougar locations. We attributed cougar locations with percentage of cumulative rainfall above or below the monthly rainfall average for the GYNR, 1948–2004 (Western Regional Climate Center, 2005).

Model Selection and Survival Surface

We used an information-theoretic approach (Burnham and Anderson 2002) and Akaike's Information Criterion (AIC) adjusted for small sample sizes (i.e., AIC_c) to rank models (Burnham and Anderson 2002) from the candidate list. We derived model-averaged covariate estimates (Burnham and Anderson 2002) from all a priori models and applied them to the best model to estimate annual survival of independent cougars and kittens and to develop survival surfaces for independent male and female cougars. We assessed model fit with receiver operating characteristic (ROC) curves (Boyce et al. 2002) performed with Program R package ROCR (Sing et al. 2005). Integrating the area under the ROC curve (AUC) provides an assessment of model performance (Swets 1988, Manel et al. 2001).

We assessed model fit for the study area and developed separate ROC curves for males and females contrasting known harvest locations with an equal, randomly selected number of known live cougar telemetry (VHF and GPS) locations. We attributed locations with the probability of survival (pixel size of 30 m) from the top model and with true survival (survival = 1, mortality = 0) from the harvest and telemetry data. We obtained harvest locations spanning the years 1989–2005 and recorded as township, range, and section from MDFWP. The study area boundary included portions of Montana Region 3 hunt units 313, 314, and 317. To further assess predictive capabilities, we applied our model an additional 50 km east and 80 km north of the study area boundary (including Region 3 hunt units 310, 311, 316, and 362 and remaining portions of units 313, 314, and 317) and again assessed model fit with ROC AUC for males and females.

We used the finite rate of increase function in the PopTools (PopTools version 3.0.5, www.cse.csiro.au/poptools, accessed 20 Jun 2008) extension for Excel (Microsoft Corporation, Redmond, Washington) to estimate population growth rates (λ) during the PW and DW studies. We used study phase specific maternity rates (m_x) and age specific survival estimates for females from birth (age class zero) to age 14 years as matrix inputs. Because the simple deterministic models we used assume closed population structure (i.e., no immigration or emigration), we adjusted survival rates for yearling females based on our estimates of immigration and emigration (T. K. Ruth, unpublished data). We used PopTools to evaluate the sensitivity and elasticity of lambda to changes in age-specific survival and reproductive rates (Caswell 2001). Following Harris et al. (2006, 2007) and Schwartz et al. (2010) we determined a threshold female survival rate that resulted in population growth ($\lambda \geq 1.0$) and chose this value of female survival to identify source and sink areas in the GYNR.

RESULTS

Adult and Independent Subadult Survival

We monitored 104 adult and independent, pre-dispersal cougars during the PW (30 F, 20 M) and DW (27 F, 27 M) phases of our study (Table 1) for a total 1,911 cougar months. Number of individuals monitored annually ranged from 1 to 16 and 0 to 12 for females and males, respectively, during the PW study phase and did not differ ($\chi^2_1 = 0.003$, $P = 0.958$) from the DW study in which number of individuals monitored per year ranged from 1 to 17 females and 0 to 8 males (Table 1, Fig. 1A). There was no difference in median length of monitoring for female (Mann–Whitney $U = 315.5$, $P = 0.152$) or male (Mann–Whitney $U = 233.5$, $P = 0.428$) cougars between study phases.

Six of 123 a priori models had $\Delta AIC_c < 2$ (Table 2), indicating similar support for these models (Burnham and Anderson 2002); they accounted for 89% of AIC_c weights among the candidate model set. Covariates common to these models were sex, age, age^2, km/km^2 of total roads during the cougar hunting season, and annual elevation.

Evidence ratios using AIC_c weights indicated weak support for the best model over other models in the set; model 1 had 1.4 times support over model 2 and 2.7 times support over

Table 1. Numbers of adult and independent, non-dispersing cougars, total and average months radio-monitored, and mortalities by study phase and sex for cougars on the Greater Yellowstone Northern Range, 1987–2005.

			Months available				Mortalities		
Phase	Sex	No. cougars	Total	$\bar{x}$	Median	SD	Human	Natural	Total
Pre-wolf	Female	30	578	19.3	10.0	20.4	2	6	8
	Male	20	285	14.3	7.5	17.3	3	2	5
	Subtotal	50	863	17.3	9.0	19.2	5	8	13
During wolf	Female	27	764	28.3	19.0	25.9	2	7	9
	Male	27	284	10.5	4.0	13.0	3	8	11
	Subtotal	54	1,048	19.4	11.5	22.2	5	15	20
Total		104	1,911	18.4	10.0	20.7	10	23	33

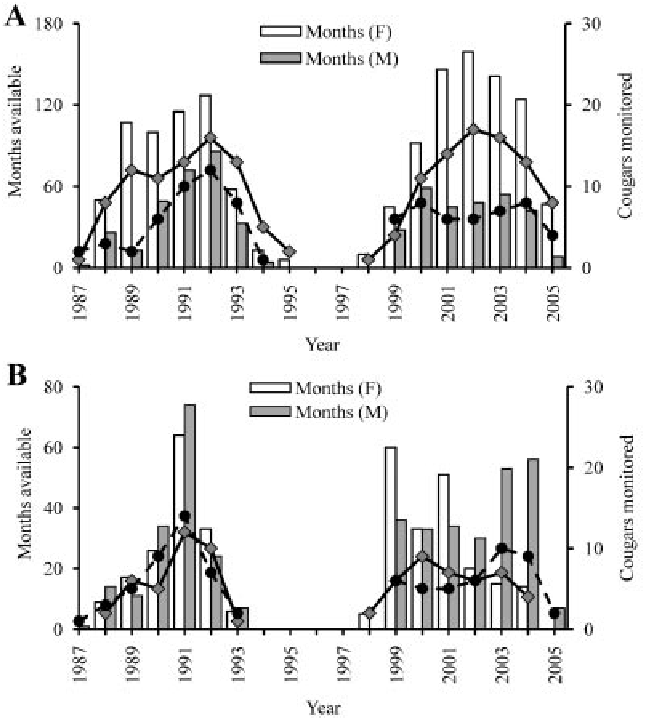

Figure 1. Number of independent cougars (A) and dependent kittens (B) we radio monitored, and total months of availability by sex, for pre-wolf (1987–1995) and during wolf (1998–2005) monitoring phases on the Greater Yellowstone Northern Range. We depict the number of females (F) with gray diamonds and males (M) with black circles.

model 6. The second through sixth models contained the same suite of top model covariates, as well as the additional covariates of annual wolf use, annual density of adult male cougars, season, and study phase. Survival was negatively affected by increasing annual wolf use and positively affected as the density of adult male cougars increased. Temporal covariates of season and phase had negative effects on survival with survival slightly lower during summer and in the DW study phase. Models 2–6 differed by 1–2 parameters from our best model (model 1), and likelihood ratio tests comparing nested models yielded $0.117 \leq P \leq 0.817$ suggesting that additional covariates did not add to the overall model. In addition, 95% confidence intervals for the β coefficients for annual wolf use, annual adult male cougar density, season, and study phase bounded zero, suggesting uncertainty in the predictive power of these covariates. These models (and covariates) were probably not strongly supported because they were influenced by the top 4 covariates (Burnham and Anderson 2002:131) and had confidence intervals that overlapped zero. We derived model averaged beta estimates (Table 3) for covariates in the top model to use in constructing survival surfaces.

Results from the best model (Table 3) indicated that survival of adult and independent, pre-dispersal cougars was influenced by 1) sex—females had higher survival rates than males; 2) age—survival increased with increasing age and females between 1 yr and 10 yr of age had survival >0.80, males 3–9 yr old had survival of 0.70–0.81 (Fig. 2A); 3) road density—survival declined with increasing km of road/km^2 during the cougar hunting season; and 4) elevation—cougars had improved survival at higher elevations.

Road density during the cougar hunting season was better supported than total annual road density. Road density calculated with a 2.59 km^2 moving window outperformed the 500-m^2 moving window. The β coefficients for all the road density covariates were negative and 95% confidence intervals did not bound zero (Table 3), indicating the influence of roads was well supported in our best model. Cougar survival decreased with increasing density of roads; however, road densities >1.58 km/km^2 had little additional effect on survival (Fig. 2B).

Annual elevation was an important covariate and it outperformed seasonal elevation by 8.84 ΔAIC_c. The 95% confidence intervals for the β coefficient did not bound zero (Table 3), indicating clear support for the positive influence of elevation on cougar survival (Fig. 2C).

Although the effects of study phase were not clear, model results indicated that PW females (0.880, $\text{SE} = 0.002$) and PW males (0.746, $\text{SE} = 0.008$) had slightly higher mean rates of survival than did DW study females (0.842, $\text{SE} = 0.008$) and males (0.676, $\text{SE} = 0.027$). Causes of mortality (human, predation, and natural or accidental) were similar between PW and DW phases ($\chi^2_2 = 0.878$, $P = 0.645$). During both studies and across all years, mortal-

Table 2. Top 6 of 123 a priori models* we used to assess impact of individual and temporal covariates on survival of adult and independent subadult cougars on the Greater Yellowstone Northern Range prior to (1987–1994) and during wolf reestablishment (1998–2005). All models also contain an intercept that accounts for one parameter.

Model[a]	AIC_c	No. parameters	ΔAIC_c	Model likelihood	AIC_c weights	Deviance
1. Sex + Age + Age^2 + Hunttrd54 + Elevann	301.719	6	0	1	0.260	289.675
2. Sex + Age + Age^2 + Hunttrd54 + Elevann + Wolfann	302.328	7	0.609	0.738	0.191	288.269
3. Sex + Age + Age^2 + Hunttrd54 + Elevann + Wolfann + Amcougann	303.066	8	1.347	0.510	0.132	286.990
4. Sex + Age + Age^2 + Hunttrd54 + Elevann + Amcougann	303.504	7	1.785	0.410	0.106	289.445
5. Sex + Age + Age^2 + Season + Hunttrd54 + Elevann + Wolfann	303.615	8	1.896	0.388	0.101	287.540
6. Phase + Sex + Age + Age^2 + Hunttrd54 + Elevann	303.680	7	1.961	0.375	0.097	289.621

* Difference in Akaike's Information Criterion adjusted for small sample size [ΔAIC_c] < 2.0.

[a] Sex = gender of cougar; Age + Age^2 = quadratic term for cougar age, which was calculated using midpoint of radio location interval and birth date of the individual; Hunttrd54 = total road density (roaded 30-m cells/2.59 km^2) in hunt areas during the cougar hunting season; Elevann = average elevation (km); Wolfann = average annual wolf use days; Amcougann = minimum annual density of adult male cougars per 1,000 km^2; Season = winter (1 Nov–30 Apr) or snow free (1 May–31 Oct). Model covariates are further described in Table S2 available online at www.onlinelibrary.wiley.com.

Table 3. Model averaged beta estimates on the logit scale for covariates in the top a priori model we used to assess impact of individual and temporal covariates on estimates of independent cougar survival on the Greater Yellowstone Northern Range, prior to (1987–1994) and during wolf reestablishment (1998–2005).

			95%CI	
Parameter[a]	**Beta coeff.**	**SE**	**Lower**	**Upper**
Intercept	−4.419	2.706	−10.331	1.493
Sex	−1.186	0.407	−1.986	−0.386
Age	0.559	0.194	0.174	0.944
Age^2	−0.050	0.013	−0.076	−0.023
Hunttrd54	−0.032	0.007	−0.046	−0.018
Elevann	3.925	1.248	1.458	6.392

[a] Sex = gender of cougar; Age = cougar age calculated using midpoint of radio location interval and birth date of the individual; Age^2 = included as quadratic term for cougar age; Hunttrd54 = total road density in hunt areas during the cougar hunting season; Elevann = average elevation (km). Model covariates are further described in Table S2 available online at www.onlinelibrary.wiley.com.

ities peaked in December ($n = 6$) and again in July with the highest number of deaths ($n = 4$) occurring in July in the DW study. Human hunting accounted for 38.5% of total mortality during the PW study and 25% of mortality in the DW study (Table 1). In the PW and DW phases 62% and 75% of mortalities, respectively, were due to natural causes. During the PW study, natural deaths included intraspecific killing (37.5%), death from an unknown predator (12.5%), and disease or accidents (50%). Intraspecific killing accounted for 33.3%, wolves for 26.7%, and disease or accidents for 40% of natural deaths in the DW study.

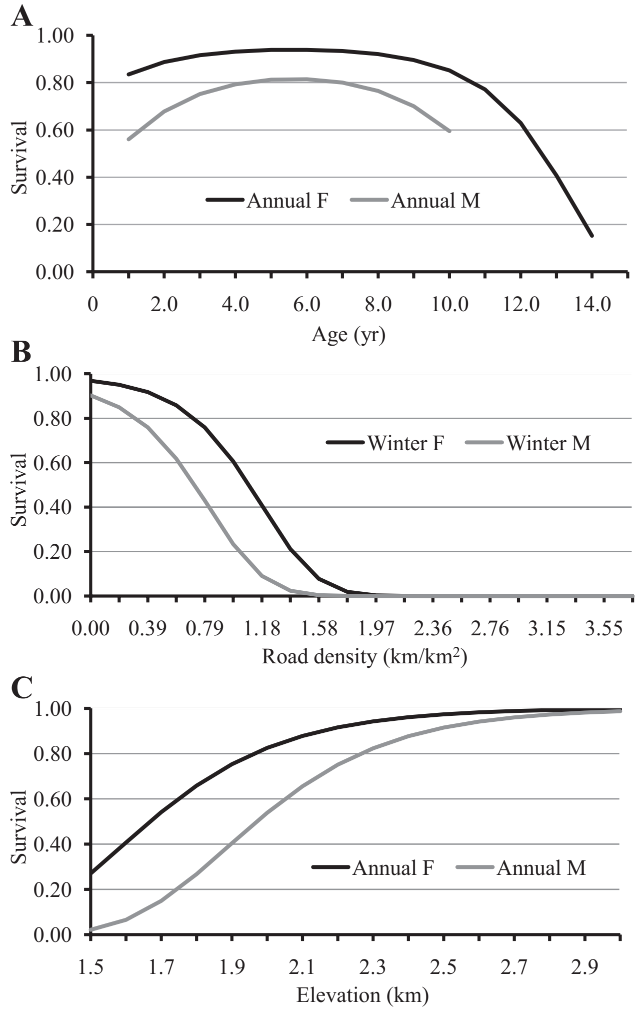

Figure 2. Annual, age-specific survival estimates of independent cougars (A); the influence of road density (km/km^2) during the cougar hunting season on winter survival estimates (B); and the influence of elevation (km) on annual survival estimates (C) of adult and independent, pre-dispersal female (F) and male (M) cougars on the Greater Yellowstone Northern Range, 1987–2005. We computed estimates using βs from the top model (Table 3).

Kitten Survival

Our survival sample contained 106 dependent kittens radio-monitored in 24 litters during the PW (27 F, 27 M) and 24 litters in the DW (24 F, 28 M) phases of our study for a total 767 cougar–months (Table 4). There was no difference between numbers of individuals monitored per year between study phases and sexes ($\chi^2_1 = 0.133$, $P = 0.754$). Number of kittens monitored per year ranged from 1 to 12 and 1 to 14 for females and males, respectively, during the PW study with 0–9 females and 0–10 males monitored in the DW study (Table 4 and Fig. 1B). There was no difference in median length of monitoring (Mann–Whitney $U = 645.5$, $P = 0.286$) for female kittens between study phases. Median length of monitoring was less for male kittens in the PW than in the DW study (Mann–Whitney $\text{U} = 626.0$, $P = 0.029$).

Our estimates of $\hat{c}$ for kitten survival ranged from 0.839 to 3.637 and averaged 1.527, indicating the fates of siblings were generally not independent, as evidenced by 9 litters in which kittens died at the same time and of similar causes. Littermates were killed in single events from wolves ($n = 1$ litter), infanticidal male cougars ($n = 5$ litters), or orphaning due to the death of their mother ($n = 3$ litters). Thus, we used the value of 1.53 for $\hat{c}$ to adjust the quasi-likelihood estimate in Program MARK.

Four of 90 candidate models with $\Delta\text{QAIC}_c < 2$ included the following covariates: age, age^2, season, and biomass of elk calves (Table 5). These models accounted for 80% of AIC_c weights among the candidate model set. Evidence ratios using the QAIC_c weights indicated weak support for the best model over other models in the set; model 1 had 1.9 times support over model 2 and 2.7 times support over model 4. When we added annual adult male density to the model with age, season, and elk calf biomass and compared it against the model with seasonal adult male density, it lowered the former model by 1.245 ΔQAIC_c units. Adding seasonal wolf use to the top model did not improve model

Table 4. Number of cougar kittens, total and average months radio-monitored, and mortalities by study phase and sex for cougars on the Greater Yellowstone Northern Range prior to (1987–1994) and during wolf reestablishment (1998–2005).

			Months available				Mortalities			
Phase	**Sex**	**No. kittens**	**Total**	$\bar{x}$	**Median**	**SD**	**Human**	**Natural**	**Undetermined**	**Total**
Pre-wolf	Female	27	155	5.7	5.0	4.3	0	5	6	11
	Male	27	165	6.1	5.0	4.0	1[a]	7	2	10
	Subtotal	54	320	5.9	5.0	4.1	1	12	8	21
During wolf	Female	24	197	8.3	6.5	6.2	1	6	1	8
	Male	28	250	8.9	8.5	5.0	0	10	2	12
	Subtotal	52	447	8.6	7.0	5.5	1	16	3	20
Total		106	767	7.2	5.0	5.0	2	28	11	41

[a] Removed by Montana Fish, Wildlife, and Parks after mother was killed by hunters.

Table 5. Top 4 of 90 a priori models* we used to assess impact of individual and temporal covariates on survival of cougar kittens on the Greater Yellowstone Northern Range prior to (1987–1994) and during wolf reestablishment (1998–2005). All models also contain an intercept that accounts for one parameter.

Model[a]	$QAIC_c$	No. parameters	$\Delta QAIC_c$	Model likelihood	AIC_c weights	QDeviance
1. Age + Age^2 + Season + Calfbio + Amcougseas	144.412	6	0	1	0.112	132.301
2. Age + Age^2 + Season + Calfbio + Amcougann	145.657	6	1.245	0.537	0.060	133.546
3. Age + Age^2 + Season + Calfbio + Amcougseas + Wolfseas	146.253	7	1.842	0.398	0.045	132.106
4. Age + Age^2 + Season + Calfbio	146.392	5	1.980	0.372	0.042	136.313

[*] Difference in quasi-likelihood modified Akaike's Information Criterion adjusted for small sample size [$\Delta QAIC_c$] < 2.0.

[a] Age + Age^2 = quadratic term for cougar age, which was calculated using midpoint of radio location interval and birth date of the individual; Season = winter (1 Nov–30 Apr) or snow free (1 May–31 Oct); Calfbio = total calf biomass in metric tons; Amcougseas = minimum seasonal density of adult male cougars per 1,000 km^2; Amcougann = minimum annual density of adult male cougars per 1,000 km^2; Wolfseas = average wolf use days during winter and snow-free months. Model covariates are further described in Table S2 available online at www.onlinelibrary.wiley.com.

fit (likelihood ratio test, $\chi^2_1 = 0.195$, $P = 0.658$) yet $\Delta QAIC_c$ indicated similar support for this model with other top models (Burnham and Anderson 2002). Survival was negatively affected by increasing seasonal wolf use (model 3) and positively affected as annual density of adult male cougars increased (model 2). There was uncertainty in the predictive power of seasonal wolf use and annual male cougar density as 95% confidence intervals for the β coefficients bounded zero.

The best-fitting model (Table 6) had 6 parameters and detected variation in survival between ages of dependent kittens, season, biomass of elk calves, and seasonal minimum density of adult male cougars. Kitten survival increased rapidly and reached an asymptote of 0.90 between 0.6 yr and 0.7 yr (7–8 months) of age (Fig. 3A). Survival of kittens was lower during winter (0.755, Nov–Apr), a time when cougars and wolves were condensed on winter range, than during snow-free months (0.910, Mar–Oct, Fig. 3B). The primary cougar breeding season also occurred during late winter (Mar–Apr). The temporal covariate of elk calf biomass had a positive influence on kitten survival; survival increased with increasing minimum estimates of calf biomass (Fig. 3C). The top model included seasonal density of adult male cougars and it improved the model with age, season, and elk calf biomass by 1.98 $\Delta QAIC_c$ units. Kitten survival increased with adult male density (Table 6). The 95% confidence interval for the model-averaged β coefficient for adult male density bounded zero, suggesting uncertainty in the predictive power of this covariate. Prior to model averaging, however, the 95%CI (0.019–1.670) for the adult male density β coefficient (0.844) did not bound zero. Winter male density varied from 0.91/1,000 km^2 (1989) to 1.82/

Table 6. Model averaged beta estimates on the logit scale for covariates in the top a priori model we used to assess impacts of individual and temporal covariates on estimates of cougar kitten survival on the Greater Yellowstone Northern Range prior to (1987–1994) and during wolf reestablishment (1998–2005).

			95%CI	
Parameter[a]	**Beta coeff.**	**SE**	**Lower**	**Upper**
Intercept	−4.595	2.158	−8.824	−0.366
Age	13.917	3.046	7.947	19.888
Age^2	−6.024	1.966	−9.877	−2.171
Season	1.769	0.717	0.364	3.174
Calfbio	0.700	0.308	0.096	1.305
Amcougseas	0.853	0.455	−0.040	1.745

[a] Age = cougar age calculated using midpoint of radio location interval and birth date of the individual; Age^2 = included as quadratic term for cougar age; Season = winter (1 Nov–30 Apr) or snow free (1 May–31 Oct); Calfbio = total calf biomass in metric tons; Amcougseas = minimum seasonal density of adult male cougars per 1,000 km^2. Model covariates are further described in Table S2 available online at www.onlinelibrary.wiley.com.

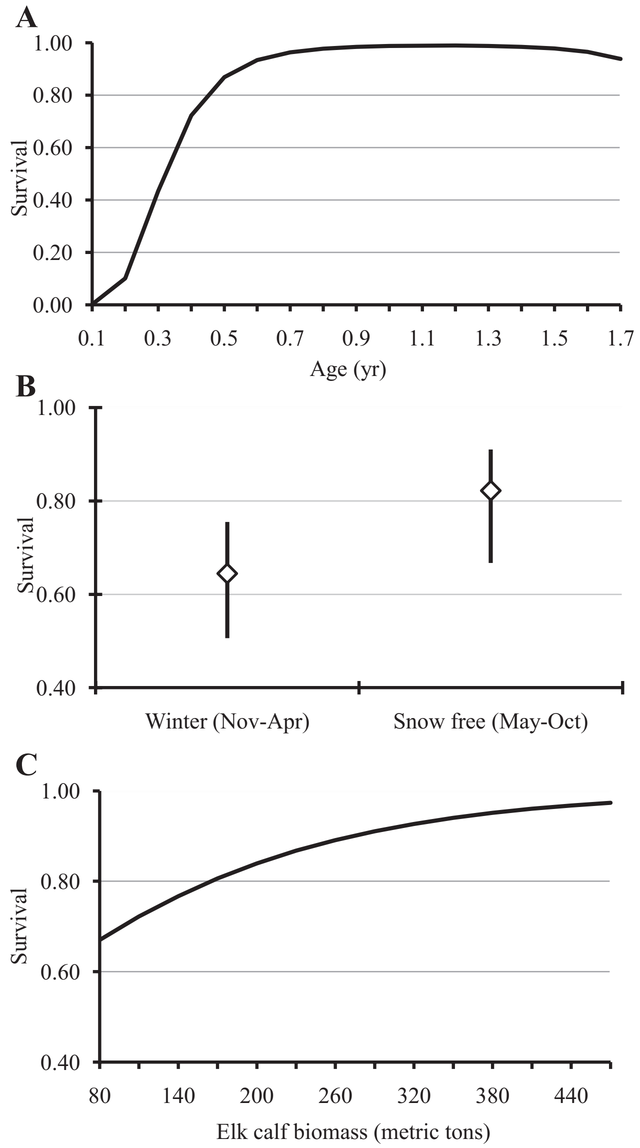

Figure 3. Annual, age specific survival estimates of cougar kittens (A), the effect of season (B) on estimates of kitten survival, and the influence of elk calf biomass (metric tons) on annual survival estimates of cougar kittens across the range of minimum estimates of elk calves (C) on the Greater Yellowstone Northern Range, 1987–2005. We computed estimates using βs from the top model (Table 6).

1,000 km^2 (1993) with annual mean age of 3.7–5.2 yr during the PW phase as males immigrated at an average rate of 1.7/yr and established home ranges. In the DW phase, male density increased from 1.76/1,000 km^2 in winter 1998–1999 to 2.93/1,000 km^2 in winter 2000–2001 and then declined to 1.03/1,000 km^2 by 2005 as adult males died. Annual mean age of adult males during the DW phase ranged from 4.2 to 7.1 yr and new males immigrated at an average rate of 0.9/yr.

Although phase was not included in our top model, annual kitten survival was slightly lower during the PW study (0.462) than the DW study (0.585). Causes of mortality (predation, orphaning or malnutrition, unknown) of kittens were similar between PW and DW phases ($\chi^2_2 = 5.932$, $P = 0.052$). In the PW and DW phases, 29% and 39% of total mortalities, respectively, were due to natural causes. However, during the PW study, 43% of kitten mortality (Table 4) resulted from infanticide and we suspected that 2 of the undetermined mortalities were related to infanticide. The DW study represented a time of greater territorial stability of dominant adult males and we documented only one (5%) kitten mortality due to infanticide. Orphaning and malnutrition accounted for 10% of natural deaths in the PW study and 40% of mortality during the DW study. Another 35% of mortalities during the DW study were due to predation by wolves or bears. One female kitten (14 months of age) was killed by hunters during the hunting season in the DW study. Most kitten mortality occurred in winter (PW = 81%, DW = 65%, $\chi^2_1 = 3.72$, $P = 0.05$) and was associated with infanticide in the PW study and wolves and orphaning or malnutrition in the DW study.

Survival Surface and Model Fit

We used model-averaged covariate estimates from our top model to create a survival surface for independent female and male cougars on the GYNR. Because our best model included road density during cougar hunting, we incorporated this seasonal effect when creating the survival surface. Thus, we created an annual surface by multiplying a surface that incorporated density of roads during the 4 months of the cougar hunting season (Dec–Mar) by a surface that removed the effect of roads for the 8 months when cougar hunting did not occur, such that:

$$\begin{aligned}&\text{Annual survival surface}\\&\quad = (\text{roads during hunt surface})^4\\&\qquad \times (\text{no roads during hunt surface})^8\end{aligned}$$

Results of ROC curve analysis indicated a good model fit for both female cougars (AUC = 0.81, 95%CI = 0.70–0.92, $n = 35$ harvest locations) and male cougars (AUC = 0.84, 95%CI = 0.74–0.94, $n = 49$ harvest locations) for our study area. When we applied our model further north and northwest beyond the study area boundary, our model provided a fair fit for female (ROC AUC = 0.73, 95%CI = 0.65–0.81, $n = 82$ locations) and male cougars (ROC AUC = 0.73, 95%CI = 0.67–0.80, $n = 137$ locations).

Mean survival for independent female cougars was 0.880 and 0.842 from our PW and DW studies, respectively. Using our survival estimates, PW $m_x = 0.75$ and DW $m_x = 0.44$, our estimates of population trajectory were $\lambda \geq 1.04$ in the PW study and $\lambda \geq 0.83$ in the DW study. Sensitivity and elasticity analyses (age specific sensitivity = 0.01–0.72, age specific elasticity = 0.01–0.11) supported the large influence of female survival on cougar population growth as found by Lambert et al. (2006). We found that $\lambda \geq 1.0$ when survival of 2–12-year-old independent females was ≥ 0.93 for the PW study and 1.00 for the DW phase. By assuming that maintaining $\lambda \geq 1.0$ across variation in m_x and emigration of 1-year old females requires female survival ≥ 0.93, we identified and mapped source (survival ≥ 0.93) and sink (survival < 0.93) habitats from survival probabilities (Fig. 4; see Schwartz et al. 2010).

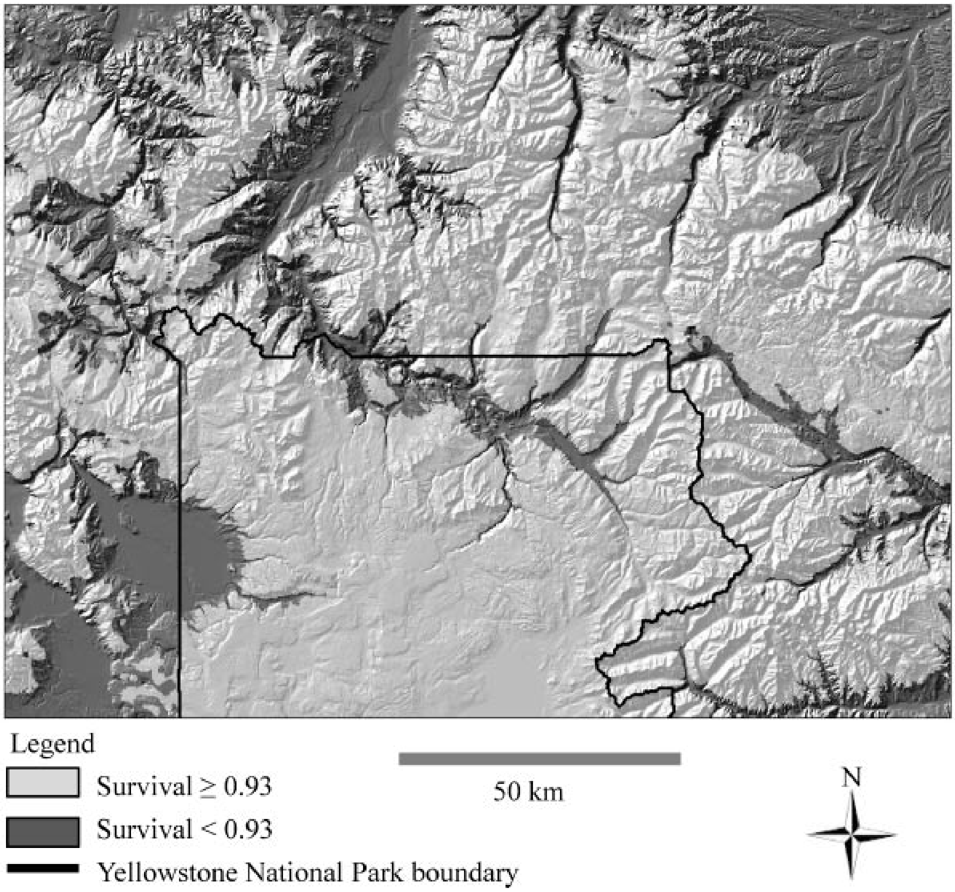

Figure 4. Survival surface reflecting threshold values of survival for independent female cougars; areas ≥0.93 indicate source habitat (white) and areas <0.93 indicate sink habitat (dark gray) on Greater Yellowstone's Northern Range, 1987–2005. We applied model averaged covariate estimates to the best model (Table 3) to estimate survival.

DISCUSSION

Quigley and Hornocker (2010:65) noted, "Two important extremes are evident in mortality factors for cougar populations, one human caused and one driven by internal strife (supplemented by other factors, such as disease and old age)." Cougar survival on the GYNR was largely a function of demography, density, and human influences stemming from sport-hunting.

Adult and Independent Subadult Survival

With the exception of the evaluation by Biek et al. (2006) of feline immunodeficiency virus (FIV) infection on cougar survival, our study is the first to evaluate factors influencing cougar survival in a multi-model approach. By far the most important determinants of survival were age and sex of the cougar, elevation, and density of roads in a cougar's home range during the cougar hunting season. Survival increased as females and males aged but then rapidly declined at older ages: >10 yr for females and >8 yr for males. Similar to other studies of hunted cougar populations (Cunningham et al. 1995, Lambert et al. 2006, Robinson et al. 2008) and in contrast to one non-hunted population (Logan and Sweanor 2001), female cougars in our study area had higher survival than males. Selective harvest of males could have contributed to observed differences in female and male survival in our study. Cougar hunters may selectively harvest males, particularly when competition between hunters is low, becoming less selective when demand exceeds harvest quotas and competition is high (Anderson and Lindzey 2005). During our PW study, 73% of harvest on the north end of our study area was males, suggesting selection for this gender, whereas males (55%) and females (45%) were harvested more equitably during the DW study. Because we combined adults and independent subadults for these analyses, our results do not reflect differences in harvest structure between these 2 age classes. Two female and 3 male cougars killed by hunters during the PW study were adults. In the DW study, 2 adult females and 3 subadult males were killed by hunters.

Annual elevation was important in our models, supporting the hypothesis that regardless of season, survival can be expected to be higher at higher elevations, a result similar to that found for grizzly bears in the GYE (Schwartz et al. 2010). For cougars outside or overlapping Park or Wilderness, elevation likely captured access to cougars by hunters starting from trailheads or roads originating in the Gardiner and Paradise valleys. Although a seasonal effect was not supported in our top model set, cougars are constrained to lower elevations where prey occurs during winter and spatial overlap with wolves can increase as winter progresses (Alexander et al. 2006). Overall, elevation may represent a combination of factors that influence survival, perhaps including some that we did not consider or include in our analysis.

Road density outside YNP during the cougar hunting season was an important predictor of cougar survival. Road densities $\geq$1.58 km/km^2 had no additional effect on survival as estimated survival dropped to zero. On average, adult and subadult cougars in our sample only spent about 27% of their time in areas open to hunting during winter. Thus, although cougars spent proportionally more time in areas with no hunting access (Park or Wilderness), road access had a significant negative effect on survival for cougars that overlapped or lived outside the park during winter. Our study sample underrepresented independent subadults because we excluded them from analysis once they dispersed beyond the study boundary. Of 38 successful dispersers in the DW phase, 29% were killed prior to establishment during the hunting season at 18 months to 3 years of age and 18% were killed during the hunting season at >3 years of age. On the GYNR, survival rates for adult and subadult cougars combined were lower than mean survival estimates for adult males where no hunting occurred (0.91 M, 0.82 F, Logan and Sweanor 2001), were higher than heavily hunted populations (0.64 pooled adults on Monroe, Utah study area, Stoner et al. 2006; 0.33 adult M, 0.77 adult F, Lambert et al. 2006), and fell within annual estimates reported in other populations where mortality from hunting, vehicle collisions, and depredation removals were the leading causes of death (0.69–0.92 pooled M-F, Anderson et al. 1992; 0.75 pooled adults, Beier and Barrett 1993; 0.12–1.0 M, 0–0.81 F, Cunningham et al. 1995; 0.76 pooled adults on Oquirrhs, Utah study area, Stoner et al. 2006).

Road density calculated with a 2.59 km^2 moving window outperformed the 500-m^2 moving window, suggesting that the larger spatial scale better accounted for the relationship between hunter access and roads and that cougars were not necessarily killed near roads. Although some cougars may quickly tree short distances from roads, others are likely treed and killed at distances represented by the 2.59 km^2 moving window because houndsmen release dogs on tracks left from the previous night and a cougar may have traveled far from the road. Although traveling cougars have shown aversion to paved roads during the day, dirt roads and other low vehicle use roads may facilitate cougar movements (Van Dyke et al. 1986, Belden and Hagedorn 1993, Sweanor et al. 2000, Dickson et al. 2005). Cougars that travel snow-compacted roads leave tracks visible to houndsmen driving vehicles or snowmachines. Road access and snow conditions were key factors influencing distribution of hunting pressure and harvest of cougars in western Montana (Murphy 1983).

The possible effect of increased wolf presence on survival was small compared with effects of age, sex, elevation, and density of roads during the hunting season. Wolves caused 15% of adult cougar deaths and all occurred during winter. Our estimates of annual survival were much higher than those reported for cougars approximately 10 years after wolf reestablishment in the North Fork of the Flathead, Montana (0.29 M, 0.65 F, Ruth 2004*a*) where hunting and starvation were the primary sources of mortality and higher than those in Banff National Park during wolf recolonization (0.51 annual rate for pooled sexes, Kortello et al. 2007). Although the influence of increasing wolf use is not clear from our survival modeling, cougars responded to increasing wolf use by concentrating their activities in more topographically complex habitats (Ruth and Buotte 2007). In Banff National Park, Kortello (2007) found that as wolf use increased during winter, cougars shifted to areas with more human development and activity. If cougars in source areas avoid wolves by shifting into or overlapping areas managed as sinks, then source populations could become affected by management outside their boundaries. The direction cougars shift will likely be determined by the availability of complex terrain and other habitat characteristics (e.g., higher human density) that may limit wolf use. Shifts into good quality, occupied cougar habitat could lead to the perception of a growing cougar population and increased quotas, particularly if those areas are managed as sinks. The likelihood of harvest will still depend on the amount of road access in the area of interest. Considering that areas managed for cougar harvest are likely to be managed for wolf harvest as well, competition between the 2 species may be moderated by the effects of hunting.

Kitten Survival

Dependent siblings should not be assumed to have independent fates in survival analyses. Siblings in litters are usually left in a group while their mother hunts. Thus, littermates may equally have an increased risk of mortality from other cougars, wolves, bears, or loss of their mother. Violation of the independence assumption causes sample data to be overdispersed relative to a binomial model, which leads to underestimates of sampling variances (Schwartz et al. 2006, Bishop et al. 2008), a result supported by our analysis of kitten survival.

Estimates of kitten survival in New Mexico (0.59–0.66, Logan and Sweanor 2001) were higher than ours (0.46) in the PW phase and similar to those (0.59) in the DW phase. Kitten survival in a heavily hunted population in Washington (0.57, Lambert et al. 2006) was also similar to our DW survival but higher than kitten survival in the PW phase. The New Mexico and Washington estimates, however, reflect an assumption of independence of survival within litters.

Unlike adult cougars, gender of kittens had little influence on their survival to independence from their mother, similar to findings of Logan and Sweanor (2001) and Laundré et al. (2007). Also similar to findings of Logan and Sweanor (2001), kittens of both sexes had higher mortality at $\leq$4 months of age. Consequently, litters detected at ages >4 months will generally have smaller mean sizes and result in higher estimated rates of survival than those detected at younger ages (Murphy 1998, Ross and Jalkotzy 1992, Logan and Sweanor 2001:119, Quigley and Hornocker 2010).

Our finding that increased density of adult male cougars positively influenced kitten survival is consistent with SSI theory. Although SSI theory proposes that increased removal of adult males can negatively influence kitten survival (Stringham 1980) we suggest the mechanism is not explicitly density of males but rather territorial stability within the adult male social class that may drive SSI in cougars (see Logan and Sweanor 2010). Sustained removal of male cougars does not always result in reduced cougar density, yet can result in high levels of immigration (Robinson et al. 2008) and territorial instability. Thus, in other hunted populations, kitten survival may be inversely related to density. When possible, analyses similar to ours should first evaluate home range stability prior to using density as a covariate and compare it with a temporally changing spatial covariate. A younger age structure is characteristic of heavily hunted populations (Logan and Sweanor 2001, Anderson and Lindzey 2005, Stoner et al. 2006). The high degree of infanticide observed during the PW phase and mostly absent in the DW phase is consistent with an increasing cougar population with frequent annual immigration, younger age structure, and poorly defined male territorial boundaries in the PW phase. However, immigration of new males did not preclude resident males and newly established residents from acting as primary breeders in the PW study (Murphy 1998). In brown bears, both resident and immigrant males may be infanticidal (Miller et al. 2003, Swenson 2003). In 2 of 5 litters during our PW study, infanticidal males were resident breeders. Although breeding opportunities for males are not enhanced unless the whole litter is lost, mothers may defend kittens, resulting in partial loss of litters or the death of mothers and kittens alike (Logan and Sweanor 2001, Miller et al. 2003). Two maternal females were killed by males in the PW study and one litter was killed at the same time as the mother.

There was seasonality to infanticide in our study area; except for one kitten killed in October, all cases of infanticide occurred during winter. Winter density of adult males had a stronger influence on kitten survival, presumably because cougars were condensed on winter ranges, resulting in greater overlap. Infanticide in the PW phase occurred concurrent with newly established males vying for territories (lower density but increasing population) and increased winter overlap, which negatively influenced kitten survival. Conversely, we observed lower rates of infanticide and increased kitten survival in the DW phase when there was greater territorial stability (and higher density) of adult males and females. Breeding also began in January–February and peaked in March–April during both study phases. Males could encounter females unfamiliar to them, or unattended litters, with infanticide a result of males seeking breeding opportunities (Logan and Sweanor 2001).

Whether predation, reduced competition, or individual behavior are motives for some infanticide in cougars and whether infanticide may result in breeding opportunities for infanticidal males remain as questions and may not be consistent across time, within or among areas. We expected but did not observe similar rates of infanticide in the DW study if predation or competition for food resources were strong motives for infanticide. Further, in all 5 cases of infanticide in our PW study, it was unclear whether infanticidal males were sires of litters they killed or of subsequent litters. In New Mexico, infanticidal males were not sires of the litters they killed and they consumed kittens killed during infanticidal events (Logan and Sweanor 2001). On average, the loss of litters accelerated the time for females to breed again by about 5 months (Logan and Sweanor 2001). Other studies documented few cases of infanticide in a population with high male harvest in Wyoming (C. R. Anderson, Jr., Colorado Division of Wildlife, personal communication) and in a reestablishing population in South Dakota (D. Thompson, Wyoming Game and Fish Department, personal communication).

Minimum annual estimates of biomass of elk calves had a strong positive influence on kitten survival. Although the trend in overall elk calf biomass was greater in the PW study, the analyses incorporated year-to-year changes in calf abundance (PW range = 0.9–4.7 metric tons, DW range = 0.8–2.4 metric tons) and functioned in an additive manner to influence kitten survival. Similar to findings of Logan and Sweanor (2001), timing of peak births of kittens coincided with the birth of primary prey, elk calves and deer fawns, in June and July. Abundance and availability of this food source may be essential to supporting litters of offspring to independence. Cougar mothers may forage at greater distances and for longer periods from kittens when calves and fawns are fewer (Laundré and Hernández 2007), potentially exposing kittens to greater risk of predation from male cougars or other carnivores (Logan and Sweanor 2001). Alternatively, Logan and Sweanor (2001) found kitten survival did not appear to be sensitive to the population dynamics of deer and suggested a time lag preceded lower survival in response to a reduced prey base. Laundré et al. (2007) documented a time lag; survival of cougar young declined the year of and 2 years after a mule deer decline, but survival rates returned to predecline levels once cougar numbers adjusted downward to lower abundance of prey.

The effect of wolf presence on survival was small compared with effects of kitten age, season, biomass of elk calves, and seasonal density of adult male cougars. However, kitten deaths due to wolves represented 10–39% of observed average annual kitten production (10.2 kittens/yr over 6 yr) and 7–23% of observed average annual litters (4.3 litters/yr over 6 yr) produced on the GYNR. Although cougars showed spatial avoidance of wolves (Ruth and Buotte 2007, Kortello et al. 2007), the need to access prey may limit avoidance during winter.

Birth pulse did not appear in any of our top models, suggesting this covariate did not have a strong influence on kitten survival. However, models that included the primary birth peak (May–Jul) indicated a positive effect on kitten survival ($\beta = 1.12$, 95%CI = 0.24–2.00 for model = intercept + age + age^2 + bpeak1). Inclusion of the secondary peak (Sep–Oct) with the primary peak did not have a similar outcome; the beta coefficient was negative with a 95% confidence interval that bounded zero for the covariate

Bpeak2. Although there was lack of support for Logan and Sweanor's (2001) hypothesis using the longer birth period, they cautioned that the hypothesis is dependent upon being able to detect kittens born during non-favorable times of the year and being able to quantify their survival. Of the litters we documented, 10% were born outside the 2 birth peaks, which perhaps influenced the lack of relationship to survival. However, betas in models that included only the primary birth peak (which is more pronounced in northern than southern latitudes) had a positive effect on kitten survival indicating support for Logan and Sweanor's (2001) hypothesis.

Our study prior to and after wolf reintroduction provides one of the few long-term telemetry-based studies on cougars in North America. Although our analysis linked factors to interspecific, intraspecific, and hunting-caused mortality, we could not explain all proximate causes of mortality, including disease and accidents, with our analysis. However, Biek et al. (2006) found no evidence that FIV-infected cougars in our study population experienced an increased risk of infection with other feline pathogens and they found no support for an overall reduction in cougar survival caused by chronic FIV infection compared with effects of age, sex, and sampling site. In addition, our study ended prior to determining causes of an apparent decline in the cougar population and whether the decline was sustained. As a consequence, we recommend similar efforts to understand factors influencing cougar survival in ecosystems where wolves are present or expected to reestablish. Such efforts should be long-term (>10 yr) to incorporate variation in cougar, wolf, and prey densities.

Survival Surface and Source-Sink

On the GYNR, low elevations and increasing density of roads, particularly in areas open to hunting, posed greater mortality risk for cougars than in areas of low road density and higher elevations. Our results provide quantitative support to findings of Murphy (1983) for cougars and are consistent with findings for other carnivores (wolves: Person and Russell 2008; grizzly bears: Mattson et al. 1987, McLellan and Shackleton 1988, Schwartz et al. 2010).

Our model provided a good fit between areas predicting low survival and harvest data in Montana and provides the ability to map factors currently influencing cougar survival in the GYNR landscape. Because locations of cougars harvested in Montana were recorded to the nearest section, there was spatial ambiguity as to their exact location with possible error of 1 km (C. Anderson, Jr., unpublished data), which may have influenced the predictive power (ROC AUC) of our model. The predictive power declined slightly as we extended beyond the study area boundary indicating caution in broad application of survival models to large geographic areas or in using our results to establish road density standards in the GYE or other areas (see also Schwartz et al. 2010). In addition, our models highlight covariates that influence survival under current conditions, but they neither predict future conditions (Schwartz et al. 2010) nor indicate which habitats are currently used by cougars. A next step is construction of models that predict cougar habitat use and which are then integrated with our survival models as suggested by Schwartz et al. (2010). Further, Runge et al. (2006) suggest that estimates of emigration are important for delineating source habitats and for evaluating how local populations function with respect to a larger system. Evaluating factors influencing survival and probabilistic classification of source-stable-sink habitats at various local scales, as the landscape changes, and testing across regions could identify different covariates and enhance understanding of where and at what times certain habitats function as sources or sinks.

MANAGEMENT IMPLICATIONS

We recommend that managers take several measures to enhance cougar population management that is based on a source-sink strategy. Managers can identify or create source areas by delineating productive cougar habitats (generally greater than 1,000–2,200 km^2; Beier 1993, Logan and Sweanor 2001) that encompass prey winter ranges and few roads, such as national parks and wilderness areas, or by establishing such areas as refuges with no hunting. The size and function of apparent source populations should be initially verified and then periodically re-verified with any new effects considered as fluctuations in cougar fecundity and survival, changes in road densities, and interactions with competing carnivores may preclude their consistent function in supporting source populations. Because hunting can influence survival of cougars in adjacent untargeted areas, particularly those that are small in size, minimizing road density or limiting road access in critical winter habitats could be applied in an adaptive management approach to enhance protection of certain source populations. Managers should expect highly effective removal of cougars from habitats rendered accessible to sport hunters due to high road density and low elevation and such areas are easily identified and mapped using Geographic Information Systems. We caution that where cougar populations are managed to sustain high annual removal (sinks), immigration from neighboring areas or spatial shifts by adults from adjacent sources may mask actual population declines, leading to the common perception of population growth or stability, and pressure to increase or maintain current harvests (Robinson et al. 2008). Additionally, sinks or areas that experience functional recovery from natural population declines may experience low kitten survival when turnover of males is high or males are newly established. Sink habitats may also already have lower breeding potential due to social instability and can be expected to strongly rely on annual immigration from source populations. At the regional scale, documenting the juxtaposition and connectivity between source and sink populations is critically important to cougar management and conservation planning.

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