

PREDATOR-SPECIFIC MORTALITY OF PRONGHORN ON YELLOWSTONE'S NORTHERN RANGE

Kerey K. Barnowe-Meyer^{1,3}, P.J. White², Troy L. Davis², and John A. Byers¹

ABSTRACT.—Yellowstone National Park supports a small population (<300) of pronghorn (*Antilocapra americana*). Some individuals migrate during summer to areas characterized by reduced visibility, mixed habitat types, and a diverse predator community. Across areas selected by migratory and nonmigratory pronghorn, we documented cause-specific mortality of adults and fawns and assessed relative risk of predation by various predators. Coyotes (*Canis latrans*) accounted for 56% of adult predation and up to 79% of fawn predation. Cougars (*Puma concolor*) and wolves (*Canis lupus*) accounted for additional predation of adults, while cougars, black bears (*Ursus americanus*), and Golden Eagles (*Aquila chrysaetos*) were documented killing fawns on rare occasions. Our results suggest that even when pronghorn are in the presence of multiple predator species, coyote predation on adults and fawns may predominate for populations inhabiting shrubsteppe habitat. However, the risk of predation by sympatric predators, particularly cougars, may be high for female pronghorn selecting mixed cover types during migration or for birthing purposes. While the direct effect of wolves on overall mortality was low, wolves may indirectly influence survival rates of adult females and fawns by altering the behavior and space use of sympatric predators, particularly coyotes.

Key words: pronghorn, Yellowstone, predation, coyotes, wolves, cougars, survival, mortality, *Antilocapra americana*.

Pronghorn (*Antilocapra americana*) inhabiting the northern range of Yellowstone National Park are listed as a species of special concern by the National Park Service, with heavy predation and poor winter range conditions placing the population at severe risk of extinction (National Research Council 2002, Boccadori et al. 2008). Coyotes (*Canis latrans*) are variably common across areas selected by Yellowstone pronghorn (Crabtree and Sheldon 1999) and have long been implicated as the main source of predation on pronghorn adults and fawns (Skinner 1922, Murie 1940, O'Gara 1968). However, the diversity and abundance of predators on Yellowstone's northern range have increased in recent decades (Bangs and Fritts 1996, Smith et al. 2003, Harris et al. 2007). Few pronghorn populations are exposed to the diversity of predators now present in Yellowstone, yet the relative extents to which coyotes and other species currently prey on Yellowstone pronghorn are unknown. Coyotes, bobcats (*Lynx rufus*), and Golden Eagles (*Aquila chrysaetos*) are the most common predators of pronghorn across western North America (reviewed in O'Gara and Shaw 2004). Other predators known to take adult pronghorn or

fawns in some populations include domestic dogs (*Canis lupus familiaris*), cougars (*Puma concolor*), badgers (*Taxidea taxus*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), and red foxes (*Vulpes vulpes*; O'Gara and Shaw 2004). All of these predator species are present in and adjacent to Yellowstone National Park. In addition, gray wolves (*Canis lupus*), wolverines (*Gulo gulo*), and lynx (*Lynx canadensis*) are present in Yellowstone at variable densities and are capable of taking fawns opportunistically. Incidental predation by the numerous predators present in Yellowstone may significantly impact overall juvenile survival in this pronghorn population.

The Yellowstone pronghorn population is partially migratory, with some individuals migrating from the winter range to higher-elevation summering areas within the park (White et al. 2007). The factors responsible for the maintenance of partial migration in this population are poorly understood, yet the increasing proportion of migrants in this population over the past decade (White et al. 2007) may signal important changes in habitat quality or predation risk over time. Data on predator-specific mortality would aid ongoing

¹Department of Biological Sciences, University of Idaho, Moscow, ID 83844-3051.

²National Park Service, Yellowstone National Park, WY 82190.

³E-mail: kkbarnowe-meyer@vandals.uidaho.edu

studies of spatial variation in predation risk and pronghorn reproductive success in this population. In the Gardiner Basin north of Yellowstone, domestic dogs may pose some predation risk to nonmigrant pronghorn on privately-owned portions of the winter range, while bobcats, lynx, Golden Eagles, gray wolves, cougars, badgers, grizzly and black bears, red foxes, and wolverines are generally found in interior areas of the park accessed solely by migrant pronghorn. The effects of wolf reintroduction on migrant pronghorn fawn survival is a topic of significant research interest because wolves were hypothesized to reduce coyote densities in some areas as a result of interspecific competition (White and Garrott 2005). Differences in the frequency and source of predation between areas are unknown yet may drive the migratory tendencies and demographics of this population (Taylor and Norris 2007).

The diverse predator community of Yellowstone National Park provides a model setting in which to assess the relative impact of numerous sympatric predators on adult and juvenile pronghorn survival. Our objectives were to identify the major and minor predators of Yellowstone pronghorn and to assess relative predation risk among summering areas selected by migrants and nonmigrants. Across these areas, we documented the frequency of predator-specific mortality of pronghorn adults and fawns and qualitatively assessed the risk from each predator species. Our results have significance for the management of Yellowstone's at-risk pronghorn population as well as other populations inhabiting mixed habitat types and areas possessing diverse predator communities. These data also have significance for research involving the migration, dispersal, and range expansion of pronghorn and other ungulate populations worldwide.

STUDY AREA

Pronghorn inhabit various open portions (approximately 330 km²) of the northern range of Yellowstone National Park in Montana and Wyoming (Fig. 1). Pronghorn movements in winter are restricted to the arid and windswept basin surrounding Gardiner, Montana, an area of approximately 30 km² below 1700 m elevation (Fig. 2; Barmore 1980). The habitat in this area is open grassland and shrub-

steppe, interspersed with abandoned agricultural fields dominated by exotic grasses and forbs, active agricultural fields, and nonvegetated areas (Boccardori et al. 2008). Between April and October each year, a portion of the Yellowstone pronghorn herd migrates over Mt. Everts (Fig. 2) to summer ranges within the park between 1500 and 2500 m elevation (White et al. 2007, Boccardori et al. 2008). These areas are characterized by a diversity of habitat types, including grasslands, shrub-steppe, nonvegetated thermal features, coniferous forests, and subalpine meadows (Despain 1990). Following birthing and several weeks of isolation in late May and June, pronghorn females congregate within several largely discrete shrubsteppe areas until autumn migration (White et al. 2007). Resident individuals occupy the winter range year-round for foraging, birthing, and fawn rearing (White et al. 2007, Boccardori et al. 2008). Pronghorn share portions of their total annual range with coyotes, gray wolves, cougars, grizzly bears, black bears, Golden Eagles, bobcats, badgers, red foxes, wolverines, lynx, and domestic dogs (outside the park). Sympatric ungulates include moose (*Alces alces*), bison (*Bison bison*), elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), mountain goats (*Oreamnos americanus*), and bighorn sheep (*Ovis canadensis*). Small mammal species available as alternate prey for some predators include deer mice (*Peromyscus maniculatus*), microtine rodents (*Microtus* spp.), pocket gophers (*Thomomys talpoides*), and Uinta ground squirrels (*Spermophilus armatus*).

METHODS

We captured adult female pronghorn in the winters of 1999–2005 via darting from the ground and net-gunning from a helicopter (Firchow et al. 1986), and we fitted individuals with either a very-high-frequency (VHF) or a global-positioning-system (GPS) radio-collar with a mortality sensor on a 6-hour delay (Lotek Wireless Inc., Newmarket, Ontario, Canada). Capture operations were conducted in accordance with guidelines set forth by the American Society of Mammalogists (Animal Care and Use Committee 1998). To detect mortality events, we visually located 40 radio-collared adult female pronghorn approximately

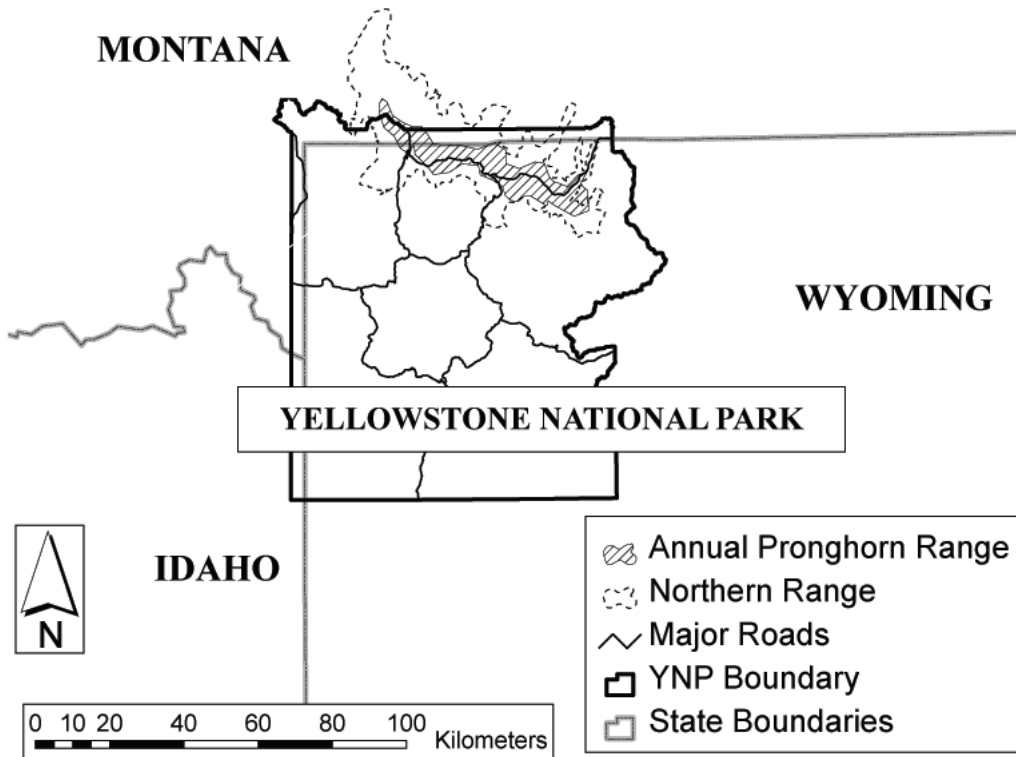


Fig. 1. Study area and approximate range of pronghorn within and adjacent to Yellowstone National Park, Montana and Wyoming.

twice weekly during spring, summer, and autumn, and twice monthly during winter in 1999–2001 and 2004–2006. We excluded newly captured adults (≤ 2 weeks post-capture) from analysis to avoid biasing winter estimates of relative predation towards those predators (coyotes) most common on the winter range where captures occurred.

We attached solar-powered, eartag radio-transmitters with mortality sensors on a 12-hour delay (Advanced Telemetry Systems, Inc., Isanti, MN) to 28 fawns captured within 4 days of birth in 1999, 2000, and 2001. Fawns were captured by hand using methods that did not predispose individuals to predation (Byers 1997a). We monitored signals from instrumented fawns daily to detect mortality events. When transmitters indicated death, we attempted to recover the tag or collar and to record information on its location, presence of bite marks or other physical damage, and whether any remnants of the carcass were present. When the carcass was relatively intact, we used descriptions of predator-kill

characteristics in O’Gara and Shaw (2004) to identify the predator species involved. Fawns were monitored until 1 August of each year. Additional fawn mortality data (noted in text) were obtained from opportunistic discovery of fawn mortality events involving noninstrumented fawns from 1999 through 2006.

RESULTS

Rapid carcass use by predators and scavengers made determination of cause of death difficult in many instances. Cause-specific adult mortality ($n = 22$) included 13 predator kills (5 coyotes, 3 cougars, 1 wolf, and 4 undetermined predators), 8 deaths due to undetermined causes, and 1 death due to birthing complications. We witnessed 1 instance in which a coyote attacked and killed an instrumented pronghorn mother on the day after she had given birth. Two of the cougar predation events on adults occurred within migration corridors in the period immediately following birthing. Of those adult mortality events for which a

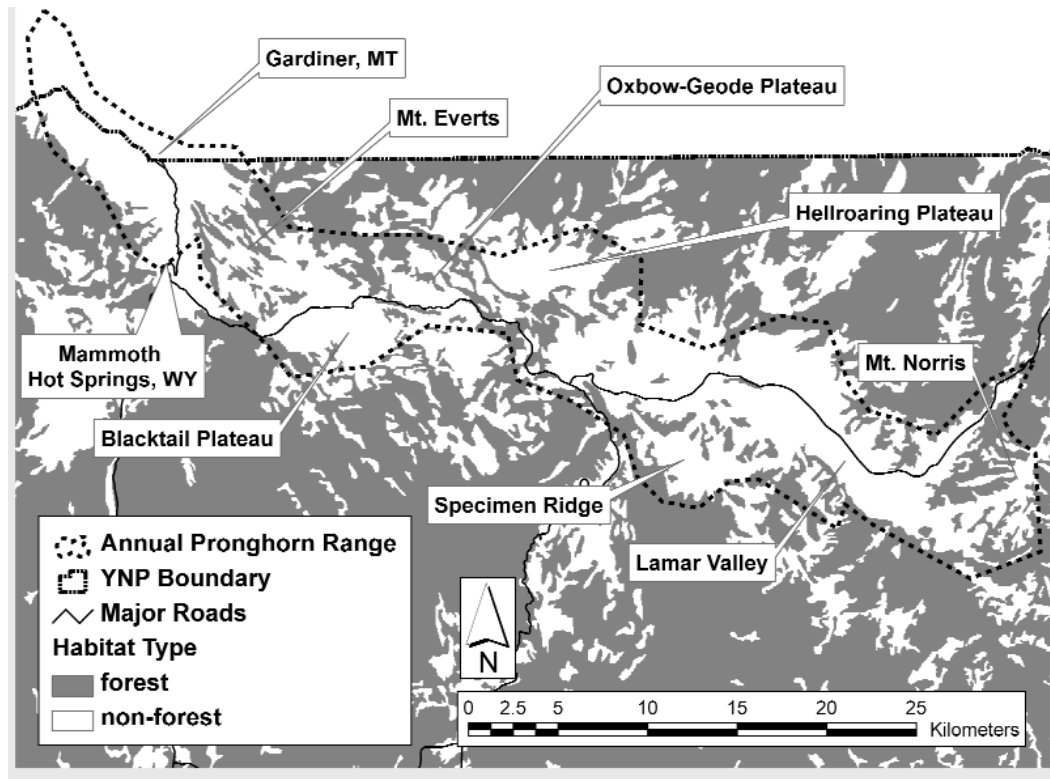


Fig. 2. Forested and nonforested habitat types within the approximate yearly range of pronghorn in and adjacent to Yellowstone National Park, Montana and Wyoming. Migrant pronghorn occupy areas from Mt. Everts east to Mt. Norris during the summer months.

predator species could be implicated, 56% (5 of 9) involved coyotes.

Pronghorn give birth across Yellowstone's northern range, from low elevations in the Gardiner Basin to the slopes of Mt. Norris (Fig. 2), in most major habitat types (K.K. Barnowe-Meyer unpublished data). Four of 28 tagged fawns (14%) survived to August: 2 born to migrant females and 2 born to nonmigrant females. Eight of 28 tagged fawns disappeared without leaving any physical evidence of mortality, and 2 died of undetermined causes. Of those instrumented fawns known to have been killed by predators ($n = 14$), 6 (43%) were killed by coyotes, 5 (36%) were scavenged and likely killed by coyotes, 1 (7%) was killed by a raptor (likely a Golden Eagle), and 2 (14%) were killed by an unidentified predator. Of the 6 coyote-killed fawns, we witnessed 2 events directly. Also, we recovered 4 of the 5 coyote-scavenged fawn eartags ≤ 30 m from coyote dens; all tags showed bite marks. The small

size of pronghorn fawn carcasses and their rapid consumption by predators (Robinson 1952) suggest that secondhand scavenging opportunities may have been limited. Coyotes therefore accounted for between 43% (6 of 14) and 79% (11 of 14) of total predation on instrumented fawns.

Between 1999 and 2006, three additional instances were documented involving predator effects on noninstrumented fawns. Coyote predation on an instrumented adult female one day following birthing (noted previously) resulted in the orphaning of twin fawns. Also noted previously, cougar predation on an instrumented adult female in 2004 orphaned a single fawn within the Mt. Everts migration corridor connecting the winter range with the interior summering areas (Fig. 2). The fate of these orphaned fawns could not be determined, but all were orphaned within 2 weeks of birth. Finally, a black bear was observed opportunistically killing a bedded, 10-day-old

fawn in 2004. The bear quickly carried the noninstrumented fawn into a timbered area while being observed by a small group of alarmed adult female pronghorn nearby.

DISCUSSION

Predation was the most common proximate cause of death for both adult female pronghorn ($\geq 59\%$) and fawns ($\geq 67\%$) in Yellowstone; these values likely underestimate actual predation rates, because we were unable to assign cause of death in some instances. Data suggest that coyotes are the main predator of both adults and fawns. When we included only those instances when species-specific predation could be determined, coyotes were responsible for 56% of adult female predation and up to 79% of fawn predation during our study. Prior to wolf reintroduction, coyote densities exceeded 1.0 per km² in many areas of Yellowstone's northern range (Crabtree and Sheldon 1999). This value is equivalent to or higher than coyote densities in areas occupied by pronghorn populations elsewhere (Barrett 1984, Dunbar and Giordano 2002, Jacques et al. 2007). In general, areas of high coyote density in Yellowstone (open, low-lying, mesic shrubsteppe habitat; Crabtree and Sheldon 1999) are also those selected by many female pronghorn prior to and following birthing (K.K. Barnowe-Meyer unpublished data). Researchers are currently investigating differences in coyote densities between migrant and nonmigrant areas.

Cougars and wolves accounted for the balance of predator-specific mortality on adult females (33% and 11%, respectively). Cougars, Golden Eagles, and black bears killed some fawns, either through direct predation or by orphaning dependent fawns. Our modest sample sizes prevented a thorough examination of quantitative differences in species-specific predation rates on migrant and nonmigrant pronghorn in Yellowstone. However, coyote predation affected both migrant and nonmigrant pronghorn, while cougar, Golden Eagle, black bear, and wolf predation occurred solely in areas accessed by migrants during the summer. Nonmigrants do enjoy limited seasonal access to partially timbered areas surrounding the Gardiner Basin, yet these areas appear to lack the frequent presence of several species of predators, notably wolves.

Cougars have been documented killing adult pronghorn in several populations, generally at low rates (Knipe 1944, Shaw 1977, Anderson and Lindzey 2003). However, cougars caused 42% of adult pronghorn mortality during one study in central Arizona (Ockenfels 1994), and a single cougar was documented killing over 60 adult pronghorn during a 2-year period in Texas (Engstrom and Maxwell 1988). Heavy cougar predation on fawns has been reported in central Arizona (53% of total mortality; S. Schuetze 1992, cited in O'Gara and Shaw 2004) and Texas ($\leq 20\%$ of total mortality; Canon and Bryant 1992). Cougars were the second-most-common source of predation on adult Yellowstone pronghorn during our study, with most predation occurring in and adjacent to areas of heavy vegetative cover where visibility was reduced. Cougars are present in many timbered areas utilized by migrating Yellowstone pronghorn (Murphy 1998, Ruth 2004). Pronghorn constituted only 0.3% of prey items consumed by cougars on Yellowstone's northern range from 1987 to 1996 (Murphy 1998). However, the proportion of Yellowstone pronghorn migrating during this period was low (20%–25%; Scott and Geisser 1996, Caslick 1998) relative to our study period (approximately 70%; White et al. 2007). Forested areas are common on Mt. Everts (White et al. 2007); on the periphery of the Blacktail, Oxbow-Geode, and Hellroaring plateaus; and on the slopes surrounding the Lamar Valley floor and Specimen Ridge (Fig. 2). These areas are only available to and utilized by migrant pronghorn.

Golden Eagles have been documented killing pronghorn adults and fawns in many populations (Beale 1978, Autenrieth 1982, Byers 1997b). Though data are anecdotal, Golden Eagles are locally common in areas of high small-mammal abundance in Yellowstone, particularly in the Lamar Valley, where many pronghorn give birth. Pronghorn females actively defend fawns from attack by chasing eagles and standing over fawns (Woods 1925, Byers 1997b). Because of terrain variability and the movement of females away from bedded fawns for limited periods while browsing (Byers 1997b), Golden Eagles likely prey upon a small number of fawns each year.

Black and grizzly bears occasionally prey upon fawns (Murie 1935), and a black bear was observed opportunistically taking one fawn during this study. Bears of both species range

widely in Yellowstone but may be associated with certain areas during the pronghorn fawning period. Grizzly and black bears prey heavily on elk calves during the pronghorn fawning season (Barber-Meyer et al. 2008) and may pose a heightened risk to fawns in major calving areas, particularly in the Lamar Valley (Barber-Meyer et al. 2008). Grizzly bears congregate at relatively high elevation in late spring (about 2400 m; Haroldson et al. 2002), and black bears often follow receding snow lines to access emerging vegetation during this period (Jonkel and Cowan 1971, Amstrup and Beecham 1976). These seasonal trends may result in occasional grizzly and black bear predation on pronghorn fawns in isolated and high-elevation areas selected by some migrant pronghorn (K.K. Barnowe-Meyer unpublished data). However, no evidence of pronghorn consumption was detected in a recent diet study on Yellowstone's grizzly bears (Mattson 1997).

Although badgers, bobcats, lynx, wolverines, foxes, and domestic dogs may prey occasionally on pronghorn fawns (O'Gara and Shaw 2004), we did not detect predation by these species on pronghorn. Field observations suggest that badgers are variably common in sagebrush-dominated areas along the Yellowstone and Lamar rivers, east of Gardiner (K.K. Barnowe-Meyer personal observation). Bobcats are rarely observed in Yellowstone, and the species' distribution and abundance within the park are unknown. Lynx are virtually never seen in the park (Murphy et al. 2006) and probably seldom encounter pronghorn fawns because of differential habitat use. Wolverines are present in Yellowstone at low densities within areas accessed by some migrant pronghorn (Consolo-Murphy and Meagher 1995) and may occasionally encounter fawns in high-elevation areas. Domestic dogs may account for some predation of nonmigrant fawns north of the park near Gardiner, Montana. Though red foxes can impact fawn survival under certain circumstances (O'Gara and Shaw 2004), ungulates do not constitute a significant portion of red fox diets in Yellowstone (Van Etten 2006).

Wolf predation on Yellowstone pronghorn has been documented on numerous occasions since wolf reintroduction in 1995 (Phillips and Smith 1997, Smith et al. 1998, 2004, 2005, 2007, Smith and Guernsey 2001). However,

overall predation rates have been low ($\leq 1\%$ of summer diets; Smith et al. 2007), suggesting that direct wolf predation on Yellowstone pronghorn is largely opportunistic. The broader ecosystem effect of wolves on pronghorn fawn survival is currently being assessed. Although Yellowstone's northern range supports a relatively high density of wolves (Smith et al. 2003), the pronghorn winter range inhabited by nonmigrant pronghorn year-round is relatively wolf-free (Kauffman et al. 2007). There is speculation that the reintroduction of wolves may indirectly contribute to increased recruitment of migrant Yellowstone pronghorn by reducing the coyote population in areas of high wolf use (Crabtree and Sheldon 1999, White and Garrott 2005, Berger and Gese 2007). Research on this topic is ongoing. The long-term effects of wolf presence on other sympatric predators, such as cougars, are unknown at this time.

Migration or dispersal to nearby, yet non-contiguous, areas often necessitates individual movements through areas of suboptimal habitat (Trainer et al. 1983, Sawyer et al. 2005, White et al. 2007). For migrant ungulates, these movements often carry direct fitness costs (Nicholson et al. 1997, reviewed in Bolger et al. 2008). Pronghorn exhibit increased alertness when visibility decreases, suggesting greater perceived risk of predation in thickly vegetated areas (Goldsmith 1990). The renowned visual acuity and running speed of pronghorn are curbed by reduced visibility and rugged terrain, increasing the likelihood of capture by a variety of predators. Ockenfels (1994) noted an association between cougar kill sites and rugged or thickly vegetated terrain. Pronghorn in Yellowstone traverse narrow, nonforested corridors on Mt. Everts and the Oxbow-Geode Plateau during migration, with some corridors on Mt. Everts narrowing to no more than 50–60 m in width (White et al. 2007). Several other migratory pronghorn populations face constricted or partially forested migration corridors (Trainer et al. 1983, Foster 1988, Sawyer et al. 2005). Our results suggest that pronghorn face an increased risk of predation from cougars within thickly vegetated migration corridors in Yellowstone and may face similar risk in populations elsewhere.

The adult mortality we observed in the period immediately following parturition highlights the influence of habitat selection

during and following birthing on female and fawn vulnerability to predation. Rugged and densely vegetated areas likely restrict defensive efforts employed by females to protect nearby fawns (Byers 1997b). Though coyotes may be encountered in many habitat types across western North America (Koehler and Hornocker 1991, Crabtree and Sheldon 1999, Kamler and Gipson 2000, Arjo and Pletscher 2004), additional predator species (notably cougars, bobcats, and black bears) may be encountered by female pronghorn selecting rugged or mixed habitat types adjacent to open areas (Amstrup and Beecham 1976, Koehler and Hornocker 1991, Neale and Sacks 2001). Maternal defense efforts, normally employed against smaller predators (Lipetz and Bekoff 1980, Byers 1997b), may also be less effective against these larger species. In addition, the increased vulnerability of adult females following parturition increases the risk of *de facto* fawn mortality resulting from the orphaning of dependent fawns. During birthing, as during migration, pronghorn may increase their susceptibility to opportunistic predation by numerous predator species by selecting rugged or thickly vegetated areas. Despite these risks, Yellowstone females selecting rugged and partially forested areas for birthing tend to exhibit higher reproductive success than females selecting more open, lower-elevation habitat (K.K. Barnowe-Meyer unpublished data). Overall predation risk in the former areas may be lower due to less-frequent selection of high-elevation, rugged areas by Yellowstone coyotes (Crabtree and Varley 1995, Moorcroft et al. 2006).

The factors ultimately governing fawn survival in this population are still under investigation. We are currently assessing spatial and temporal variation in forage quality across areas utilized by Yellowstone pronghorn. Dunbar (2002) found little evidence of disease in this population, and available data suggest that Yellowstone pronghorn retain relatively high levels of genetic diversity (Lee 1994, Lou 1998). Despite the greater diversity of predators in migrant areas, preliminary data suggest that migrant fawn survival exceeds that of nonmigrants (K.K. Barnowe-Meyer unpublished data). Our results indicate that spatial variation in the predation risk posed by coyotes may underlie significant variation in total predation risk to pronghorn fawns. The extent to which coyote

predation is influenced by sympatric predator species, habitat attributes, and other factors is an area of intense research interest. The reintroduction of wolves into Yellowstone was hypothesized to have a variety of ecosystem-level effects (Buskirk 1999, Johnson and Crabtree 1999). To date, peer-reviewed studies investigating the realized impact of wolves on apex and mesopredators in Yellowstone have been scarce (Switalski 2003, Wilmers et al. 2003). Further work is needed to investigate the extent to which wolves, habitat characteristics (Gese et al. 1996), and social factors (Moorcroft et al. 2006) influence the predation risk posed by coyotes on Yellowstone's northern range.

ACKNOWLEDGMENTS

Financial support for this project was provided by the Bernice Barbour Foundation, Montana State University, the National Park Service, the University of Idaho, and the Yellowstone Park Foundation. We thank V. Boccadori, D. Chalfant, H. Harris, C. Hernandez, J. Mack, W. Maples, K. Nittinger, G. Obrist, A. Playter, K. Pullen, M. Robinson, L. Stinson, D. Thompson, and B. Whitfield for data collection efforts. We are grateful to K. Tonnessen and the Rocky Mountains Cooperative Ecosystem Studies Unit for facilitating funding agreements, and are grateful to Hawkins & Powers Aviation, Helicopter Capture Services, Leading Edge Aviation, and Montana Aircraft for support with pronghorn capture and aerial telemetry.

LITERATURE CITED

- AMSTRUP, S.C., AND J. BEECHAM. 1976. Activity patterns of radio-collared black bears in Idaho. *Journal of Wildlife Management* 40:340–348.
- ANDERSON, C.R., JR., AND E.G. LINDZEY. 2003. Estimating cougar predation rates from GPS location clusters. *Journal of Wildlife Management* 67:307–316.
- ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79:1416–1431.
- ARJO, W.M., AND D.H. PLETSCHER. 2004. Coyote and wolf habitat use in northwestern Montana. *Northwest Science* 78:24–32.
- AUTENRIETH, R.E. 1982. Pronghorn fawn habitat use and vulnerability to predation. *Proceedings of the 10th Biennial Pronghorn Antelope Workshop* 10:112–131.
- BANGS, E.E., AND S.H. FRITTS. 1996. Reintroducing the gray wolf to central Idaho and Yellowstone National Park. *Wildlife Society Bulletin* 24:402–413.

- BARBER-MEYER, S.M., L.D. MECH, AND P.J. WHITE. 2008. Survival and cause-specific elk calf mortality following wolf restoration to Yellowstone National Park. *Wildlife Monographs* 169:1–30.
- BARMORE, W.J. 1980. Population characteristics, distribution and habitat relationships of six ungulates in northern Yellowstone Park. Utah State University, Logan.
- BARRETT, M.W. 1984. Movements, habitat use, and predation on pronghorn fawns in Alberta. *Journal of Wildlife Management* 48:542–550.
- BEALE, D.M. 1978. Birth rate and fawn mortality among pronghorn antelope in western Utah. *Proceedings of the 8th Biennial Pronghorn Antelope Workshop* 8:445–446.
- BERGER, K.M., AND E.M. GESE. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology* 76:1075–1085.
- BOCCADORI, S.J., P.J. WHITE, R.A. GARROTT, J.J. BORKOWSKI, AND T.L. DAVIS. 2008. Yellowstone pronghorn alter resource selection after sagebrush decline. *Journal of Mammalogy* 89:1031–1040.
- BOLGER, D.T., W.D. NEWMARK, T.A. MORRISON, AND D.F. DOAK. 2008. The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters* 11:63–77.
- BUSKIRK, S.W. 1999. Mesocarnivores in Yellowstone. Pages 165–187 in T.W. Clark, A.P. Curlee, S.C. Minta, and P.M. Kareiva, editors, *Carnivores in ecosystems: the Yellowstone experience*. Yale University Press, New Haven, CT.
- BYERS, J.A. 1997a. Mortality risk to young pronghorns from handling. *Journal of Mammalogy* 78:894–899.
- _____. 1997b. American pronghorn: social adaptations and the ghosts of predators past. University of Chicago Press, Chicago, IL.
- CANON, S.K., AND F.C. BRYANT. 1992. Survival of Trans-Pecos pronghorn. *Proceedings of the 15th Biennial Pronghorn Antelope Workshop* 15:67–77.
- CASLICK, J.W. 1998. Yellowstone pronghorns: relict herd in a shrinking habitat. *Yellowstone Science* 6:20–24.
- CONSOLO-MURPHY, S.L., AND M. MEAGHER. 1995. The status of wolverine, lynx, and fisher in Yellowstone National Park. Pages 57–62 in A.P. Curlee, A.M. Gillesberg, and D. Casey, editors, *Greater Yellowstone predators: ecology and conservation in a changing landscape*. *Proceedings of the 3rd Biennial Conference on the Greater Yellowstone Ecosystem*. Yellowstone National Park and Northern Rockies Conservation Cooperative, Jackson, WY.
- CRABTREE, R.L., AND J.W. SHELDON. 1999. The ecological role of coyotes on Yellowstone's northern range. *Yellowstone Science* 7:15–23.
- CRABTREE, R.L., AND J.D. VARLEY. 1995. The ecological and sociodemographic role of the coyote on Yellowstone's northern range. Pages 63–84 in A.P. Curlee, A.M. Gillesberg, and D. Casey, editors, *Greater Yellowstone predators: ecology and conservation in a changing landscape*. *Proceedings of the 3rd Biennial Conference on the Greater Yellowstone Ecosystem*. Yellowstone National Park and Northern Rockies Conservation Cooperative, Jackson, WY.
- DESPAIN, D.G. 1990. *Yellowstone vegetation: consequences of environment and history in a natural setting*. Roberts Rinehart Publishers, Boulder, CO.
- DUNBAR, M.R. 2002. Physiological ecology of pronghorn of Yellowstone National Park, Wyoming. *Proceedings of the Yellowstone Pronghorn Conservation Assessment Workshop*. Mammoth Hot Springs, WY.
- DUNBAR, M.R., AND M.R. GIORDANO. 2002. Abundance and condition indices of coyotes on Hart Mountain National Antelope Refuge, Oregon. *Western North American Naturalist* 62:641–647.
- ENGSTROM, M.D., AND T.C. MAXWELL. 1988. Records of mountain lion (*Felis concolor*) from the Edwards Plateau of Texas. *Texas Journal of Science* 40:450–452.
- FIRCHOW, K.M., M.R. VAUGHAN, AND W.R. MYTTON. 1986. Evaluation of the hand-held net gun for capturing pronghorns. *Journal of Wildlife Management* 50:320–322.
- FOSTER, C.L. 1988. Migration of Fort Rock and Duncan Reservoir pronghorn, Oregon. *Proceedings of the 13th Biennial Pronghorn Antelope Workshop* 13:72–82.
- GESE, E.M., R.L. RUFF, AND R.L. CRABTREE. 1996. Intrinsic and extrinsic factors influencing coyote predation of small mammals in Yellowstone National Park. *Canadian Journal of Zoology* 74:784–797.
- GOLDSMITH, A.E. 1990. Vigilance behavior of pronghorns in different habitats. *Journal of Mammalogy* 71:460–462.
- HAROLDSON, M.A., M.A. TERNENT, K.A. GUNTHER, AND C.C. SCHWARTZ. 2002. Grizzly bear denning chronology and movements in the Greater Yellowstone Ecosystem. *Ursus* 13:29–37.
- HARRIS, R.B., G.C. WHITE, C.C. SCHWARTZ, AND M.A. HAROLDSON. 2007. Population growth of Yellowstone grizzly bears: uncertainty and future monitoring. *Ursus* 18:168–178.
- JACQUES, C.N., J.A. JENKS, J.D. SIEVERS, D.E. RODDY, AND F.G. LINDZEY. 2007. Survival of pronghorns in western South Dakota. *Journal of Wildlife Management* 71:737–743.
- JOHNSON, K.A., AND R.L. CRABTREE. 1999. Small prey of carnivores in the Greater Yellowstone Ecosystem. Pages 239–263 in T.W. Clark, A.P. Curlee, S.C. Minta, and P.M. Kareiva, editors, *Carnivores in ecosystems: the Yellowstone experience*. Yale University Press, New Haven, CT.
- JONKEL, C.J., AND I. MCT. COWAN. 1971. The black bear in the spruce-fir forest. *Wildlife Monographs* 27:3–57.
- KAMLER, J.F., AND P.S. GIPSON. 2000. Space and habitat use by resident and transient coyotes. *Canadian Journal of Zoology* 78:2106–2111.
- KAUFFMAN, M.J., N. VARLEY, D.W. SMITH, D.R. STAHLER, D.R. MACNULTY, AND M.S. BOYCE. 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology Letters* 10:690–700.
- KNIPE, T. 1944. The status of the antelope herds of northern Arizona. P-R Project 9R, Arizona Game and Fish Commission, Phoenix, AZ.
- KOEHLER, G.M., AND M.G. HORNOCKER. 1991. Seasonal resource use among mountain lions, bobcats, and coyotes. *Journal of Mammalogy* 72:391–396.
- LEE, T.E.J. 1994. Mitochondrial DNA and allozyme analysis of North American pronghorn populations. *Journal of Wildlife Management* 58:307–318.
- LIPETZ, V.E., AND M. BEKOFF. 1980. Possible functions of predator harassment in pronghorn antelopes. *Journal of Mammalogy* 61:741–743.
- LOU, Y. 1998. Genetic variation of pronghorn (*Antilocapra americana*) populations in North America. Doctoral dissertation, Texas A&M University, College Station.

- MATTSON, D.J. 1997. Use of ungulates by Yellowstone grizzly bears. *Biological Conservation* 81:161–177.
- MOORCROFT, P.R., M.A. LEWIS, AND R.L. CRABTREE. 2006. Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. *Proceedings of the Royal Society B: Biological Sciences* 273:1651–1659.
- MURIE, A. 1940. Ecology of the coyote in the Yellowstone. National Park Service Fauna Series No. 4, U.S. Government Printing Office, Washington DC.
- MURIE, O.J. 1935. Food habits of the coyote in Jackson Hole, Wyoming. U.S. Department of Agriculture Circ. 362, Washington, DC.
- MURPHY, K.M. 1998. The ecology of the cougar (*Puma concolor*) in the northern Yellowstone ecosystem: interactions with prey, bears, and humans. Doctoral dissertation, University of Idaho, Moscow.
- MURPHY, K.M., T.M. POTTER, J.C. HALFPENNY, K.A. GUNTHER, M.T. JONES, P.A. LUNDBERG, AND N.D. BERG. 2006. Distribution of Canada lynx in Yellowstone National Park. *Northwest Science* 80:199–206.
- NATIONAL RESEARCH COUNCIL. 2002. Ecological dynamics on Yellowstone's northern range. National Academy Press, Washington, DC.
- NEALE, J.C.C., AND B.N. SACKS. 2001. Resource utilization and interspecific relations of sympatric bobcats and coyotes. *Oikos* 94:236–249.
- NICHOLSON, M.C., R.T. BOWYER, AND J.G. KIE. 1997. Habitat selection and survival of mule deer: trade-offs associated with migration. *Journal of Mammalogy* 78:483–504.
- OCKENFELS, R.A. 1994. Mountain lion predation on pronghorn in central Arizona. *Southwestern Naturalist* 39:305–306.
- O'GARA, B.W. 1968. A study of the reproductive cycle of the female pronghorn. Doctoral dissertation, University of Montana, Missoula.
- O'GARA, B.W., AND H.G. SHAW. 2004. Predation. Pages 337–377 in B.W. O'Gara and J.D. Yoakum, editors, *Pronghorn: ecology and management*. University Press of Colorado, Boulder.
- PHILLIPS, M.K., AND D.W. SMITH. 1997. Yellowstone Wolf Project: Biennial Report, 1995–1996. Yellowstone National Park, Mammoth Hot Springs, WY.
- ROBINSON, W.B. 1952. Some observations on coyote predation in Yellowstone National Park. *Journal of Mammalogy* 33:470–476.
- RUTH, T.K. 2004. Ghost of the Rockies: the Yellowstone cougar project. *Yellowstone Science* 12:13–24.
- SAWYER, H., F. LINDZEY, AND D. MCWHIRTER. 2005. Mule deer and pronghorn migration in western Wyoming. *Wildlife Society Bulletin* 33:1266–1273.
- SCOTT, M.D., AND H. GEISSER. 1996. Pronghorn migration and habitat use following the 1988 Yellowstone fires. Pages 123–132 in J.M. Greenlee, editor, *Ecological implications of fire in the Greater Yellowstone*. Proceedings of the 2nd Biennial Conference on the Greater Yellowstone Ecosystem. USDI National Park Service, Yellowstone National Park, Mammoth, WY.
- SHAW, H.G. 1977. Impact of mountain lions on mule deer and cattle in northwestern Arizona. Pages 17–32 in R.L. Phillips and C. Jonkel, editors, *Proceedings of the 1975 Predator Symposium*. University of Montana Forestry and Conservation Experimental Station, Missoula.
- SKINNER, M.P. 1922. The prong-horn. *Journal of Mammalogy* 3:82–105.
- SMITH, D.W., AND D.S. GUERNSEY. 2001. Yellowstone Wolf Project: Annual Report, 2001. Yellowstone National Park, Mammoth Hot Springs, WY.
- SMITH, D.W., K.M. MURPHY, AND D.S. GUERNSEY. 1998. Yellowstone Wolf Project: Annual Report, 1998. Yellowstone National Park, Mammoth Hot Springs, WY.
- SMITH, D.W., R.O. PETERSON, AND D.B. HOUSTON. 2003. Yellowstone after wolves. *BioScience* 53:330–340.
- SMITH, D.W., D.R. STAHLER, AND D.S. GUERNSEY. 2004. Yellowstone Wolf Project: Annual Report, 2004. Yellowstone National Park, Mammoth Hot Springs, WY.
- _____. 2005. Yellowstone Wolf Project: Annual Report, 2005. Yellowstone National Park, Mammoth Hot Springs, WY.
- SMITH, D.W., D.R. STAHLER, D.S. GUERNSEY, M. METZ, E. ALBERS, L. WILLIAMSON, N. LEGERE, E. ALMBERG, AND R. MCINTYRE. 2007. Yellowstone Wolf Project: Annual Report, 2007. Yellowstone National Park, Mammoth Hot Springs.
- SWITALSKI, T.A. 2003. Coyote foraging ecology and vigilance in response to gray wolf reintroduction in Yellowstone National Park. *Canadian Journal of Zoology* 81:985–993.
- TAYLOR, C.M., AND D.R. NORRIS. 2007. Predicting conditions for migration: effects of density dependence and habitat quality. *Biology Letters* 3:280–283.
- TRAINER, C.E., M.J. WILLIS, G.P. KEISTER, JR., AND D.P. SHEEHY. 1983. Fawn mortality and habitat use among pronghorn during spring and summer in southeast Oregon, 1981–1982. Oregon Department of Fish and Wildlife Research Report 12, Portland, OR.
- VAN ETTEN, K. 2006. Habitat selection by red fox in Yellowstone National Park and mechanisms of coexistence with coyotes. Doctoral dissertation, Colorado State University, Fort Collins.
- WHITE, P.J., T.L. DAVIS, K.K. BARNOWE-MEYER, R.L. CRABTREE, AND R.A. GARROTT. 2007. Partial migration and philopatry of Yellowstone pronghorn. *Biological Conservation* 135:518–526.
- WHITE, P.J., AND R.A. GARROTT. 2005. Yellowstone's ungulates after wolves—expectations, realizations, and predictions. *Biological Conservation* 125:141–152.
- WILMERS, C.C., R.L. CRABTREE, D.W. SMITH, K.M. MURPHY, AND W.M. GETZ. 2003. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. *Journal of Animal Ecology* 72:909–916.
- WOODS, S.H. 1925. The pronghorned antelope: America's own—shall we permit its extermination? *American Forests and Forest Life* 31:649–651.

Received 17 January 2008

Accepted 17 October 2008