



Energy Disturbance and Productivity of Mule Deer Habitat in Sage-Grouse Core Areas^{☆,☆☆}



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ABSTRACT

Anthropogenic development impacts habitat use by many rangeland species including mule deer (*Odocoileus hemionus*). Recent policies, including Wyoming's Sage-Grouse Executive Order, have been implemented to conserve habitat and populations of greater sage-grouse (*Centrocercus urophasianus*). Core Areas (CAs), designated for sage-grouse conservation by the Wyoming policy, are likely less disturbed than non-CA, predictably providing protection for nontarget species, such as mule deer, that share substantial habitat with sage-grouse. Our objectives focused on examining the influence of Wyoming's CAs on mule deer including 1) quantifying oil and gas development within crucial winter range and Hunt Areas (HAs) with respect to CA overlap and 2) using fawn-to-female ratios (fawns · 1 adult female⁻¹) to evaluate whether deer populations overlapping CAs were more productive. We used oil and gas well data from the Wyoming Oil and Gas Conservation Commission and fawn-to-female ratios for 103 mule deer HAs derived from Wyoming Game and Fish Department data across designated mule deer crucial winter ranges (1980–2013) and statewide mule deer HAs (1995–2013). Numbers and trends in well pads were lower within CA-overlapped deer winter range than non-CA-overlapped winter ranges during 1980–2013. Mule deer HAs overlapped by CAs also displayed lower trends of well pads as the percentage of CA overlap increased. Trend in fawn-to-female ratios (mean = 0.69, range: 0.55–0.83) was higher in HAs with ≥70% CA overlap compared with a slight but significant negative trend in fawn-to-female ratios (mean = 0.64, range: 0.53–0.73) in HAs with no CA overlap (≤1%) from 1995–2013. HAs with CA overlap ≥ 70% exceeded 0.66 fawns-to-female, a threshold indicative of an increasing population. The relative change in fawn-to-female ratios has important implications to conservation of mule deer populations.

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Introduction

Conservation of ungulates is increasingly complex as their habitats are subject to expanding human development from natural resource extraction, urbanization, industrial infrastructure, and agricultural expansion. The global demand for energy is estimated to increase by 40% within the next 20 yr, accelerating oil, gas, coal, and renewable energy development (International Energy Agency 2015). Expanding energy development 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). Impacts from anthropogenic development can

negatively affect mule deer use of winter ranges (Sawyer et al. 2006), migration routes (Sawyer et al. 2009a; Lendrum et al. 2013; Sawyer et al. 2013), and other seasonal habitats (Blum et al. 2015). Similar avoidance of human activity has been observed with other ungulate species including elk (*Cervus elaphus*; Kuck et al. 1985; Buchanan et al. 2014), pronghorn (*Antilocapra americana*; Beckman et al. 2012), and caribou (*Rangifer tarandus* ssp.; Cameron et al. 2005; Sorensen et al. 2007; Polfus et al. 2011) that inhabit areas with mining, oil and gas development, or other human-associated infrastructure. Avoidance of human infrastructure by ungulates can compromise vital rates including survival due to use of less desirable habitat leading to increased energetic costs (Parker and Robbins 1984; Parker and Gillingham 1990; Rumble et al. 2005), impacts to parturition and recruitment (Cook et al. 2004; Tollefson et al. 2011), increased winter mortality (Parker et al. 2005), and increased potential for direct mortality through vehicle collisions and predation (Vors et al. 2006). In response to these impacts, state wildlife management agencies such as the Wyoming Game and Fish Department (WGFD) have developed protective stipulations to minimize the impacts of development on mule deer (WGFD 2009). Stipulations include recommendations of no human activity within WGFD-

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designated mule deer crucial winter range from 15 November to 30 April. However, these stipulations are only recommendations—they are not a rule of law or enforceable policy and may not be implemented by land management agencies.

Many western states have implemented conservation policies to protect greater sage-grouse (*Centrocercus urophasianus*; hereafter, sage-grouse) and their habitats at landscape scales (State of Wyoming, 2008, 2010, 2011; Stiver 2011; State of Idaho, 2012; State of Montana 2014; State of Nevada 2014; State of Oregon 2015). Wyoming was the first state to implement protective policy through its Sage-grouse Executive Order ([SGEO] State of Wyoming, 2008, 2010). The SGEO is a natural resource policy designed to maintain or improve sage-grouse habitat and populations in Wyoming by minimizing density and size of anthropogenic disturbances in designated sage-grouse Core Areas (CAs; State of Wyoming, 2008, 2010, 2011). CAs were delineated through mapping of high breeding density areas (2005–2007), calculated on the basis of population-weighted density of sage-grouse lek counts (Doherty et al. 2010) in areas with limited human development (State of Wyoming, 2008, 2010). The SGEO management strategy constrains energy development and other surface-disturbing activities across approximately 24% of Wyoming. Consequently, as a regulatory mechanism, the SGEO, as applied within CAs, may provide protections to mule deer more effectively than specific mule deer seasonal range stipulations.

Greater limits placed on development and other anthropogenic activities in landscapes encompassed by CAs in Wyoming should yield benefits to large, mobile species such as mule deer. The SGEO prescribes disturbance density levels that should not exceed $1 \cdot 2.6 \text{ km}^{-2}$ ($1 \cdot 640 \text{ ac}^{-1}$) within a defined analysis area (e.g., Holloran 2005; Doherty 2008) and total surface disturbance acreage should not exceed 5% of the analysis area (State of Wyoming 2011). Mule deer may respond favorably to practices that minimize development and result in less fragmentation and disturbance from human activity improving use of formerly avoided habitat (Sawyer et al. 2009b). Improved habitat quality is reflected in population parameters such as higher pregnancy, increases in fawn-to-adult female (fawns $\cdot 1$ adult female $^{-1}$; hereafter, fawn-to-female) ratios, and higher adult winter survival (Tollefson et al. 2010; Bergman et al. 2014). Fawn-to-female ratios are a common metric to assess productivity of deer herd units (Rabe et al. 2002; Skalski et al. 2005). Such data have been collected and recorded by the WGFD since the 1960s (WGFD Job Completion Reports; WGFD unpublished data).

Sage-grouse CAs are part of a policy-driven, land-protection mechanism and may protect important seasonal habitats for mule deer, the benefits of which may be reflected in a population response. Therefore the primary purpose of our study was to evaluate whether landscapes overlapped by sage-grouse CAs provide benefits to seasonally important mule deer habitat and populations in Wyoming. Sage-grouse have been proposed as an umbrella species (Rich and Altman 2001; Rowland et al. 2006; Hanser and Knick 2011)—a species whose habitat encompasses and may benefit another species (Noss 1990). We thus secondarily examined evidence to ascertain whether sage-grouse may function as an umbrella species for mule deer (Gamu et al. 2013). Our objectives included 1) quantifying oil and gas development in both mule deer crucial winter range and WGFD HAs in respect to CA overlap and 2) using fawn-to-female ratios, evaluate whether mule deer populations overlapping CAs received fitness benefits. We first predicted that mule deer crucial winter range and WGFD HAs occurring within CAs would have less anthropogenic disturbance than crucial winter ranges or HAs outside of CAs, respectively. Second, we predicted that mule deer populations using HAs overlapped by CAs would display higher productivity as measured by fawn-to-female ratios than mule deer populations that utilized areas outside of CAs. If data support both predictions, they provide evidence that the policy enacted in Wyoming to protect sage-grouse has the potential to also benefit mule deer, and in that respect sage-grouse can be viewed as an umbrella for mule deer.

Methods

Study Area

We conducted our evaluations within occupied mule deer range across Wyoming, United States. Specifically, we focused on WGFD-designated crucial winter ranges within current occupied sage-grouse range (Fig. 1) and statewide WGFD mule deer population HAs (Fig. 2). The WGFD identifies “crucial” ranges as the determining factor in the long-term ability of a wildlife population to maintain itself at or above WGFD population objectives. Winter ranges are populated by mule deer during winter months (Garrot et al. 1987; Brown 1992) where WGFD prescribes seasonal stipulations of no human activity from 15 November through 30 April on designated crucial winter ranges (WGFD 2009). Typically, crucial winter ranges consist of areas that provide western or southern exposure and windswept landscapes and support sagebrush (*Artemisia* L. spp.)/antelope bitterbrush (*Purshia tridentata* [Pursh] DC.) vegetative complexes, or combinations of these characteristics.

One-hundred-forty mule deer HAs ranging in size from 98 to 13 661 km^2 (mean = 1 852 km^2) occur across Wyoming and are delineated to encompass subpopulations of mule deer within 39 larger herd units. HAs include mule deer habitats overlapped by sage-grouse CAs within the sagebrush-dominated basins in the western, central, and northeastern portions of the state and often coincide with energy development. The Wyoming Basins are in the western half of the state and consist of multiple basins between mountain ranges (Rowland and Leu 2011). Major basins include the Bighorn, Great Divide, Green River, and Shirley. Wyoming Basins are considered a stronghold for sage-grouse because range-wide they contain the second largest area of sage-grouse habitat (Wisdom et al. 2011) and the largest sage-grouse populations (Doherty et al. 2015). Northeastern Wyoming rangelands include the Thunder and Powder River Basins, where sage-grouse populations are not as robust as in the Wyoming Basins (Garton et al. 2011; Doherty et al. 2015; WAFWA 2015). Wyoming Basins' vegetation consists typically of shrub steppe dominated by Wyoming big sagebrush (*A. t.* Nutt. subsp. *wyomingensis* Beetle & Young) and mountain big sagebrush (*A. t.* Nutt. subsp. *vaseyana* [Rydb.] Beetle) but also includes areas of black (*A. nova* A. Nelson) and low sagebrush (*A. arbuscula* Nutt.), whereas northeast Wyoming contains comparatively less sagebrush and more grass coverage (Rowland and Leu 2011; Knight et al. 2014). Common grasses

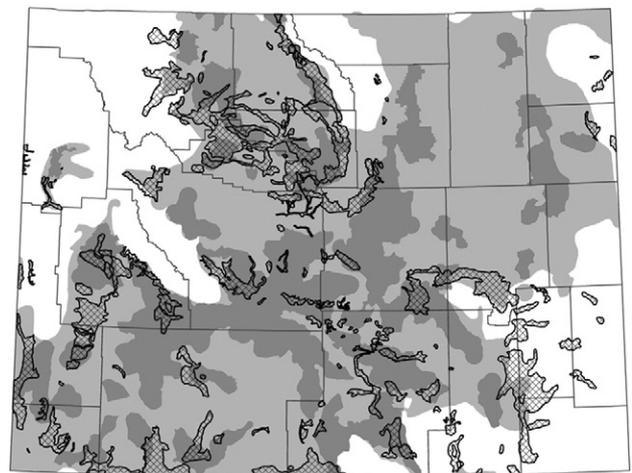


Figure 1. Mule deer crucial winter range (hashed polygons) overlaying sage-grouse Core Areas in dark gray in Wyoming, 1980–2013. Light gray shading indicates current distribution of sage-grouse (Schroeder et al. 2004). Mule deer and Core Area delineations by Wyoming Game and Fish Department (Core Area Version 3, State of Wyoming 2010).

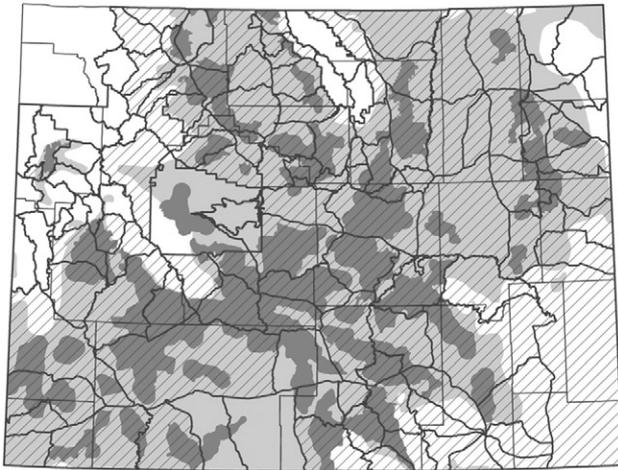


Figure 2. Location of 103 (hatched) of 140 (outlined) current (2015) Wyoming Game and Fish Department Mule Deer Hunt Areas overlaid on 31 Core sage-grouse population areas (dark-gray areas), Wyoming, 1995–2013. Light gray-shaded areas represent sage-grouse range where non-Core sage-grouse populations occur within current sage-grouse range (Schroeder et al. 2004). Mule deer and Core Area delineations by Wyoming Game and Fish Department (Core Area Version 3, State of Wyoming 2010).

in the Wyoming Basins and northeast Wyoming include bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve), needle and thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth), western wheatgrass (*Pascopyrum smithii* [Rydb.] Á. Löve), and a variety of blue grasses (*Poa* L. spp.) Forbs vary in abundance depending on precipitation and soil characteristics. Invasive grass species such as cheatgrass (*Bromus tectorum* L.) are common in northeastern Wyoming and are becoming more common in the Wyoming Basins. Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) and ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) occur on rocky uplifts and in river drainages.

HAs lying entirely within mountain ranges in Wyoming typically do not overlap energy development. However, HAs overlapping mountain ranges with adjacent foothills and lower elevation rangelands typically include some level of energy or extractive resource development. Wyoming mountain ranges encompass temperate forests with tree species at moderate elevations including lodgepole (*Pinus contorta* Douglas ex Loudon) and ponderosa pines (*P. ponderosa* Lawson & C. Lawson), and quaking aspen (*Populus tremuloides* Michx.). Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), and Englemann spruce (*Picea engelmannii* Parry ex Engelm.) form forests at higher elevations. The shortgrass prairie in the southeast corner of the state is composed of grasses including blue grama (*Bouteloua gracilis* [Willd. ex Kunth] Lag. ex Griffiths), buffalo grass (*B. dactyloides* [Nutt.] J.T. Columbus), western wheatgrass, and needle and thread.

Experimental Design

We obtained statewide mule deer crucial winter range delineations from WGFD for 2007–2013 and compared boundaries with older winter range maps. As boundary changes were minimal, we used the 2013 map as the representative winter range layer from 1980 to 2013. We selected mule deer HAs that had consistent boundaries and demographic data from 1995 to 2013, resulting in 103 of 140 (74%) useable HAs. We overlapped sage-grouse CA boundaries with crucial winter ranges and intersected areas of commonality to distinguish CA-overlapped winter range (WR-Core) from non-Core-overlapped winter range (WR-Noncore; ArcGIS Version 10.1, Environmental Systems Research Institute, Redlands, CA). We used these spatial regions to evaluate a temporal

increase in well pads from 1980–2013. Similarly, we intersected CA with HAs to distinguish between Core-overlapped HAs (HA-Core) and non-Core HAs (HA-Noncore). In addition, we calculated the percent overlap of CA within individual mule deer HAs from 1995 to 2013 to develop categories of percent overlap with CA. WR-Core and HA-Core (categories) served as treatments, whereas WR-Noncore and HA-Noncore served as respective controls in our well pad analysis.

We collected data on numbers of active wells from the Wyoming Oil and Gas Conservation Commission (2014) oil and gas well database dating from 1980–2013. Plugged, abandoned, or inactive wells were not included because mule deer exhibit avoidance of active wells (Sawyer et al. 2006). We calculated average well pad size on the basis of the average size of 100 randomly chosen well pads digitized in GIS (Geographic Information Systems 10.1, ESRI, Redlands, CA). Using the average well pad size, we calculated an average well pad radius of 60 m. If the 60-m radius of a well pad intersected the 60-m radius of another pad, these pads were merged into one well pad. We tallied the number of oil and gas well pads for each year 1980–2013 for winter range and 1995–2013 for HAs. We included the years 1980–2013 for winter range and 1995–2013 for HAs. The different time frames we analyzed coincided with consistent boundary delineations for both crucial winter ranges and HAs and consistent population management objectives for HAs (S. Smith, WGFD, personal communication). Lands encompassed by CAs served as functional CAs even before CA designation (2008), as evidenced by high sage-grouse population densities (Doherty et al. 2010) and minimal oil and gas development resulting in positive sage-grouse population response (Gamo and Beck 2017).

Fawn-to-female ratio data for mule deer were obtained from 1995–2013 WGFD HA annual reports. The WGFD conducts and compiles annual mule deer winter counts via aerial and ground surveys across the state following protocols that are similar to other western states in late November through early December (Rabe et al. 2002). Animals are then classified into adult males, adult females, and fawns, and observers strive to obtain sample sizes that are sufficiently precise to compute 90% confidence intervals for WGFD population estimates (Czaplewski et al. 1983; WGFD, Job Completion Reports, unpublished data). Records of these counts are input into a database and summarized by the WGFD in annual Job Completion Reports (WGFD unpublished data; Cheyenne). The primary change that occurs within HAs has historically been the number of permits made available. In addition, the focus of harvest has been directed at males or in combination with females and fawns being harvested through “any deer” tags (Job Completion Reports, WGFD). We calculated fawn-to-female ratios for each HA for 1995–2013. We then grouped HAs into multiple quantiles on the basis of their respective land area percentage of overlap with sage-grouse CA. Quantiles included $\leq 1\%$, $\geq 20\%$, $\geq 40\%$, $\geq 60\%$, and $\geq 80\%$ overlap. We considered an overlap of $\leq 1\%$ as representative of non-Core overlap, and this level served as a control, whereas other groupings served as treatments. Finally, if we found a measureable difference from one quantile to the next we evaluated the halfway point between the two quantiles to further pinpoint the percent overlap at which the difference occurred.

Statistical Analyses

We utilized analysis of covariance (ANCOVA; PROC GLM, SAS 9.4, SAS Institute, Cary, NC) to compare trends in well pad development between WR-Core and WR-Noncore from 1980 to 2013. We compared the main effects of WR-Core to WR-Noncore with time being the covariate. We further utilized ANCOVA to evaluate differences in the trend of well pad increases between the HA-Core quantiles ($\geq 20\%$, $\geq 40\%$, $\geq 60\%$, $\geq 80\%$) and HA-Noncore ($\leq 1\%$). Finally, we utilized ANCOVA to evaluate differences in mule deer fawn-to-female ratio trends between HA-Core ($\geq 20\%$, $\geq 40\%$, $\geq 60\%$, $\geq 80\%$) and HA-Noncore quantiles ($< 1\%$), 1995–2013. The ANCOVA procedure we employed used a suite of four models and systematically compared among models to determine the best fit for

the comparison among the two trend lines from linear regressions (Weisberg 1985). The models were as follows:

$$\text{Model 1 : } \hat{y} = b_{0,1}W_1 + b_{0,2}W_2 + b_{1,1}Z_1 + b_{1,2}Z_2$$

$$\text{Model 2 : } \hat{y} = b_{0,1}W_1 + b_{0,2}W_2 + b_1X_1$$

$$\text{Model 3 : } \hat{y} = b_0 + b_{1,1}Z_1 + b_{1,2}Z_2$$

$$\text{Model 4 : } \hat{y} = b_0 + b_1X$$

where b_0 was the y-intercept, b_1 was the slope estimate, W was a label term, and Z was the value associated with the corresponding W , and X is time. We first tested model 1 against model 2 to test the null hypothesis that the slopes of Core and non-Core response variables (well pads and fawn-to-female ratios) trends were identical versus the alternate that they were different ($\alpha = 0.10$). If the null hypothesis was accepted, we then tested model 2 against model 4 to test the null hypothesis that the slopes were identical between Core and non-Core areas, as well as the y- intercepts being identical between the two areas versus the alternate that the slopes were identical but the y-intercepts were different. In addition, if upon visual inspection of the plots of the compared slopes the y-intercepts were clearly distinct, we first tested model 1 against model 3 to test the null hypothesis that the y-intercepts were identical between Core and non-Core areas versus the alternate that they were different. If the null hypothesis was accepted, we then tested model 3 against model 4 to test the null hypothesis that the y-intercepts were identical between Core and non-Core areas, as well as the slopes being identical between the two areas versus the alternate that the y-intercepts were identical but the slopes were different. We tested for normal probabilities and used Ordinary Least Squares assuming residuals were normally distributed. Model significance testing was accomplished using an F -test.

The WGFD considers fawn-to-female ratios exceeding 0.66 to be indicative of a growing mule deer population, whereas lower ratios represent decreasing populations (Unsworth et al. 1999). Thus, to further evaluate the influence of CA on mule deer productivity, we used a one-sample t -test ($\alpha = 0.10$) to compare mean fawn-to-female ratios from 1995 to 2013 for HA quantiles ($\leq 1\%$, $\geq 20\%$, $\geq 40\%$, $\geq 60\%$, $\geq 70\%$, $\geq 80\%$) to a baseline ratio of 0.66. We excluded one fawn-to-female ratio data set from HA-Core with ≥ 80 CA overlap because this observation did not meet sample size requirements for fawn-to-female ratio analysis (Czaplewski et al. 1983).

Results

Winter Range Well Pad Density

We evaluated 3502 HA-by-year combinations across 34 yr (1980–2013) in 103 mule deer HAs within Wyoming. Total active well pads within mule deer WR-Core increased from 28 in 1980 to 81 in 2013 (Fig. 3) and well pad density increased from 0.3 to 1.0 well pads $\cdot 100 \text{ km}^{-2}$ during the same time. Correspondingly, in WR-Noncore, total well pad numbers increased from 840 in 1980 to 2 176 in 2013 and well pad density changed from 5.1 to 13.4 well pads $\cdot 100 \text{ km}^{-2}$. The increasing trend in well pads differed ($F_{1,64} = 1383.89, P < 0.01, r^2 = 0.99$) as WR-Core ($\beta_1 = 1.89, SE = 0.84, DF_{\text{error}} = 64, P = 0.03$) gained fewer well pads than WR-Noncore ($\beta_1 = 46.04, SE = 0.84, DF_{\text{error}} = 64, P < 0.01$) from 1980–2013.

Hunt Area Well Pad Density

The number of active well pads within the 103 mule deer HAs varied on the basis of percent overlap with sage-grouse CAs, but all overlap groupings showed increased numbers through time. We included the observation at the $\geq 70\%$ quantile, as we found a change occurred between the ≥ 60 and $\geq 80\%$ quantiles (Table 1). A corresponding change in well pad density was noted as HA-Noncore well pad density increased from 3.1 to $18.2 \cdot 100 \text{ km}^{-2}$ during 1995–2013. Similarly, in HA-Core

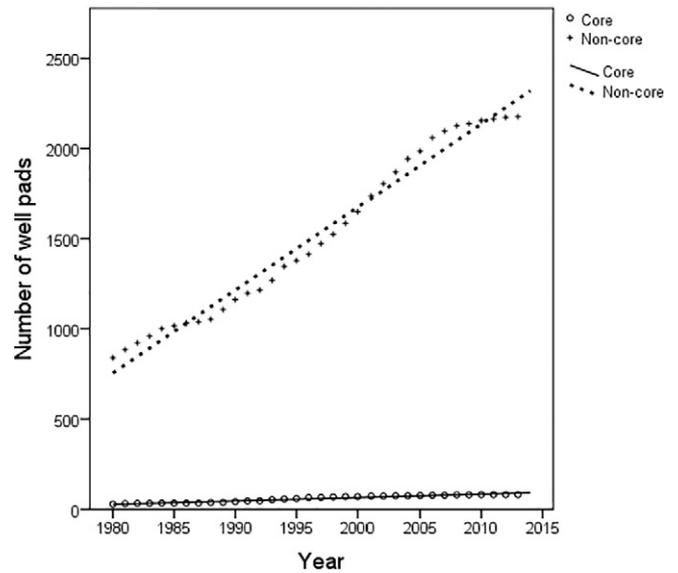


Fig. 3. Well pad comparison between Core and non-Core sage-grouse population areas overlapped with mule deer crucial winter range areas in Wyoming, 1980–2013. Linear trend lines are provided for comparisons.

$\geq 20\%$ well pad density increased from 4.9 to $10.7 \cdot 100 \text{ km}^{-2}$ and from 4.3 to $8.3 \cdot 100 \text{ km}^{-2}$ in HA-Core $\geq 40\%$. HA-Core $\geq 60\%$ well pad density changed from 4.9 to $6.7 \cdot 100 \text{ km}^{-2}$ and HA-Core $\geq 70\%$ well pad density changed from 4.3 to $5.5 \cdot 100 \text{ km}^{-2}$. Finally, HA-Core $\geq 80\%$ well pad density increased from 3.7 to $4.8 \cdot 100 \text{ km}^{-2}$ during 1995–2013.

Trend of well pad increase was higher ($P < 0.01$) in HA-Noncore compared with all HA-Core quantiles ($\geq 20\%$, $\geq 40\%$, $\geq 60\%$, $\geq 70\%$, $\geq 80\%$). The trend of well pad increase ($F_{1,35} = 34.15, P < 0.01, r^2 = 0.99$) was most similar in HA-Core $\geq 20\%$ ($\beta_1 = 467.76, SE = 37.11, DF_{\text{error}} = 34, P < 0.01$) but still less than in HA-Noncore ($\beta_1 = 570.57, SE = 37.11, DF_{\text{error}} = 34, P < 0.01$). The greatest separation in trend ($F_{1,35} = 260.12, P < 0.01, r^2 = 0.98$) occurred between HA-Core $\geq 80\%$ ($\beta_1 = 4.91, SE = 24.80, DF_{\text{error}} = 34, P = 0.84$) and HA-Noncore.

Table 1

Active well pads in mule deer Hunt Areas with $\leq 1\%$ (non-Core, control Hunt Areas), and at least 20%, 40%, 60%, 70%, and 80% overlap with sage-grouse Core Area in Wyoming, 1995–2013.

Yr	Well pads					
	$\leq 1\%$	$\geq 20\%$	$\geq 40\%$	$\geq 60\%$	$\geq 70\%$	$\geq 80\%$
1995	1 604	5 532	2 591	1 218	766	320
1996	1 622	5 184	2 630	1 239	779	328
1997	1 668	5 819	2 687	1 252	784	330
1998	1 768	6 043	2 749	1 268	791	333
1999	1 910	6 294	2 808	1 288	795	333
2000	2 331	6 552	2 860	1 301	796	333
2001	2 965	6 840	2 941	1 324	815	333
2002	3 566	7 195	3 051	1 336	823	333
2003	4 057	7 380	3 013	1 240	826	333
2004	4 744	7 739	3 120	1 249	826	326
2005	5 821	8 354	3 355	1 263	834	327
2006	7 061	9 034	3 795	1 442	841	331
2007	8 163	9 911	4 159	1 458	846	334
2008	8 230	10 591	4 443	1 478	858	337
2009	9 065	13 207	5 152	1 656	914	391
2010	9 382	13 667	5 238	1 673	920	392
2011	9 748	11 804	4 852	1 589	943	410
2012	9 946	12 033	4 955	1 623	961	416
2013	9 456	12 155	5 004	1 659	978	418

Hunt Area Fawn-to-Female Ratios

Fawn-to-female ratios varied depending on percentage of HAs that overlapped with CAs. In HA-Noncore ($\leq 1\%$ overlap with CA) fawn-to-female ratios averaged 0.64 (range: 0.53–0.73) from 1995 to 2013 (Table 2). Ratios in HA-Core ≥ 20 and ≥ 40 averaged 0.65 (range: 0.55–0.74) and 0.64 (range: 0.54–0.75), respectively. Ratios in HA-Core $\geq 60\%$ averaged 0.65 (range: 0.52–0.78) over the same time. In HA-Core $\geq 70\%$ fawn-to-female ratios averaged 0.69 (range: 0.55–0.83) and averaged 0.69 (range: 0.52–0.82) in HA-Core $\geq 80\%$.

We found no differences ($P > 0.50$) in fawn-to-female trends comparing HA-Core 20%, 40%, and 60% quantiles with HA-Noncore. The trends of fawn-to-female ratios were different, albeit negative ($F_{1,735} = 13.15$, $P < 0.01$, $r^2 = 0.04$) between HA-Core $\geq 70\%$ ($\hat{\beta}_1 = -0.001$, $DF_{\text{error}} = 736$, $P = 0.17$) and HA-Noncore ($\hat{\beta}_1 = -0.005$, $SE = 0.002$, $DF_{\text{error}} = 736$, $P = 0.23$). Fawn-to-female ratio trends differed ($F_{1,642} = 8.76$, $P < 0.01$, $r^2 = 0.03$) between the positive trend in HA-Core $\geq 80\%$ ($\hat{\beta}_1 = 0.00$, $SE = 0.003$, $DF_{\text{error}} = 641$, $P = 0.88$) compared with the negative trend in HA-Noncore ($\hat{\beta}_1 = -0.005$, $SE = 0.003$, $DF_{\text{error}} = 641$, $P < 0.01$) from 1995 to 2013 (Fig. 4).

Comparisons of mean fawn-to-female ratios in overlap groupings varied in relation to the 0.66 reference ratio for productivity (Fig. 5). HA-Noncore fawn-to-female ratios (mean = 0.63, $SE = 0.01$, $t_{33} = -2.53$, $P < 0.01$), HA-Core $\geq 20\%$ (mean = 0.64, $SE = 0.01$, $t_{58} = -2.25$, $P = 0.02$), and HA-Core $\geq 40\%$ (mean = 0.64, $SE = 0.01$, $t_{30} = -1.39$, $P = 0.09$) were < 0.66 . HA-Core $\geq 60\%$ (mean = 0.65, $SE = 0.02$, $t_{14} = -0.41$, $P = 0.34$) was not different than 0.66. Mean fawn-to-female ratios in both HA-Core $\geq 70\%$ (mean = 0.69, $SE = 0.01$, $t_9 = 3.68$, $P < 0.01$) and HA-Core $\geq 80\%$ (mean = 0.69, $SE = 0.01$, $t_4 = 2.294$, $P = 0.04$) were higher than the 0.66 threshold for positive productivity (Fig. 5).

Discussion

Wyoming CAs were designated to conserve and maintain sage-grouse populations and habitats through a detailed process of planning and managing energy development and other land surface disturbing activities through the implementation of the SGEO (State of Wyoming, 2008, 2010, 2011). By design, the SGEO limits surface disturbance size and densities within CA boundaries. Thus, a benefit of the designation and protections within CAs is its potential to conserve habitats for other wildlife species that inhabit sagebrush including mule deer

Table 2

Mean fawn-to-adult female ratios (SE) in mule deer Hunt Areas with $\leq 1\%$ (non-Core), and at least 20%, 40%, 60%, 70%, and 80% overlap with sage-grouse Core Area in Wyoming, 1995–2013.

Yr	Fawn-to-female ratios with Core Area overlap					
	$\leq 1\%$ $n = 28$	$\leq 20\%$ $n = 54$	$\leq 40\%$ $n = 28$	60% $n = 15$	70% $n = 11$	80% $n = 5$
1995	0.68 (0.02)	0.65 (0.02)	0.68 (0.04)	0.71 (0.06)	0.71 (0.08)	0.77 (0.15)
1996	0.69 (0.03)	0.71 (0.02)	0.71 (0.03)	0.71 (0.04)	0.68 (0.05)	0.65 (0.05)
1997	0.63 (0.03)	0.68 (0.02)	0.70 (0.02)	0.72 (0.03)	0.74 (0.04)	0.72 (0.06)
1998	0.73 (0.04)	0.74 (0.02)	0.75 (0.03)	0.78 (0.04)	0.83 (0.05)	0.82 (0.07)
1999	0.71 (0.02)	0.72 (0.02)	0.73 (0.03)	0.74 (0.04)	0.73 (0.05)	0.65 (0.07)
2000	0.64 (0.03)	0.64 (0.02)	0.61 (0.03)	0.60 (0.03)	0.60 (0.02)	0.62 (0.03)
2001	0.53 (0.03)	0.55 (0.02)	0.54 (0.03)	0.52 (0.04)	0.55 (0.04)	0.53 (0.04)
2002	0.56 (0.03)	0.60 (0.02)	0.58 (0.03)	0.58 (0.04)	0.59 (0.04)	0.52 (0.03)
2003	0.68 (0.03)	0.68 (0.02)	0.66 (0.03)	0.62 (0.05)	0.64 (0.06)	0.59 (0.10)
2004	0.61 (0.02)	0.66 (0.02)	0.67 (0.03)	0.69 (0.05)	0.71 (0.05)	0.65 (0.07)
2005	0.72 (0.04)	0.68 (0.02)	0.70 (0.02)	0.73 (0.03)	0.77 (0.03)	0.74 (0.04)
2006	0.65 (0.02)	0.63 (0.02)	0.61 (0.02)	0.60 (0.03)	0.64 (0.02)	0.67 (0.03)
2007	0.63 (0.02)	0.62 (0.02)	0.61 (0.02)	0.61 (0.04)	0.66 (0.04)	0.70 (0.05)
2008	0.59 (0.03)	0.63 (0.02)	0.65 (0.02)	0.66 (0.03)	0.71 (0.03)	0.70 (0.04)
2009	0.65 (0.03)	0.60 (0.01)	0.62 (0.02)	0.63 (0.03)	0.67 (0.04)	0.67 (0.06)
2010	0.59 (0.02)	0.62 (0.02)	0.64 (0.02)	0.66 (0.04)	0.71 (0.05)	0.75 (0.06)
2011	0.60 (0.02)	0.60 (0.02)	0.61 (0.03)	0.62 (0.04)	0.65 (0.04)	0.65 (0.05)
2012	0.63 (0.04)	0.59 (0.02)	0.58 (0.03)	0.59 (0.04)	0.62 (0.05)	0.57 (0.07)
2013	0.58 (0.03)	0.60 (0.02)	0.58 (0.03)	0.57 (0.04)	0.63 (0.04)	0.70 (0.06)

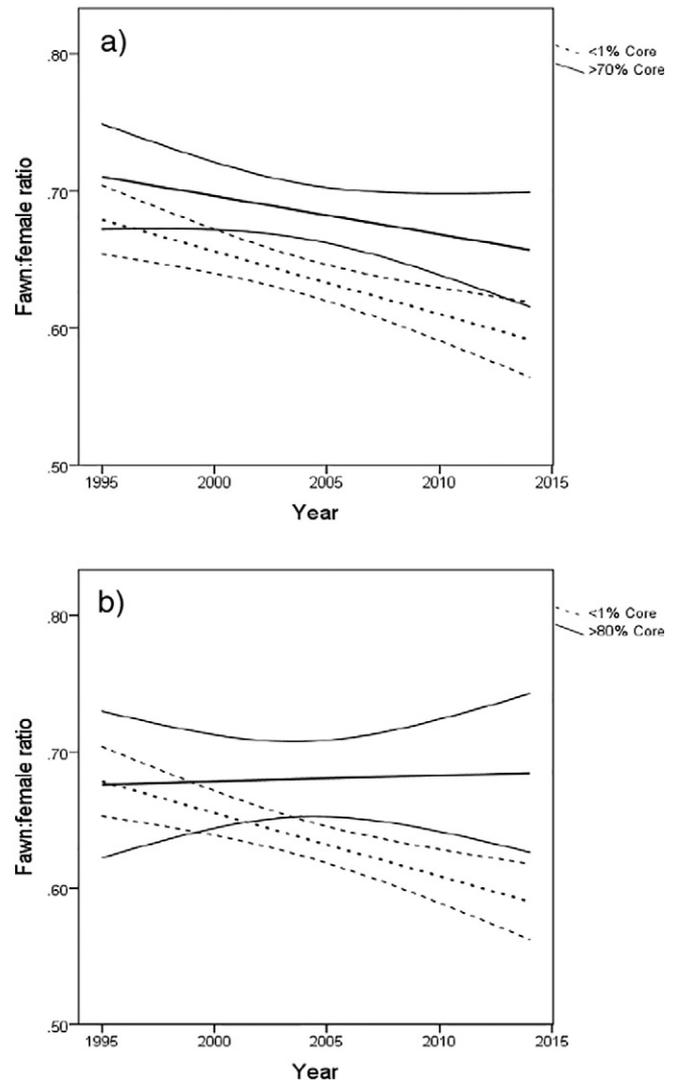


Figure 4. Fawn-to-female ratio comparison between (a) $\geq 70\%$ and (b) $\geq 80\%$ Core versus $\leq 1\%$ Core (non-Core, controls) overlapped mule deer Hunt Areas in Wyoming, 1995–2013. Linear trends with 95% confidence intervals are provided for comparisons.

(Gamo et al. 2013). Our first objective was to evaluate whether energy development was lower in mule deer winter ranges overlapped by sage-grouse CAs. We evaluated well pad densities in both winter ranges (1980–2013) and HAs (1995–2013) by comparing the number of well pads in CA-overlapped crucial winter range and HAs to non-Core winter range and HAs, respectively. We predicted well pad densities would be less in winter range associated with CA. In addition, we compared long-term annual totals of well pads through time to evaluate differences in trends of well pad numbers within Core and non-Core-overlapped winter range (1980–2013) and HAs (1995–2013). In both cases, we found well pad numbers and trends of well pads were lower in CA-overlapped winter range and HAs. Our second objective was to evaluate whether mule deer HAs overlapped by CAs received fitness benefits through fawn-to-adult female ratios. We found trends in fawn-to-female ratios began to show increases when overlap with CAs reached $\geq 70\%$ and more definitively at $\geq 80\%$. Considering that CAs were drawn encompassing high-value habitat for sage-grouse with areas of low development, it was not surprising these areas appeared beneficial for mule deer.

The Wyoming SGEO delineated CAs, as mandated through the 2008 Wyoming Governor's Executive Order, provide restrictions with more authority than WFGD winter mule deer stipulation recommendations.

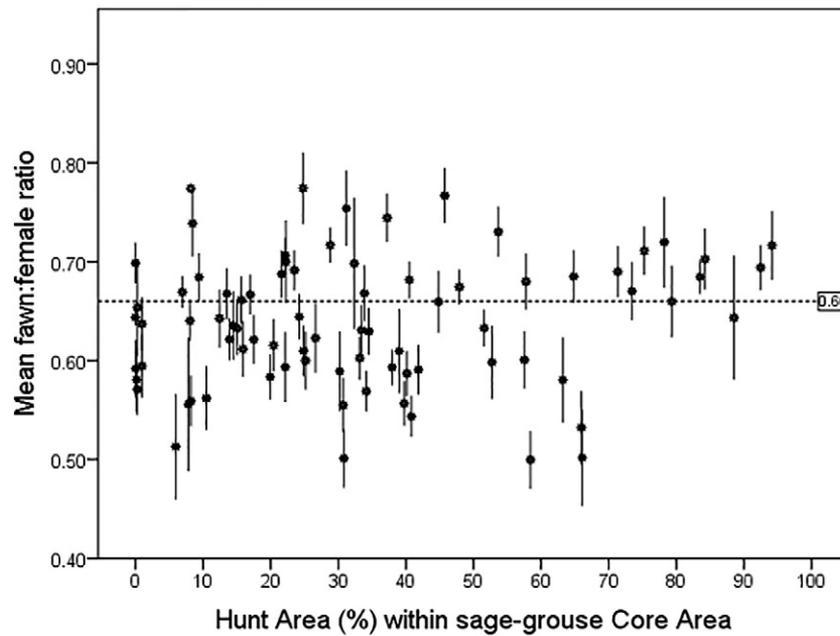


Fig. 5. Mean fawn-to-female ratios (\pm SE) for mule deer by the percentage Core Area overlap in 103 Hunt Areas, Wyoming, 1995–2013. The dashed horizontal line indicates a level (0.66) for fawn-to-female ratios above which populations are increasing (Unsworth et al. 1999).

Crucial winter range protections, which help limit human associated disturbance, are important as they can reduce impacts to already stressed animals and ultimately impact survival through severe winters (Bartmann and Bowden 1984; Parker and Robbins 1984; Bishop et al. 2005). Within the Pinedale, Wyoming area, development on winter range has contributed to reductions in mule deer utilizing the area (WGFD, unpublished report). Mule deer avoided oil and gas development infrastructure in the upper Green River Basin of western Wyoming by selecting habitats ≥ 3 km from active fields as development increased through time on important winter ranges (Sawyer et al. 2006). Timing of mule deer migration was also influenced by anthropogenic disturbance in northwestern Colorado as mule deer hastened their travel through higher well pad density areas (0.19 km^{-2}) compared with less densely ($< 0.01 \text{ km}^{-2}$) developed areas (Lendrum et al. 2013). Mule deer avoided oil and gas infrastructure out to 600–800 m in a study evaluating use of shale oil and gas development in northwestern Colorado (Northrup et al. 2015). Mule deer avoided areas of higher disturbance within mine complexes spending more time within less disturbed areas in southwestern Idaho (Blum et al. 2015). Such changes in wintering and migratory behavior may ultimately influence mule deer survival. Our results demonstrated crucial winter ranges overlapped by sage-grouse CAs indeed had much less development, based on oil and gas well pads, than did nonoverlapped HAs. Suggested SGEO disturbance densities ($0.38 \cdot \text{km}^{-2}$) for Wyoming are about 5- to 7-fold below well pad densities of 2.0 and $2.8 \cdot \text{km}^{-2}$ described by Sawyer et al. (2013) and Lendrum et al. (2012), respectively, which were attributed to changes in migratory behavior in mule deer. Thus, areas encompassed by CAs limit development to a level much less than that which initiates migratory behavior changes in mule deer.

Similar to the effect on crucial winter ranges, CAs provided landscapes of minimized well pad densities within mule deer HAs. No HA was completely encompassed by sage-grouse CA, but areas with at least 70–80% overlap revealed a higher trend in fawn-to-female ratios as opposed to non-Core-overlapped areas. In addition, HAs with $\geq 70\%$ overlap with CA maintained fawn-to-female ratios above 0.66 indicative of an increasing population (Unsworth et al. 1999). Unfortunately, only 11 of 103 HAs (10.7% of total we analyzed) encompassed $\geq 70\%$ overlap

with CA. Furthermore, the fawn-to-female ratio in HAs with $\geq 60\%$ overlap with CA did not differ from $0.66 \text{ fawns} \cdot 1 \text{ adult female}^{-1}$, indicating stable productivity in these HAs. Higher fawn-to-female ratios for mule deer in areas with less CA overlap may occur on a more local basis, but we were unable to detect these effects due to the scale of our analysis. Our data provide evidence suggesting CA landscapes may contribute to conditions that allow for increased fecundity.

An important outcome of the implementation of the SGEO, particularly through the establishment of CAs, is that greater emphasis placed on conserving habitat for sage-grouse over large landscapes may provide benefits for other species such as mule deer (Gamo et al. 2013; Copeland et al. 2014). Noss (1990:360–361) defined surrogate species as “a species with large area requirements, which if given sufficient protected habitat area, will bring many other species under protection.” In other words, the SGEO provides the protections or regulatory status suggested by Hanser and Knick (2011) enhancing sage-grouse’s ability to serve as an umbrella species for mule deer. Umbrella species are a type of surrogate species that may provide conservation benefits to “background” species (Caro 2003; Roberge and Angelstam 2004; Caro 2010), and in this case mule deer overlap with sage-grouse habitat. For example, Copeland et al. (2014) found sage-grouse CAs overlapped with 66–70% of mule deer migration corridors, 74–75% of stopover areas, and 52–91% of wintering areas for two mule deer populations in western Wyoming. The landscapes encompassed by CA (24% of the surface of Wyoming) include 33% of mule deer crucial winter range (Gamo et al. 2013). In their assessment of 10 000 randomly sampled plots, Copeland et al. (2014) found average disruption (number of surface disturbances; e.g., well pads) was $0.1 \cdot \text{km}^{-2}$ and average surface disturbance was 1.6% compared to $3.8 \cdot \text{km}^{-2}$ and 5.9% for a developed site, respectively. These findings suggest mule deer migration corridors overlapped by conserved lands, which included CA in the upper Green River Basin in Wyoming, were afforded better protections than those outside of conserved lands. However, there are other aspects related to oil and gas development including size and arrangement of well pads that may influence use of corridors, a factor that we did not address. Our findings, including increased protections of crucial winter range from development and productive fawn-to-female ratios within

≥ 70% CA-overlapped HAs, suggest lands serving as sage-grouse CAs, which overlap mule deer habitat, may benefit mule deer.

Implications

Landscape conservation practices are becoming more critical in maintaining viable habitat for wildlife, including relatively widespread and abundant rangeland species such as mule deer. In addition to providing protections to mule deer habitat, policies that reduce development within CAs may increase protections for up to 33% of WGFD-designated winter range and overlapped HAs (Gamo et al. 2013). Conservation measures are invaluable to stem the decline in mule deer across western North America (de Vos et al. 2003). Variation in rangeland carrying capacity, disease, drought, predation, and other factors may limit recruitment of fawns into mule deer populations. However, incorporating conservation strategies for other species such as sage-grouse may provide for broad-scale conservation of associated species including mule deer (Rowland et al. 2006; Gamo et al. 2013; Copeland et al. 2014).

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