



Original Article

Energy Development and Hunter Success for Mule Deer and Pronghorn in Wyoming

R. SCOTT GAMO,¹ Wyoming Game and Fish Department and Department of Ecosystem Science and Management, University of Wyoming, Cheyenne, WY 82006, USA

KURT T. SMITH, Department of Ecosystem Science and Management, University of Wyoming, Laramie, WY 82071, USA

JEFFREY L. BECK, Department of Ecosystem Science and Management, University of Wyoming, Laramie, WY 82071, USA

ABSTRACT Infrastructure associated with energy development influences hunter access and introduces disturbance activities to landscapes that can influence habitat selection and behavior of ungulates. Consequently, habitat loss and hunter access concerns must be addressed by wildlife managers as they consider management of populations of western big game species including mule deer (*Odocoileus hemionus*) and pronghorn (*Antilocapra americana*). We evaluated whether increased energy development, as quantified through change in well pad density, has affected hunter success of mule deer and pronghorn. Ungulates tend to avoid energy development; therefore, we also evaluated whether hunting statistics can be used to identify potential effects of energy development on mule deer and pronghorn. We included data from 22 of 39 mule deer and 34 of 46 pronghorn Herd Units across Wyoming, USA, from 1980 to 2012. On average, well pad densities across mule deer Herd Units increased from 0.01 km² in 1980 to 0.06 km² in 2012, and well pads in pronghorn Herd Units increased from 0.01 km² to 0.12 km² during the same period. Our results indicated that hunter success for mule deer in Wyoming was positively associated with hunter effort, whereas pronghorn hunter success was negatively associated with hunter effort. Hunter success for both species was unaffected by well pad density. We identified a change in mule deer and pronghorn harvest success associated with hunter numbers and effort; however, harvest statistics were not informative in identifying impacts from energy development on mule deer or pronghorn populations. © 2017 The Wildlife Society.

KEY WORDS *Antilocapra americana*, harvest, *Odocoileus hemionus*, oil and gas development, resource extraction.

Ungulate habitat and population management is increasingly complex as landscapes continue to be subject to expanding human influences from energy extraction, industrialization, agricultural development, and urbanization. For example, the global demand for energy is estimated to increase by 40% within the next 20 years, leading to elevated coal, gas, oil, and renewable energy development (International Energy Agency 2015), which is projected to result in >200,000 km² of land utilized by various forms of energy development in the United States by 2035 (McDonald et al. 2009). Human-created surface disturbances such as mines, oil and gas well pads, logging, and roads contribute to habitat use changes by caribou (*Rangifer tarandus*; Cameron et al. 2005, Vors et al. 2006, Sorensen et al. 2007, Polfus et al. 2011), elk (*Cervus elaphus*; Thomas et al. 1979, Lyon 1983, Kuck et al. 1985, Millspaugh et al. 2000, Rowland et al. 2000, Rumble and Gamo 2011, Webb et al. 2011a, Buchanan et al. 2014), mule deer (*Odocoileus hemionus*; Rost and Bailey 1979;

Thomas et al. 1979; Medcraft and Clark 1986; Gamo and Anderson 2002; Sawyer et al. 2006, 2009, 2013; Lendrum et al. 2012), and pronghorn (*Antilocapra americana*; Ockenfels et al. 2000, Gamo and Anderson 2002, Sheldon 2005, Gavin and Komers 2006, Beckmann et al. 2012).

Negative effects to ungulates from energy development have often been associated with human activity (e.g., Sawyer et al. 2006, 2009; Buchanan et al. 2014). Energy development often includes increased road networks (Bureau of Land Management [BLM] 2003) to facilitate transportation of material, equipment, and personnel to and from well pads and other infrastructure points. In addition to increasing activity, increases in energy development and its associated increase in roads may facilitate hunter distributions through enhanced access to potential hunting areas (Gratson and Whitman 2000, Lebel et al. 2012). Hunter access influences harvest of ungulates; for example, Gratson and Whitman (2000) found that as hunter densities increased as a result of greater access, harvest success decreased. Others have noted that elk mortality, mainly due to harvest, increased with hunter access and densities (Unsworth et al. 1993, Cole et al. 1997, Hayes et al. 2002, McCorquodale et al. 2003, Webb et al. 2011b). In addition, increased access through road networks within intensively farmed areas in

Received: 9 May 2016; Accepted: 29 September 2016

Published: 1 February 2017

¹E-mail: scott.gamo@wyo.gov

Minnesota, USA, likely contributed to greater white-tailed deer (*O. virginianus*) vulnerability to hunting (Brinkman et al. 2004).

Traditional means of evaluating energy-related effects on ungulates have included time- and funding-intensive studies, often using GPS- or radiocollared animals to model potential changes in habitat selection and use of developed areas (e.g., Sawyer et al. 2006, 2009; Buchanan et al. 2014). However, harvest data are readily available and generally integrated into annual monitoring plans by state wildlife agencies to obtain critical information for big game population management. The Wyoming Game and Fish Department (WGFD), USA, similar to other western state wildlife agencies, annually collects a variety of herd and hunt statistics including harvest (%; hunter success), hunter effort (days until harvest), herd age ratio, and number of hunters per Herd Unit (Rupp et al. 2000, Rabe et al. 2002). Big game populations are increasingly exposed to increasing levels of disturbances in states such as Wyoming where energy development continues to expand. Evaluating ungulate population response to anthropogenic activities such as energy development may be possible through correlation of anthropogenic infrastructure with annual harvest and herd status data. Increased road networks developed to access energy resources may increase hunter access, but they may also increase avoidance of habitat by big game species. Analyses of these data may provide managers with meaningful information to better manage ungulate populations in landscapes facing increasing energy development.

Our primary objective was to evaluate whether increased energy development, as quantified through change in well

pad densities, has altered hunter success for mule deer and pronghorn in Wyoming. Ungulates tend to seasonally avoid energy development; therefore, it may be expected that hunter success is negatively related to development activities. However, increased hunter access has been associated with increased hunter success in ungulate populations. Therefore, we predicted that avoidance behaviors of mule deer and pronghorn associated with development would result in lower hunter success. The alternative prediction was that likely increased access associated with increased energy development should result in greater success for mule deer and pronghorn hunters.

STUDY AREA

Our analysis included data from 22 of 39 (56.4%) WGFD mule deer (Fig. 1) and 34 of 46 (73.9%) pronghorn (Fig. 2) Herd Units that occurred across Wyoming, with the exception of national parks. Boundaries of the Herd Units included in our evaluations were consistent over the 30 years of our analysis (S. Smith, WGFD, personal communication) and delineated and mapped by WGFD staff through annual ground or aerial observations of areas frequented by mule deer and pronghorn. Herd Units encompassed ungulate populations in a diversity of forest, sagebrush (*Artemisia* spp.), and short-grass prairie ecosystems throughout Wyoming (Knight et al. 2014). Areas where energy development and Herd Units overlapped most often co-occurred within the sagebrush-dominated basins in the

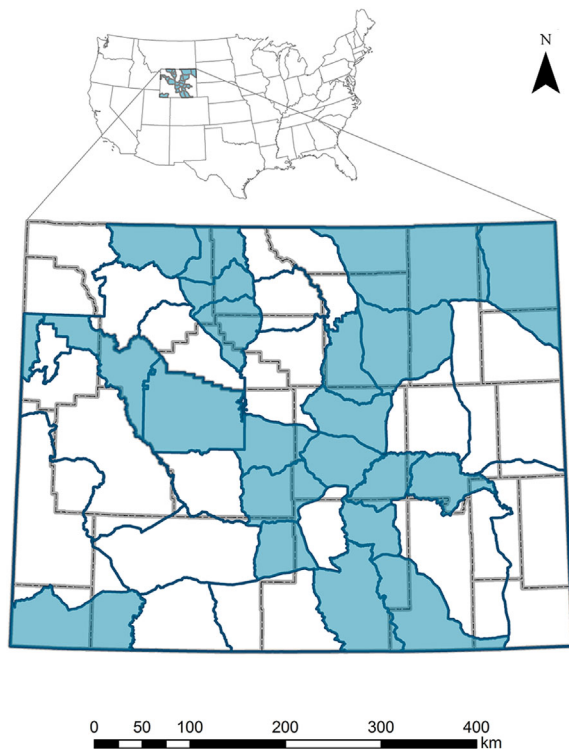


Figure 1. Location of the 22 Mule Deer Herd Units (shaded in blue) evaluated in Wyoming, USA, 1980–2012.

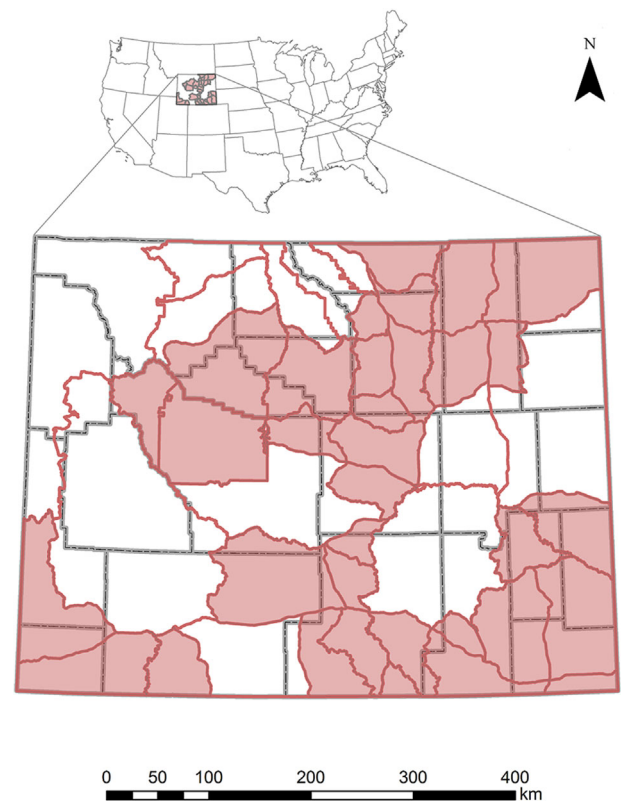


Figure 2. Location of 34 Pronghorn Herd Units (shaded in red) evaluated in Wyoming, USA, 1980–2012.

western and northeastern portions of Wyoming. The Wyoming Basin occurred within the western half of Wyoming and consisted of multiple basins between mountain ranges (Rowland and Leu 2011). Major basins included the Bighorn, Great Divide, Green River, and Shirley. Vegetation in these basins generally consisted of shrub steppe dominated by Wyoming big sagebrush (*A. tridentata wyomingensis*), but also included areas of black (*A. nova*) and low sagebrush (*A. arbuscula*; Rowland and Leu 2011, Knight et al. 2014). Common grasses included bluebunch wheatgrass (*Pseudoroegneria spicata*), needle and thread (*Hesperostipa comata*), western wheatgrass (*Pascopyrum smithii*), and a variety of blue grasses (*Poa* spp). Cheatgrass (*Bromus tectorum*), an invasive annual, was becoming more common.

Northeastern Wyoming rangelands, including the Powder River Basin, consisted of sagebrush-dominated shrub steppe assimilating with mixed-grass prairie toward the South Dakota, USA, border (Knight et al. 2014). Shrub steppe habitat was characterized by Wyoming big sagebrush, silver sagebrush (*A. cana*), and a diversity of herbaceous plants comprising the understory. Common forbs included desert alyssum (*Alyssum desertorum*), milkvetches (*Astragalus* spp.), and scarlet globemallow (*Sphaeralcea coccinea*). Common native grasses included blue grama (*Bouteloua gracilis*), bluebunch wheatgrass, prairie junegrass (*Koeleria macrantha*), and western wheatgrass. Nonnative grasses included crested wheatgrass (*Agropyron cristatum*) and cheatgrass (Thelenius et al. 1994). Rocky Mountain juniper (*Juniperus scopulorum*) and ponderosa pine (*Pinus ponderosa*) occurred on rocky uplifts and in river drainages.

Herd Units lying entirely within mountain ranges in Wyoming typically did not overlap with energy development. However, Herd Units overlapping mountain ranges with adjacent foothills and rangelands typically included some level of energy or extractive resource development. Wyoming mountain ranges encompassed temperate forests with species including Douglas fir (*Pseudotsuga menziesii*), Englemann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), ponderosa pine, and quaking aspen (*Populus tremuloides*). The short-grass prairie in the southeast corner of the state consisted of grasses including blue grama, buffalo grass (*Bouteloua dactyloides*), western wheatgrass, and needle and thread (USDA NRCS 2016).

METHODS

Study Design

We evaluated hunter data from 1980 to 2012 for mule deer and pronghorn in Wyoming. We utilized WGFD harvest data collated and calculated at the Herd Unit level across the state on an annual basis (Wyoming Game and Fish Department 1980–2012). The 22 mule deer and 34 pronghorn Herd Units we selected for our analyses had consistent boundaries and data collection over the timeframe we evaluated. These Herd Units also provided good geographical representation of the state (Figs. 1 and 2). The WGFD administered both general and limited draw

hunts for each ungulate species. The designation of hunts can change from year to year within the Hunt Areas that comprise Herd Units in regard to season length and tag allocation based on estimated animal abundance. The primary change that occurred within Hunt Areas has historically been the number of permits made available. In addition, the focus of harvest has been directed at male animals or in combination with females and fawns being harvested through any deer or any antelope tags (Wyoming Game and Fish Department 1980–2012). Wyoming Game and Fish Department used a solicited mailed or online hunter report system to collect hunter-related data. Statistics determined from these data included hunter success, hunter effort, and number of hunters. Hunter success was the percentage of license holders who were reported to be successful in harvesting a deer or pronghorn each year within respective Herd Units. Hunter effort was the average number of days hunted and included both successful and unsuccessful hunters. Number of hunters was the total number of hunters for each species in each Herd Unit and reflective of available permits. We recognized that changes in season structure in individual Hunt Areas within Herd Units may contribute to variation in reported harvest data; however, hunter effort and hunter numbers likely reflected yearly variation in season structure changes.

We used well pad density as a surrogate measure of energy development, similar to Harju et al.'s (2010) study on male greater sage-grouse (*Centrocercus urophasianus*) lek attendance response to oil and gas development in Wyoming. We contend that our choice of well pad density as an explanatory variable to evaluate how energy development may have influenced hunter access was logical because 1) it has been reported that one natural gas well is, on average, accompanied by 2 km of roads (BLM 2003) and 2) data on road network expansion in oil and gas fields were not readily available across the 33-year period of our study, whereas well pad data were recorded. We thus reasoned that areas with greater numbers of well pads were positively related to greater access, resulting in greater potential effects from energy development on hunter success. Furthermore, well pad density was area-adjusted based on the size of each Herd Unit. We collected active well data from the Wyoming Oil and Gas Conservation Commission (WOGCC) oil and gas well database from 1980 through 2012 (WOGCC 2012). We only considered active wells when they were in operation because mule deer response was shown to be associated with activity on and near well pads (Sawyer et al. 2006). We calculated average well pad size based on the average size of 100 randomly chosen well pads from across the state digitized in a Geographic Information System (\bar{x} = 60-m radius; ESRI ArcGis, Ver. 10.1). We computed the number of well pads in each mule deer or pronghorn Herd Unit by applying a 60-m radius to each well location. If the estimated radius of a well pad intersected another well pad, we merged pads together and considered them to be a single well pad. Well pad density was calculated by dividing the number of well pads by the area (km^2) of each Herd Unit.

We determined annual precipitation (cm) within each Herd Unit using data acquired from the DayMet weather information system (Thornton et al. 1997). We randomly selected 5 points from each Hunt Area within Herd Units for each year from 1980 to 2012. Herd Units consisted of 1–3 Hunt Areas, so we obtained 5–15 points/Herd Unit. We obtained weather data to estimate annual precipitation at each point. We averaged precipitation across all the points within a Herd Unit to quantify annual precipitation for that unit. Using a Geographic Information System, we calculated the percentage of public land (state and federal) within each Herd Unit by intersecting Herd Unit boundaries with public and private ownership overlays. We included land ownership to account for potential differences in access between public and private lands because restrictions to access are typically fewer on public lands.

Analyses

We used general linear mixed-effects models to evaluate the influence of predictor variables on hunter success separately for mule deer and pronghorn across Wyoming. We included the following fixed-effects variables for each year (1980–2012) in each Herd Unit: well pad density (well density), number of hunters (hunters), hunter effort (effort), annual precipitation, and percentage public land (federal and state). We included Herd Unit and year as random intercept terms to account for serial correlations with Herd Units through time. Prior to modeling, we assessed correlation among predictor variables and retained the most predictive variable (lowest Akaike's Information Criterion score) from single variable modeling if $r > |0.7|$. We visually inspected residual plots to assess linearity and homoscedasticity, and ensured that the dependent variable fit a normal distribution. We included a quadratic term for hunter effort because of a nonlinear relationship with hunter success and better model fit for both mule deer and pronghorn. To account for seasonal changes in harvest regulations (i.e., season length and tag allocation), we included number of hunters and hunter effort in modeling. For ease of model coefficient interpretation, we rescaled hunter effort by dividing by 7 to convert the number of days to harvest a mule deer or pronghorn to weeks. Similarly, we rescaled number of hunters, precipitation, and public land, by dividing values by 1,000. All statistical analyses were conducted using R statistical software using packages `fitdistrplus` and `lme4` (Bates et al. 2015, Delignette-Muller and Dutang 2015, R Core Team 2015).

RESULTS

We evaluated 726 Herd Unit \times year combinations across 33 years (1980–2012) within 22 mule deer Herd Units with consistent data collection and boundaries within Wyoming. In mule deer Herd Units, hunter success averaged 50.4% (range = 3.8–95.9%) across years and hunter effort averaged 9.2 days (range = 1.7–58.1 days) per Herd Unit. Average number of mule deer hunters in each Herd Unit was 1,823.3 (range = 18–13,686). Annual precipitation in mule deer Herd Units averaged 39.0 cm (range = 7.9–153.4 cm). Five

Table 1. Estimates and confidence intervals for variables effort (hunter effort), effort² (effort \times effort), hunters (number of hunters), precipitation (annual precipitation in cm), public (percentage public land), and well pad density used to assess mule deer hunter harvest success (%) in Wyoming, USA, 1980–2012.

Variable	Estimate	95% CI	
		Lower	Upper
Effort	-0.249	-0.274	-0.226
Effort ²	0.023	0.020	0.026
Hunters	0.019	0.010	0.027
Precipitation	0.364	-0.450	1.154
Public	0.586	-0.765	1.940
Well pad density	0.029	-0.090	0.150

of 22 (22.7%) mule deer Herd Units contained 0 well pads and well pad density averaged 0.03/km² (range = 0.0–0.61) across Herd Units. For pronghorn, we examined 34 Herd Units across 33 years that met our criteria, totaling 1,122 Herd Unit \times year combinations. Pronghorn hunter success averaged 93.2% (range = 59–100%), whereas pronghorn hunter effort averaged 2.9 days (range = 1.1–20.0 days). Average number of pronghorn hunters across Herd Units

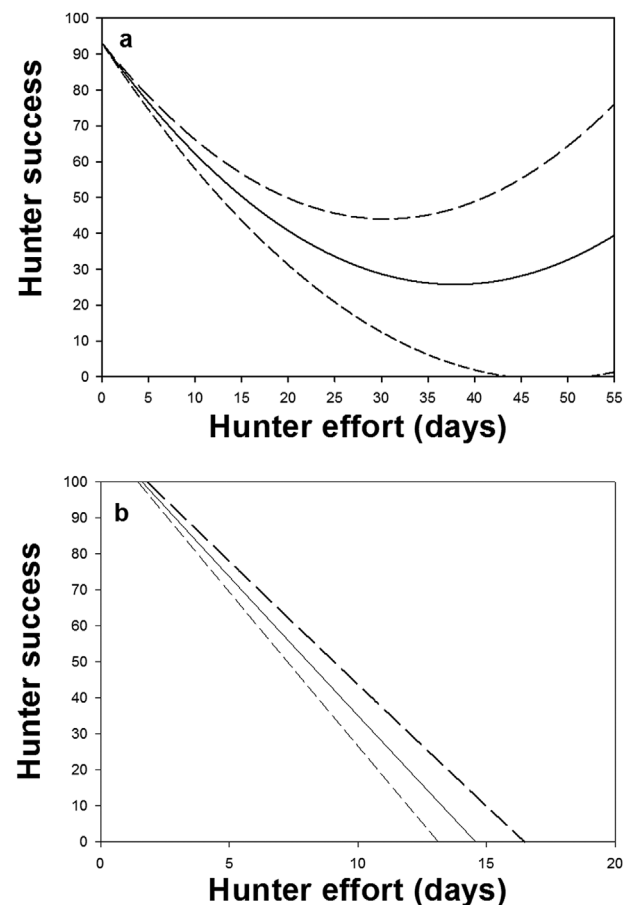


Figure 3. (a) Hunter success in response to hunter effort (days) in Wyoming Game and Fish Department Mule Deer Herd Units, USA, 1980–2012. (b) Hunter success in response to hunter effort (days) in Wyoming Game and Fish Department Pronghorn Herd Units, 1980–2012. Dashed lines are 95% confidence intervals.

was 797.5 (range = 36.0–5,509). Annual precipitation in pronghorn Herd Units averaged 39.0 cm (range = 13.7–101.2 cm). Ten of 34 (29.4%) pronghorn Herd Units had 0 well pads and well pad density averaged 0.04/km² (range = 0.0–1.40) across Herd Units.

Mule deer hunter success was positively related with a decrease in hunter effort ($\hat{\beta}_1 = -0.249$, SE = 0.012; Table 1; Fig. 3a) and an increase in number of hunters ($\hat{\beta}_1 = 0.019$, SE = 0.004; Table 1). However, 95% confidence intervals for the estimates of annual precipitation, percent public land, and well pad density overlapped 0 indicating no effect. The quadratic relationship between hunter success and effort suggested that success was negatively related with hunter effort to an intermediate point (between 35 and 40 days); thereafter, effort no longer negatively affected success. This was expected given fewer data points in the upper range of hunter effort in our data set. For the pronghorn hunter success model, the only significant variable was hunter effort (Table 2). Hunter success was negatively associated with hunter effort ($\hat{\beta}_1 = -0.547$, SE = 0.029; Table 2; Fig. 3b).

The trend in average mule deer hunter success across Herd Units did not change proportionally with average well pad density because it remained relatively constant through time (between 40% and 60% through 1980–2012), whereas well pad density in mule deer Herd Units increased 5.4-fold over the same time period from 0.01/km² in 1980 to 0.06/km² in 2012 (Fig. 4a). Pronghorn success rates remained high through time (>90%), whereas average well pad density in pronghorn Herd Units increased 9.9-fold from 0.01/km² in 1980 to 0.12/km² in 2012 (Fig. 5a). Mean hunters per Herd Unit generally decreased across time in mule deer Herd Units (Fig. 4b) reflective of fewer allocated licenses, whereas pronghorn hunter numbers fluctuated through time (Fig. 5b).

DISCUSSION

Energy development can influence access to animals and introduce additional human disturbance activities that can affect ungulate use of, and survival in, impacted landscapes (Sawyer et al. 2006, 2013; Dzialak et al. 2011; Webb et al. 2011b; Beckmann et al. 2012; Lendrum et al. 2012; Buchanan et al. 2014; Taylor et al. 2016). A better understanding of how increased development affects harvest dynamics may be

Table 2. Estimates and confidence intervals for variables effort (hunter effort), effort² (effort × effort), hunters (number of hunters), precipitation (annual precipitation in cm), public (percentage public land), and well pad density used to assess pronghorn hunter harvest success (%) in Wyoming, USA, 1980–2012.

Variable	Estimate	95% CI	
		Lower	Upper
Effort	-0.547	-0.606	-0.488
Effort ²	0.003	0.003	0.004
Hunters	0.006	-0.001	0.013
Precipitation	-0.048	-0.463	0.346
Public	0.022	-0.221	0.264
Well pad density	-0.025	-0.053	0.004

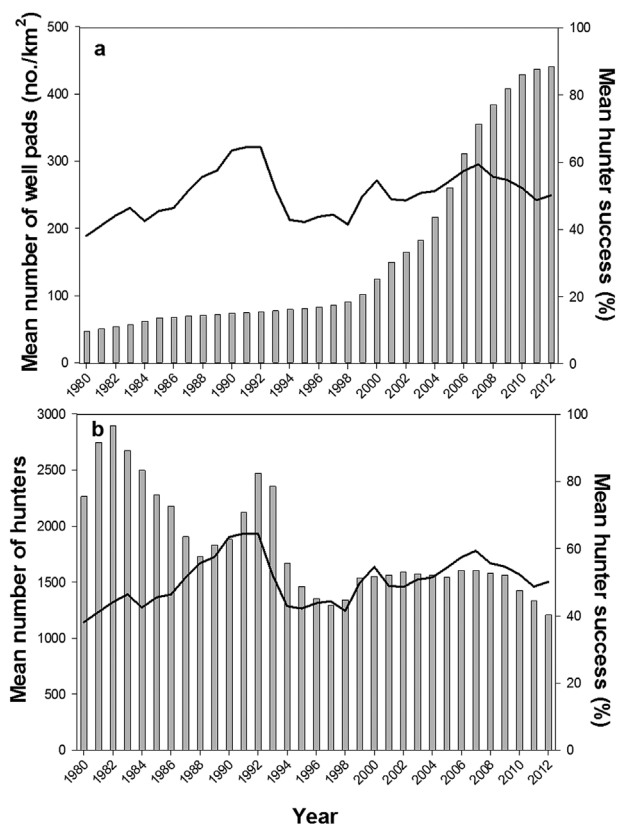


Figure 4. (a) Mean well pad density (no./km²; bars) and mean mule deer hunter success (%) (line) in Wyoming, USA, 1980–2012. (b) Mean mule deer hunters (bars) per Herd Unit and mean hunter success (%) (line) in Wyoming, 1980–2012. Well pad density data from Wyoming Oil and Gas Conservation Commission. Mule deer data reported from Wyoming Game and Fish Department Mule Deer Herd Units.

useful to managers as they consider potential effects when designing annual harvest strategies to manage big game populations. Regulated harvest is an effective tool for managing many wild ungulate populations (Stedman et al. 2004), and is extensively utilized by state agencies to reach management objectives (Rupp et al. 2000). We investigated the usefulness of harvest parameters (hunter success) as an indicator of the response by mule deer and pronghorn on extractive resource development. Specifically, we evaluated whether increased energy development, as measured by increased well pad density, was associated with harvest. Our original expectation was that any effect we might detect would be negative; consistent with the science of oil and gas development indicating a negative response for mule deer and pronghorn habitat use (Sawyer et al. 2006, 2009; Beckmann et al. 2012). Alternatively, increased hunter access may influence ungulate harvest, which may be reflected in harvest statistics (Unsworth et al. 1993, Gratson and Whitman 2000, Hayes et al. 2002, McCorquodale et al. 2003, Brinkman et al. 2004, Webb et al. 2011b). Our results suggest that hunter success for mule deer and pronghorn was not associated with well pad densities. Rather, hunter success was most associated with increased hunter effort. We predicted mule deer and pronghorn harvest success would be

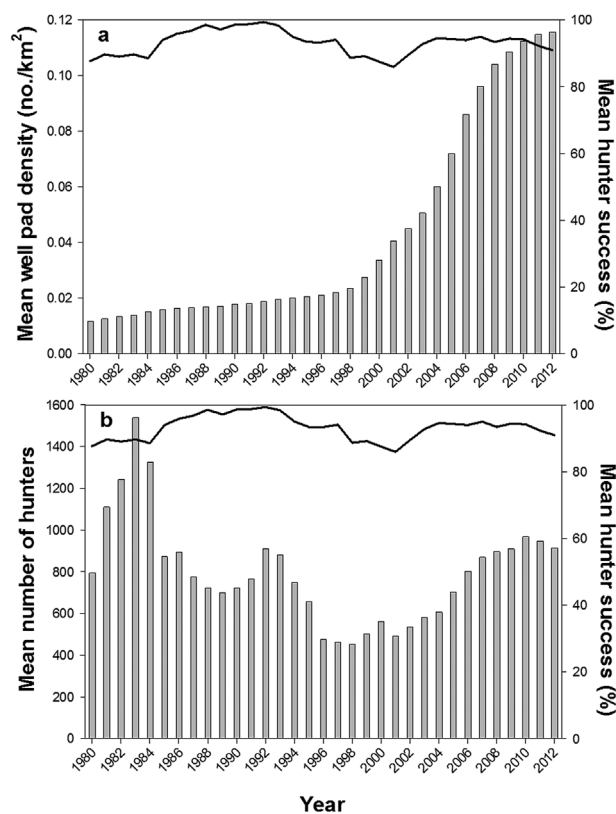


Figure 5. (a) Mean well pad density (no./km²; bars) and pronghorn hunter success (%) (line) in Wyoming, USA, 1980–2012. (b) Mean pronghorn hunters (bars) per Herd Unit and hunter success (%) (line) in Wyoming, 1980–2012. Well pad density data from Wyoming Oil and Gas Conservation Commission. Pronghorn data reported from Wyoming Game and Fish Department Pronghorn Herd Units.

informative for predicting a response to energy development. Again, analyses of harvest statistics did not reveal a relationship with either mule deer or pronghorn harvest success attributable to energy development. In addition, we were unable to detect detrimental relationships as typically revealed from response studies (e.g., avoidance of habitats, change in population size, etc.).

Mule deer hunting occurs across Wyoming in undeveloped mountain ranges, across intermountain basins, and within short-grass prairies. Energy development occurred across 77% of the 22 mule deer Herd Units we examined. Despite increased energy development across Wyoming and corresponding increase in access through associated infrastructure, hunter success remained stable over the 33-year period we examined (BLM 2003, Webb et al. 2011b). Contrary to our findings, other studies on ungulates including elk, black-tailed deer (*O. b. sitkensis*), and white-tailed deer have reported greater hunter-associated mortality with increased access (Unsworth et al. 1993, Farmer et al. 2006, Lebel et al. 2012). Similarly, Swenson (1982) found that mule deer in open habitats were more vulnerable to hunting. This may appear contradictory to what would be expected because many studies have documented avoidance behavior by ungulates when extractive energy development increases (e.g., Sawyer et al. 2006, 2009, 2013; Lendrum et al. 2012; Buchanan et al. 2014). Others found elk harvest decreased on

a per-hunter basis with increased road access where hunters on foot or off-road vehicles had greater success (Gratson and Whitman 2000). However, these studies evaluated relatively fine-scale habitat use in response to development and did not consider increased access through development at the Herd Unit level similar to our study. Thus, use of agency-collected harvest data is unlikely to be useful in identifying fine-scale impacts as can be done with more traditional means of telemetry-based and site-specific studies.

As with mule deer Herd Units, pronghorn units experienced large increases in well pad density from 1980 to 2012 indicating an expanding road network and concomitant greater hunter access. Not surprisingly, pronghorn hunting occurs within developed areas and approximately 70% of the 34 pronghorn Herd Units we examined contained well pads. Proximity to major roads was 1 of 3 factors related to greater winter mortality risk of pronghorn in the Shirley Basin of Wyoming (Taylor et al. 2016). Beckmann et al. (2012) suggested pronghorn selection of winter habitats was negatively influenced by oil and gas development. However, others have noted unaffected season-long use by pronghorn of affected areas such as surface coal mine lands (Medcraft and Clark 1986, Gamo and Anderson 2002). Wyoming historically has had large pronghorn populations with statewide populations often exceeding 300,000 individuals (Yoakum 2004a; WGFD, unpublished data). Typically, size of pronghorn populations is most influenced by weather events, particularly during severe winters that can cause population declines (Martinka 1967, Barrett 1982). Pronghorn habitat may be negatively influenced from energy development, but in general, there is less supportive evidence of this than for mule deer (Beckmann et al. 2012, Taylor et al. 2016). Pronghorn populations continue to utilize habitats within certain types of development (Medcraft and Clark 1986, Gamo and Anderson 2002, Beckmann et al. 2012, Taylor et al. 2016), and may better tolerate human activity by readily habituating to anthropogenic activities (O’Gara 2004, but see Beckmann et al. 2012). Pronghorn exist in relatively large numbers across Wyoming and it was not surprising to see consistently high success rates by pronghorn hunters because this species is generally more easily hunted in the open rangelands characterizing their habitat (Yoakum 2004b).

Wyoming mule deer populations decreased approximately 33% (WGFD, unpublished data) during our study period, concurrent with declines throughout the western United States (deVos et al. 2003). Our data revealed decreases in hunter numbers during the same period reflecting a decrease in permit allocation. Accordingly, wildlife managers made annual adjustments in hunting seasons to accommodate declining mule deer populations to maintain a relatively consistent level of harvest success, albeit harvesting fewer animals (Stedman et al. 2004). Annual adjustments to hunting seasons are typically based upon data collected each year, which provide current demographic information (Rabe et al. 2002). This system enables managers to account for fluctuating ungulate populations. In Wyoming, annual permit allocations are subject to change implemented by managers to meet management goals based not only on

annual data collection, but public input that begets season setting. Public input during the season-setting process can ultimately influence final permit numbers. Adjustments made during the season-setting process that include balancing management efforts to track wildlife populations and public opinion likely preclude the ability to fully utilize harvest metrics, such as hunter success, for evaluating potential responses by populations or habitats to energy development. In other words, the lack of stability and consistency between annual permit allocations inhibits our ability to use agency-collected data to determine whether strong relationships exist between population attributes and outside influences such as energy development. We have demonstrated that analyses of harvest metrics can provide managers with insight into the effects of hunting on some game species—specifically that managers have maintained hunter success in light of increased development.

MANAGEMENT IMPLICATIONS

Hunting seasons provide a critical opportunity to collect data that aids wildlife agencies in managing ungulate populations (Stedman et al. 2004). Managers use harvest data to assist in developing hunting strategies to maintain or reach population goals. In Wyoming, where oil and gas development is a prevalent feature, we found that increasing energy development had no apparent association with harvest success of mule deer and pronghorn. It is likely that the management processes that are involved in ultimately producing harvest parameters for each season accounted for influences on populations, including energy development. Our use of agency-collected data was useful in providing an evaluation on whether managers are adequately accounting for potential influences of increased development on harvest outcomes. We suggest managers continue to monitor herd demographics and habitat data and consider potential implications of increased development when developing harvest strategies for mule deer and pronghorn.

ACKNOWLEDGMENTS

Our research was made possible through the efforts of the many Wyoming Game and Fish Department (WGFD) biologists who collected mule deer and pronghorn herd demographic data included in our 33-year analysis. We especially acknowledge D. Legg, University of Wyoming, for his critical assistance with statistical analyses. M. Kauffman, R. Coupal, and P. Stahl from the University of Wyoming all provided helpful insights in regard to study design and analyses. We also thank J. Emmerich, S. Smith, and T. Gerhardt from WGFD for their insights. B. Brokling and K. Rogers processed spatial data for use in analyses. We thank Associate Editor C. Anderson and 2 anonymous reviewers for their thoughtful contributions, which improved our manuscript. Our research was supported by WGFD Grant Number 0020011.

LITERATURE CITED

Barrett, M. W. 1982. Distribution, behavior, and mortality of pronghorns during a severe winter in Alberta. *Journal of Wildlife Management* 46:991–1002.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. *lme4: linear mixed-effects models using Eigen and S4*. R package version 1.1-9. <http://CRAN.R-project.org/package=lme4>

Beckmann, J. P., K. Murray, R. G. Seidler, and J. Berger. 2012. Human-mediated shifts in animal habitat use: sequential changes in pronghorn use of a natural gas field in Greater Yellowstone. *Biological Conservation* 147:222–233.

Brinkman, T. J., J. A. Jenks, C. S. DePerno, B. S. Haroldson, and R. G. Osborn. 2004. Survival of white-tailed deer in an intensively farmed region of Minnesota. *Wildlife Society Bulletin* 32:726–731.

Buchanan, C. B., J. L. Beck, T. E. Bills, and S. N. Miller. 2014. Seasonal resource selection and distributional response by elk to development of a natural gas field. *Rangeland Ecology and Management* 67:369–379.

Bureau of Land Management [BLM]. 2003. Final environmental impact statement and proposed plan amendment for the Powder River Basin oil and gas project. U.S. Department of the Interior. Buffalo, Wyoming, USA.

Cameron, R. D., W. T. Smith, R. D. White, and B. Griffith. 2005. Central Arctic caribou and petroleum development: distribution, nutritional and reproductive implications. *Arctic* 58:1–9.

Cole, E. K., M. D. Pope, and R. G. Anthony. 1997. Effects of road management on movement and survival of Roosevelt elk. *Journal of Wildlife Management* 61:1115–1126.

Delignette-Muller, M. L., and C. Dutang. 2015. *Fitdistrplus: an R package for fitting distributions*. *Journal of Statistical Software* 64:1–34.

deVos, J. C. Jr., M. R. Conover, and N. E. Headrick. 2003. *Mule deer conservation: issues and management strategies*. Utah State University, Jack H. Berryman Institute Press, Logan, USA.

Dzialak, M. R., S. L. Webb, S. M. Harju, J. B. Winstead, J. Wondzell, J. P. Mudd, and L. D. Hayden-Wing. 2011. The spatial pattern of demographic performance as a component of sustainable landscape management and planning. *Landscape Ecology* 26:775–790.

Farmer, C. J., D. K. Person, and R. T. Bowyer. 2006. Risk factors and mortality of black-tailed deer in a managed forest landscape. *Journal of Wildlife Management* 70:1403–1415.

Gamo, R. S., and S. H. Anderson. 2002. Use of reclaimed minelands by pronghorn and mule deer. *Intermountain Journal of Science* 8:213–222.

Gavin, S. D., and P. E. Komers. 2006. Do pronghorn (*Antilocapra americana*) perceive roads as a predation risk? *Canadian Journal of Zoology* 84:1775–1780.

Gratton, M. W., and C. L. Whitman. 2000. Road closures and density and success of elk hunters in Idaho. *Wildlife Society Bulletin* 28:302–310.

Harju, S. M., M. R. Dzialak, R. C., Taylor, L. D. Hayden-Wing, and J. B. Winstead. 2010. Thresholds and time lags in effects of energy development on greater sage-grouse populations. *Journal of Wildlife Management* 74:437–448.

Hayes, S. G., D. J. Leptich, and P. Zager. 2002. Proximate factors affecting male elk hunting mortality in northern Idaho. *Journal of Wildlife Management* 66:491–499.

International Energy Agency. 2015. *World energy outlook 2015*. <http://www.iea.org/W/bookshop/add.aspx?id=388>. Accessed 12 Nov 2015.

Knight, D. H., G. P. Jones, W. A. Reiners, and W. H. Romme. 2014. *Mountains and plains: the ecology of Wyoming landscapes*. Second edition. Yale University Press, New Haven, Connecticut, USA.

Kuck, L., G. L. Hompland, and E. H. Merrill. 1985. Elk calf response to simulated mine disturbance in southeast Idaho. *Journal of Wildlife Management* 49:751–757.

Lebel, F., C. Dussault, A. Massé, and S. Coté. 2012. Influence of habitat features and hunter behavior on white-tailed deer harvest. *Journal of Wildlife Management* 76:1431–1440.

Lendrum, P. E., C. R. Anderson Jr., R. A. Long, J. G. Kie, and R. T. Bowyer. 2012. Habitat selection by mule deer during migration: effects of landscape structure and natural gas development. *Ecosphere* 3(9):art82.

Lyon, L. J. 1983. Road density models describing habitat effectiveness for elk. *Journal of Forestry* 81:592–613.

Martinka, C. J. 1967. Mortality of northern Montana pronghorns in severe winter. *Journal of Wildlife Management* 31:159–164.

McCorquodale, S. M., R. Wiseman, and C. L. Marcum. 2003. Survival and harvest vulnerability of elk in the Cascade Range of Washington. *Journal of Wildlife Management* 67:757–775.

McDonald, R. I., J. Fargione, J. Kiesecker, W. M. Miller, and J. Powell. 2009. Energy sprawl or energy efficiency: climate policy impacts on natural habitat for the United States of America. *PLoS ONE* 4(8):e6802.

- Medcraft, J. R., and W. R. Clark. 1986. Big game habitat use and diets on a surface mine in northeastern Wyoming. *Journal of Wildlife Management* 50:135–142.
- Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke. 2000. Elk and hunter space-use sharing in South Dakota. *Journal of Wildlife Management* 64:994–1003.
- Ockenfels, R. A., W. K. Carrel, J. C. deVos Jr., and C. L. D. Ticer. 2000. Highway and railroad effects on pronghorn movements in Arizona and Mexico. *Proceedings of the 1996 Pronghorn Antelope Workshop* 17:104.
- O’Gara, B. W. 2004. Behavior. Pages 145–194 in W. O’Gara and J. D. Yoakum, editors. *Pronghorn ecology and management*. Wildlife Management Institute. University Press of Colorado, Boulder, USA.
- Polfus, J. L., M. Hebblewhite, and K. Heinemeyer. 2011. Identifying indirect habitat loss and avoidance of human infrastructure by northern mountain woodland caribou. *Biological Conservation* 144:2637–2646.
- R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rabe, M. J., S. Rosenstock, and J. C. deVos Jr. 2002. Review of big game survey methods used by wildlife agencies of the western United States. *Wildlife Society Bulletin* 30:46–52.
- Rost, G. R., and J. A. Bailey. 1979. Distribution of mule deer and elk in relation to roads. *Journal of Wildlife Management* 43:634–641.
- Rowland, M. M., and M. Leu. 2011. Study area description. Pages 10–45 in S. E. Hanser, M. Leu, S. T. Knick, and C. L. Aldridge, editors. *Sagebrush ecosystem conservation and management: ecoregional assessment tools and models for the Wyoming Basins*. Allen Press, Lawrence, Kansas, USA.
- Rowland, M. M., M. J. Wisdom, B. K. Johnson, and J. G. Kie. 2000. Elk distribution and modeling in relation to roads. *Journal of Wildlife Management* 64:672–684.
- Rumble, M. A., and R. S. Gamo. 2011. Habitat use by elk (*Cervus elaphus*) within structural stages of a managed forest of the northcentral United States. *Forest Ecology and Management* 261:958–964.
- Rupp, S. P., W. B. Ballard, and M. C. Wallace. 2000. A nationwide evaluation of deer hunter harvest survey techniques. *Wildlife Society Bulletin* 28:570–578.
- Sawyer, H., M. J. Kauffman, A. D. Middleton, T. A. Morrison, R. M. Nielson, and T. B. Wyckoff. 2013. A framework for understanding semi-permeable barrier effects on migratory ungulates. *Journal of Applied Ecology* 50:68–78.
- Sawyer, H., M. J. Kauffman, and R. M. Nielson. 2009. Influence of well pad activity on winter habitat selection patterns of mule deer. *Journal of Wildlife Management* 73:1053–1061.
- Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. *Journal of Wildlife Management* 70:396–403.
- Sheldon, D. P. 2005. Pronghorn movement and distribution patterns in relation to roads and fences in southwestern Wyoming. Thesis, University of Wyoming, Laramie, USA.
- Sorensen, T., P. D. Mcloughlin, D. Hervieux, E. Dzus, J. Nolan, B. Wynes, and S. Boutin. 2007. Determining sustainable levels of cumulative effects for boreal caribou. *Journal of Wildlife Management* 72:900–905.
- Stedman, R., D. R. Diefenbach, C. B. Swope, J. C. Finley, A. E. Luloff, H. C. Zinn, G. J. San Julian, and G. A. Wang. 2004. Integrating wildlife and human-dimensions research methods to study hunters. *Journal of Wildlife Management* 68:762–773.
- Swenson, J. E. 1982. Effects of hunting on habitat use by mule deer on mixed grass prairie in Montana. *Wildlife Society Bulletin* 10:115–120.
- Taylor, K. T., J. L. Beck, and S. V. Huzurbazar. 2016. Factors influencing winter mortality risk for pronghorn exposed to wind energy development. *Rangeland Ecology and Management* 69:108–116.
- Thelenius, J. F., G. R. Brown, and A. L. Medina. 1994. Vegetation on semi-arid rangelands, Cheyenne River Basin, Wyoming. General Technical Report RM-GTR-263. US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- Thomas, J. W., H. Black, R. J. Sherzinger, and R. J. Pedersen. 1979. Deer and elk. Pages 104–127 in J. W. Thomas, editor. *Wildlife habitats in managed forests—the Blue Mountains of Oregon and Washington*. U.S. Department of Agriculture Forest Service, Agricultural Handbook Number 553, Washington, D.C., USA.
- Thornton, P. E., S. W. Running, and M. A. White. 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. *Journal of Hydrology* 190:214–251.
- Unsworth, J. W., L. Kuck, M. D. Scott, and E. O. Garton. 1993. Elk mortality in the Clearwater drainage of north central Idaho. *Journal of Wildlife Management* 57:495–502.
- U.S. Department of Agriculture Natural Resources Conservation Service [USDA NRCS]. 2016. The PLANTS database. National Plant Data Center, Baton Rouge, Louisiana. <http://plants.usda.gov>. Accessed 20 Sep 2016.
- Vors, L. S., J. A. Schaefer, B. A. Pond, A. R. Rodgers, and B. R. Patterson. 2006. Woodland caribou extirpation and anthropogenic landscape disturbance in Ontario. *Journal of Wildlife Management* 71:1249–1256.
- Webb, S. L., M. R. Dzialak, S. M. Harju, L. D. Hayden-Wing, and J. B. Winstead. 2011a. Effects of human activity on space use and movement patterns of female elk. *Wildlife Society Bulletin* 35:261–269.
- Webb, S. L., M. R. Dzialak, J. J. Wondzell, S. M. Harju, L. D. Hayden-Wing, and J. B. Winstead. 2011b. Survival and cause-specific mortality of female Rocky Mountain elk exposed to human activity. *Population Ecology* 53:483–493.
- Wyoming Game and Fish Department. 1980–2012. Big game job completion reports. Cheyenne, Wyoming, USA.
- Wyoming Oil and Gas Conservation Commission. 2012. WOGCC homepage. <http://www.wogcc.wyo.gov>. Accessed 15 Dec 2013.
- Yoakum, J. D. 2004a. Distribution and abundance. Pages 75–105 in W. O’Gara and J. D. Yoakum, editors. *Pronghorn ecology and management*. Wildlife Management Institute. University Press of Colorado, Boulder, USA.
- Yoakum, J. D. 2004b. Habitat characteristics and requirements. Pages 409–446 in W. O’Gara and J. D. Yoakum, editors. *Pronghorn ecology and management*. Wildlife Management Institute. University Press of Colorado, Boulder, USA.

Associate Editor: Anderson.