esa ECOSPHERE

Conserving migratory mule deer through the umbrella of sage-grouse

H. E. Copeland,[1,]† H. Sawyer,[2] K. L. Monteith,[3] D. E. Naugle,[4] A. Pocewicz,[1] N. Graf,[5] and M. J. Kauffman[6]

[1]*The Nature Conservancy, 258 Main Street, Lander, Wyoming 82520 USA*
[2]*Western Ecosystems Technology, Inc., 200 South 2nd Street, Laramie, Wyoming 82070 USA*
[3]*Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071 USA*
[4]*Wildlife Biology Program, University of Montana, Missoula, Montana 59812 USA*
[5]*Wyoming Geographic Information Sciences Center, University of Wyoming, Laramie, Wyoming 82071 USA*
[6]*U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071 USA*

Citation: Copeland, H. E., H. Sawyer, K. L. Monteith, D. E. Naugle, A. Pocewicz, N. Graf, and M. J. Kauffman. 2014. Conserving migratory mule deer through the umbrella of sage-grouse. Ecosphere 5(9):117. http://dx.doi.org/10.1890/ES14-00186.1

Abstract. Conserving migratory ungulates in increasingly human-dominated landscapes presents a difficult challenge to land managers and conservation practitioners. Nevertheless, ungulates may receive ancillary benefits from conservation actions designed to protect species of greater conservation priority where their ranges are sympatric. Greater Sage-Grouse (*Centrocercus urophasianus*), for example, have been proposed as an umbrella species for other sagebrush (*Artemesia* spp.)-dependent fauna. We examined a landscape where conservation efforts for sage-grouse overlap spatially with mule deer (*Odocoileus hemionus*) to determine whether sage-grouse conservation measures also might protect important mule deer migration routes and seasonal ranges. We conducted a spatial analysis to determine what proportion of migration routes, stopover areas, and winter ranges used by mule deer were located in areas managed for sage-grouse conservation. Conservation measures overlapped with 66–70% of migration corridors, 74–75% of stopovers, and 52–91% of wintering areas for two mule deer populations in the upper Green River Basin of Wyoming. Of those proportions, conservation actions targeted towards sage-grouse accounted for approximately half of the overlap in corridors and stopover areas, and nearly all overlap on winter ranges, indicating that sage-grouse conservation efforts represent an important step in conserving migratory mule deer. Conservation of migratory species presents unique challenges because although overlap with conserved lands may be high, connectivity of the entire route must be maintained as barriers to movement anywhere within the migration corridor could render it unviable. Where mule deer habitats overlap with sage-grouse core areas, our results indicate that increased protection is afforded to winter ranges and migration routes within the umbrella of sage-grouse conservation, but this protection is contingent on concentrated developments within core areas not intersecting with high-priority stopovers or corridors, and that the policy in turn does not encourage development on deer ranges outside of core areas. With the goal of protecting entire migration routes, our analysis highlights areas of potential conservation focus for mule deer, which are characterized by high exposure to residential development and use by a large proportion of migrating deer.

Key words: *Centrocerus urophasianus*; conservation easements; conservation effectiveness; energy development; Green River Basin; migratory corridors; mule deer; *Odocoileus hemionus*; sage-grouse core area; umbrella conservation; ungulate migration.

Received 12 June 2014; revised 5 August 2014; accepted 6 August 2014; **published** 29 September 2014. Corresponding Editor: D. P. C. Peters.

† **E-mail:** hcopeland@tnc.org

Introduction

Conserving migratory ungulates presents many challenges, because their seasonal movements are wide-ranging and cross a diversity of ecosystems with varying human land use (e.g., oil, gas, residential subdivision, agriculture, transmission, roads, and forestry). Known anthropogenic threats to migrating ungulates include energy and residential development, roadway mortality, and fencing (Grovenburg et al. 2008, Sorensen et al. 2008, Harrington and Conover 2010, Sawyer et al. 2012, Lendrum et al. 2013, Sawyer et al. 2013). In landscapes where humans and wildlife compete for similar resources, ungulate populations have generally declined as human land use intensifies. As migratory ungulates continue to decline worldwide (Berger 2004, Bolger et al. 2008), a more holistic management perspective is needed to broaden conservation efforts beyond winter and summer ranges to include migration routes as critical habitat (Berger 2004, Bolger et al. 2008, Sawyer et al. 2009, Berger et al. 2014). Conserving ungulates under these conditions will require creative and integrative solutions, one of which could be to build upon conservation strategies aimed at other species.

Mule deer (*Odocoileus hemionus*) are an iconic species indigenous to the Western US. There is concern that traditional migration routes may be threatened by increased levels of anthropogenic disturbance. Recent declines in mule deer populations have been reported throughout much of the West (deVos et al. 2003), likely a result of long-term drought and loss or fragmentation of habitat, among other factors (Bishop et al. 2009, Monteith et al. 2014). Concern for mule deer populations has prompted state management agencies and non-governmental organizations (NGOs) to explore new strategies and broaden conservation efforts to enhance protection of key mule deer habitats, such as migration routes.

The use of umbrella species has been promoted as an efficient way to conserve biodiversity by focusing on the conservation needs of one species and thereby indirectly protecting additional species occupying the same or similar ecological communities (Berger 1997). Because umbrella species are typically chosen for their need of large habitat patches, they are assumed to protect a broader suite of co-occurring species (Simberloff 1998). Some have challenged the umbrella species concept and concluded that greater care is needed in choosing surrogate species (Caro and O'Doherty 1999, Andelman and Fagan 2000, Roberge and Angelstam 2004, Ozaki et al. 2006), whereas others have suggested that a well-selected umbrella species may confer protections for additional species occupying similar habitats (Berger 1997, Fleishman et al. 2000, Rowland et al. 2006, Hanser and Knick 2011). Approximately 350 species of wildlife depend on or use sagebrush for a portion of their life cycle (Wisdom et al. 2005), so potential overlap with habitat of Greater Sage-Grouse (*Centrocercus urophasianus*), a sagebrush obligate, is high. Rowland et al. (2006) tested for habitat overlap between sage-grouse and 39 other sagebrush-associated vertebrate species, finding the greatest overlap with sagebrush obligates. Hanser and Knick (2011) observed moderate to strong associations between 13 species of passerine birds and sage-grouse, but cautioned that the effectiveness of the sage-grouse umbrella depends on maintaining the natural environment and landscape heterogeneity. Although managers have suggested that sage-grouse could be an "umbrella" for migratory mule deer (Gamo et al. 2013), no peer-reviewed studies have yet addressed this question.

In recent years, no wildlife species (indicator, flagship, umbrella, or otherwise) has received more conservation attention in the Western US than the Greater Sage-Grouse. This game bird, endemic to the sagebrush basins of the West, now occupies about half of its historic range (Schroeder et al. 2004), and populations continue to decline as sagebrush habitats are lost to development, agriculture, fire, and other factors. The overlap of large natural gas, oil, and wind resources with sagebrush habitat has exacerbated conflicts with sagebrush-dependent species like sage-grouse. Energy development reduces the amount of available habitat and increases anthropogenic disturbance, which reduces lek attendance, nest initiation rates, nesting success, and survival of adult females (Lyon and Anderson 2003, Holloran 2005, Kaiser 2006, Walker et al. 2007, Doherty et al. 2008, Harju et al. 2010, Holloran et al. 2010). Additionally, sage-grouse are highly sensitive to other types of human disturbance, such as roads, residential areas, pipelines, vehicle traffic and noise (Johnson et al. 2011, Naugle et al. 2011, Blickley et al. 2012, Knick et al. 2013, Taylor et al. 2013). Following multiple petitions for listing under the Endangered Species Act (ESA) and several years of litigation, the US Fish and Wildlife Service (USFWS) issued a listing of "warranted but precluded" in 2010, and agreed to deliver a final decision in 2015 that will determine whether the sage-grouse is listed under ESA or removed as a candidate species.

The 2010 USFWS listing decision for sage-grouse provided incentive for western states to develop proactive conservation measures that ensure species persistence and avert an ESA listing in 2015. In Wyoming, where nearly 40% of all sage-grouse occur, a process led by the Governor's Office resulted in the development and approval of the Wyoming Core Area Policy (WCAP) through an Executive Order in 2008 (State of Wyoming Executive Department 2008). The WCAP was designed to offer greater protection to lands characterized as core areas, which were initially mapped based on breeding areas (i.e., lek sites buffered by some distance) that contained 75% of the population of sage-grouse in a given region (Doherty et al. 2011). Importantly, the core area boundaries included in WCAP were adjusted to exclude federal lands approved for, or in the process of being developed for energy (e.g., wind, natural gas), and did include some areas of pre-existing development. The WCAP limits development to 5% surface disturbance over the assessment area, and an average of one disruptive activity (i.e., active oil, gas well, or mining claim) per 2.59 km^2 (640 acre section) on lands within core area boundaries, which includes 6.1 million hectares in Wyoming. Although state authority to govern decisions on federal lands is limited, the BLM issued a statewide Instructional Memorandum (Bureau of Land Management 2012) supporting the WCAP and is in the process of revising their resource management plans to align with WCAP. For the purposes of this analysis, we assumed that federal regulations abide by the WCAP.

Although stipulations of the WCAP only apply to state and federal lands, more than $100 million were invested by land trusts from 2008 to 2012 to purchase voluntary conservation easements on private lands in Wyoming in an effort to reduce development threats with an emphasis on sage-grouse conservation. Conservation easements (legal agreements with landowners to restrict development rights on their lands in exchange for tax and/or monetary incentives) have become an important tool for agencies and land trusts to achieve conservation goals and permanently restrict development on private lands (Kiesecker et al. 2007, Fishburn et al. 2009). Easements reduce anthropogenic development and favor wildlife use in sagebrush ecosystems (Pocewicz et al. 2011), but their effectiveness ultimately depends on the quality and quantity of habitat on private land, and the juxtaposition of private lands relative to key habitats. Recent analyses estimate that conservation easements may avert projected declines in sage-grouse populations in Wyoming by 9–11% (Copeland et al. 2013).

Together, the WCAP and conservation easements represent a concerted effort aimed at avoiding federal listing for the sage-grouse, which may offer contingent benefits to mule deer where their ranges are sympatric, because mule deer also rely on intact sagebrush habitat for winter range and migration routes that lead to high-elevation summer ranges. One key consideration in determining whether sage-grouse can provide an effective umbrella of conservation for mule deer is the disturbance limits set by WCAP, and if these limits provide adequate protection to maintain connectivity for migrating mule deer. The WCAP states that: (1) surface disturbance is restricted to an average of 0.39 disruptions per square kilometer (a disruption is defined by WCAP as the density of well pads and active mining operations within a project area), and (2) surface disturbance is capped at an average of 5% per 640 acres (2.59 km^2) of suitable sage-grouse habitat within the defined development project area and within a 4-mile (6.5 km) buffer around affected leks (State of Wyoming Executive Order 2011-5; Attachment B). Here we examine the likelihood that disturbance limits set within WCAP will be sufficient to keep development levels below disturbance thresholds known to impact migrating deer.

In general, mule deer winter ranges are relatively easy to delineate because of high individual fidelity and the large number of animals that congregate on them. Although deer also show strong fidelity to migration routes (Sawyer et al. 2009), delineating long-distance routes is a recent advancement stemming from improved GPS technology. Specifically, GPS data collected at fine spatiotemporal scales can be used to estimate utilization distributions (UD) that can be combined across animals to determine which route segments are used the most, and to distinguish between route segments that function as stopover habitat versus those segments used primarily for movement (Sawyer et al. 2009). Stopover sites are especially important because they allow animals to track changes in vegetation phenology; some deer populations spend up to 95% of the migration period in stopovers (Sawyer and Kauffman 2011). While winter range has traditionally been viewed as the most critical or limiting factor for mule deer populations, that paradigm has begun to shift in recent years as the importance of migration and summer nutrition for temperate ungulates has been highlighted (Cook et al. 2004, Tollefson et al. 2010, Sawyer and Kauffman 2011, Monteith et al. 2014).

The upper Green River Basin (GRB) of western Wyoming, USA, a region supporting some of the largest sage-grouse and mule deer populations in North America, has suffered dramatic declines in both species concurrent with recent natural gas development. Mule deer in this region migrate 20 to 250 km between winter ranges in the GRB and distant summer ranges in the Bridger-Teton National Forest (BTNF) (Sawyer et al. 2005). We used detailed data on mule deer wintering areas and migration routes in the GRB to evaluate sage-grouse conservation as an umbrella to sustain migratory mule deer populations. Using migration routes from two deer populations, we quantified the proportion of stopovers, movement corridors, and winter range that overlapped with sage-grouse and other conservation efforts. We then examined gaps in conservation along migration routes and within the winter-range network, and measured the relative risk of residential development to help prioritize potential conservation efforts directed towards mule deer. Finally, we evaluated if existing energy development projects that abided by prescriptions within the WCAP maintained disturbance levels below thresholds known to negatively affect migrating mule deer. Our overall goal was to evaluate the conservation effectiveness of sage-grouse as an umbrella species for another wide-ranging and migratory species.

Methods

Study area

We examined two populations of migratory mule deer that congregate on winter ranges in the GRB of western Wyoming, USA (Fig. 1). This region is characterized by high-elevation (1900–2500 m) sagebrush (*Artemisia* spp.) desert, surrounded on the east, north, and west by the Wind River, Gros Ventre, and Wyoming Range mountain ranges, respectively. Mountainous areas are dominated by conifer forests with forb and shrub understories. Land ownership in the GRB is mostly (71%) federal lands, administered by the Bureau of Land Management (BLM) and the United States Forest Service (USFS), and generally managed for multiple-use (e.g., livestock grazing, recreation, energy development, etc.). Private lands comprise 27% of the region, including mostly riparian and agricultural lands, and another 2% is managed by the state of Wyoming. Detailed descriptions of the vegetation and land-use patterns of the study areas are provided by the BLM (2008). The GRB contains two of the largest natural gas fields in the US, including the Jonah and Pinedale Anticline, which have altered large tracts of sagebrush habitat since their infill approvals (Bureau of Land Management 2000, 2008). From 2009 to 2013, 14,790 hectares of conservation easements were placed in the GRB using \$9 million in federal funds and nearly twice that amount in private or state matching funds.

Mule deer data

We used GPS data collected from 66 adult female mule deer to examine individual and population-level migration routes of mule deer in the "Mesa" and "Ryegrass" subpopulations. We

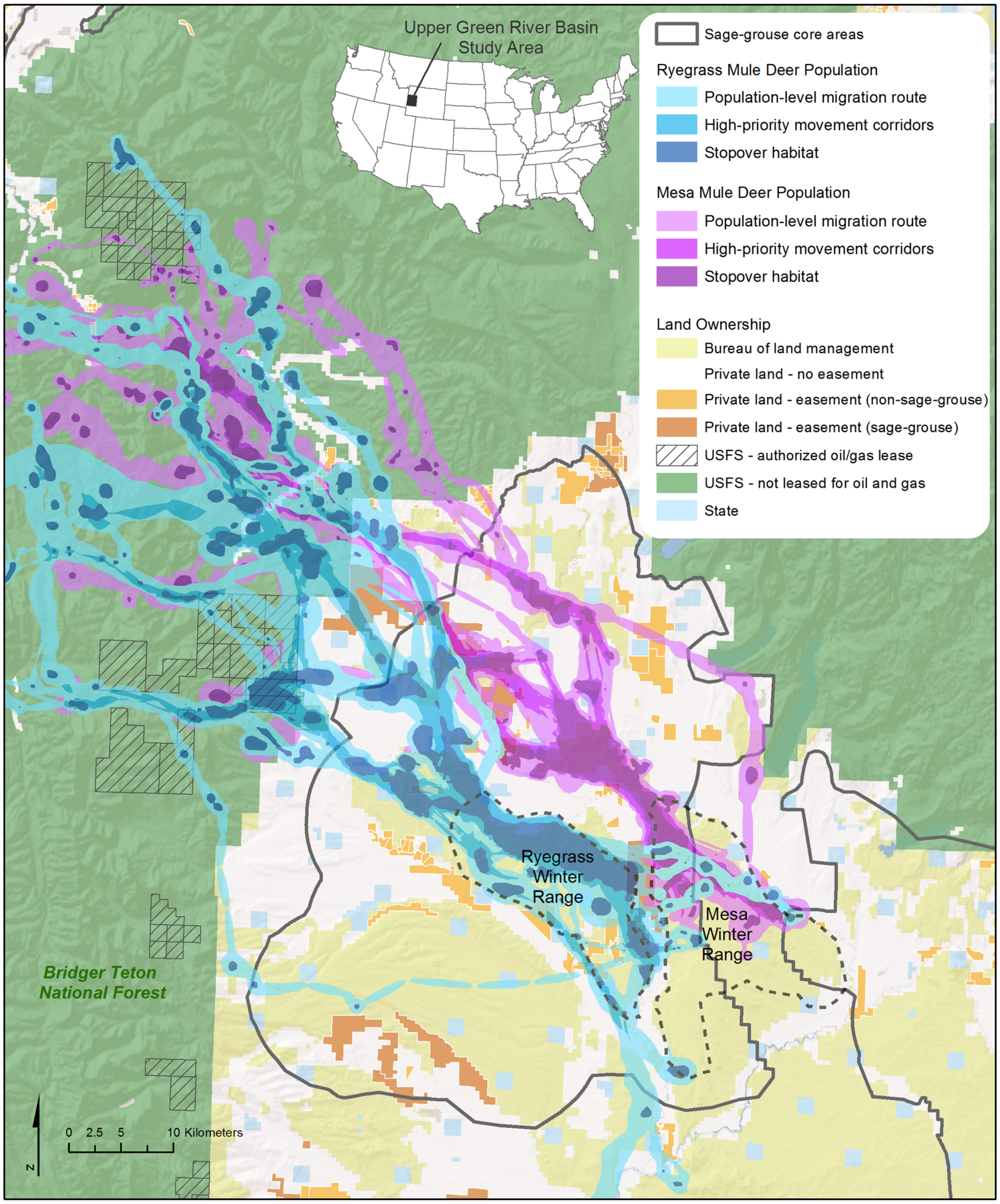

Fig. 1. Winter ranges, stopovers, and population-level migration routes (created with a BBMM) for mule deer in the Mesa and Ryegrass subpopulations, upper Green River Basin, Wyoming, USA relative to land ownership.

included individual and population-level analyses because we view these approaches as complementary and both necessary for a complete analysis. Although population-level analysis is a powerful tool to identify key routes, it fails to indicate the relative number of deer using a route and how many deer might be affected by a loss of connectivity in a particular area. Both analyses were based on GPS data of 52 migrations collected from 38 deer between 2003 and 2012 in the Mesa subpopulation, and 49 migrations collected from 28 mule deer between 2005 and 2011 in the Ryegrass subpopulation.

For the individual-level analysis, we generalized each of the spring and fall migration routes by filtering GPS locations to one point reported per day at 0900 hrs. We then converted those points to lines and smoothed each line into a single migration route for each deer.

For the population-level analysis, we used Brownian bridge movement models (BBMM; Horne et al. 2007) to estimate migration routes from GPS data that were collected at two or three hour intervals with a fix-rate success of 99%. The BBMM uses time-specific location data to estimate a probability density or utilization distribution (UD), where the probability of being in an area is conditioned on the start and end locations, the elapsed time between consecutive locations, and the speed of movement (Horne et al. 2007). We used the "*BBMM*" package in R (R Foundation for Statistical Computing, Vienna, Austria) to estimate UDs for individual migration routes. We then averaged UDs across animals in each deer population to estimate a population-level migration route (Fig. 1). The population-level migration routes provide a probabilistic measure of the migration route, where the height of the UD reflects intensity of use (Sawyer et al. 2009). We delineated stopovers as the top 15% of the UD values. To identify high priority segments within the population-level route, we estimated 95% contours of the individual UDs, overlaid them on a 50 × 50 m grid, and then calculated how many individual contours overlapped with each grid cell. High priority segments were defined as those grid cells within the population-level route that were used by at least 10% of the population (i.e., marked animals) (Sawyer et al. 2009).

Assessing umbrella protections for migration routes

Mule deer show high fidelity to their individual routes and winter ranges (Sawyer et al. 2006, Sawyer et al. 2009). We intersected crucial winter ranges (Wyoming Game and Fish Department 2012), stopover sites, high-priority movement corridors, and individual migration routes with spatial data on three levels of lands protected by conservation actions that may benefit mule deer. We included (1) lands under perpetual conservation easement (Copeland and Browning 2013), (2) USFS lands on which oil and gas leases were withdrawn or bought out through the Wyoming Range Legacy Act (L. McGee, *personal communication*) or changes in the land use management plan, and (3) federal lands within sage-grouse core areas (Bureau of Land Management 2012). Although federal subsurface leases on private lands were technically bound by the WCAP, surface restrictions do not apply and therefore residential subdivision (or other surface development) could occur on these lands. For this reason, we did not include private lands with subsurface leases in overlap calculations. In doing so, our estimates of overlap could be conservative because WCAP can provide some level of conservation on private lands. To assess the contribution of sage-grouse conservation to mule deer, we parsed protected lands in the above three categories into either relating or not relating to sage-grouse conservation. Lands relating to sage-grouse conservation included: (1) conservation easements funded through federal programs that earmark special funds for sage-grouse conservation (i.e., Farm and Ranchland Protection Program) and (2) federal lands within sage-grouse core areas (State of Wyoming Executive Department 2008). Where conservation easements fell within sage-grouse core areas, we reported the hectares of conservation easement to avoid double-counting.

Prioritizing migration route segments for conservation

While the WCAP reduces the risk of oil and gas development in the low-elevation areas of the upper GRB, it does not address the risk of residential development on private lands (Gude et al. 2006). To evaluate this risk and identify priority lands for conservation, we collected spatial data on land ownership (Sublette County 2012) and conservation easements (Copeland and Browning 2013), and parsed individual migration routes into segments that either overlapped conserved lands or did not. For each route, we calculated two scores: (1) the length weighted mean of relative residential development risk score for each unconserved segment (0 = low to 100 = high) (Beyer 2012) using a model of risk from a previous study (Copeland et al. 2013), and (2) proportion of entire route that intersected conserved lands. We classified pixels valued greater than 50 as having moderate to high risk of development.

We identified lands of greatest conservation priority by selecting parcels of private lands >40 acres (16 ha) that fell within the high-priority migration corridor, had a mean of relative residential risk ≥ 50, and lacked an existing conservation easement. We used estimates on conservation costs per hectare for Sublette County to calculate the easement cost at 50% of the estimated fair market value of $628 per hectare for irrigated parcels in Sublette County (Bastian and Foulke 2010, Copeland et al. 2013).

Estimating mule deer thresholds for disturbance and comparisons to WCAP

Anthropogenic disturbances like roads, well pads, and other infrastructure may not elicit a measureable behavioral response until some threshold is exceeded. Our understanding of such thresholds is poor, but several studies have examined the migratory behavior of mule deer relative to different levels of disturbance. Lendrum et al. (2012) observed increased step lengths when migratory mule deer moved through areas with more development (1.99 well pads/km^2) compared with those with less (0.17–1.54 well pads/km^2). In southern Wyoming, Sawyer et al. (2013) reported that mule deer migrating through areas with high levels of development detoured from their routes, increased movement rates, and reduced stopover use. In this instance, intensive development was characterized as road and well pad densities of 1.92 km/km^2 and 2.82 well pads/km^2.

Both the Sawyer et al. (2013) and Lendrum et al. (2012) studies suggest that changes in migratory behavior are expected at or above 1.99–2.82 well pads/km^2. Well-pad densities allowable under WCAP are an average 0.39 well pads/km^2, which is well below the density that might be expected to affect deer migration. Nevertheless, within the WCAP, the calculation of average well pads/km^2 is based on the project area, where size of the project area is variable and determined through a complex process of buffers applied to sage-grouse leks. Here, we compared percent disturbance and number of average disruptions of the reviewed development area with that of the intensively developed site (2.82 well pads/km^2) as reported in Sawyer et al. (2013) to determine how often disturbance levels reached thresholds that would be expected to elicit a negative response by migrating mule deer.

To characterize the range of disturbance allowed within WCAP and the frequency with which they exceeded levels identified by Sawyer et al. (2013), we estimated disturbance intensity and variability at a spatial scale relevant to migration corridors within 233 development projects reviewed under the WCAP, which we define as the "reviewed development area". We randomly placed circular buffers with a 1-km diameter (0.785 km^2; $N = 10000$) within the reviewed development projects (Fig. 2A) and generated estimates of percent disturbance and number of disruptions within each plot. A disruption is defined by WCAP as the density of well pads and active mining operations within a project area. We also randomly placed the same circular buffers ($N = 100$) within the intensively developed site reported by Sawyer et al. (2013) (Fig. 2B). We chose 1-km plots as a typical width of a mule deer migration corridor (Sawyer et al. 2009). To be consistent with the study that we used as a threshold, we only considered human disturbance, excluding disturbances of fire and agricultural conversion. Our use of the intensively developed site from Sawyer et al. (2013) as a threshold could underestimate impacts, as data from Lendrum et al. (2012) suggest that impacts are possible at lower levels of development.

Results

Among individual routes, most routes from Mesa (49 of 54 routes) and Ryegrass (49 of 51) overlapped with conserved lands for at least 50% of their route length (Fig. 3). The average overlap of migration routes with conserved lands originating from the Mesa was 65%, with about half (33%) resulting from sage-grouse conservation. For routes originating from the Ryegrass subpopulation, average overlap of migration routes with conserved lands was 69%, with 39% of the total overlap resulting from sage-grouse conservation.

High-priority movement corridors overlapped with conserved lands 66% for the Mesa and 70%

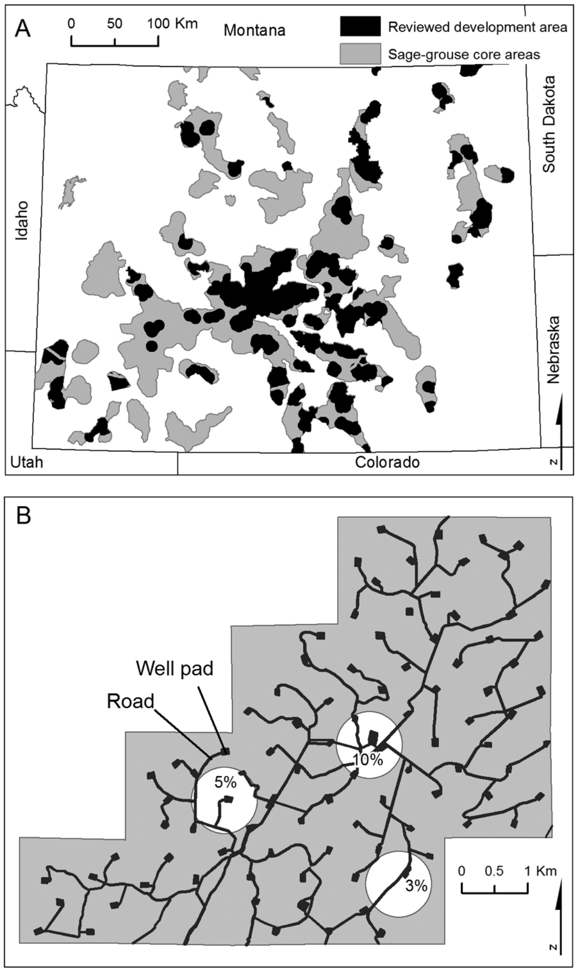

Fig. 2. Sage-grouse core areas and the reviewed development area which served as the sample area for our analysis of disturbance under the Wyoming Core Area Policy (A). Intensely developed site (Dry Cow Creek) for comparison, with 1-km sample plots and examples of different levels of disturbance (3%, 5%, 10%) (B).

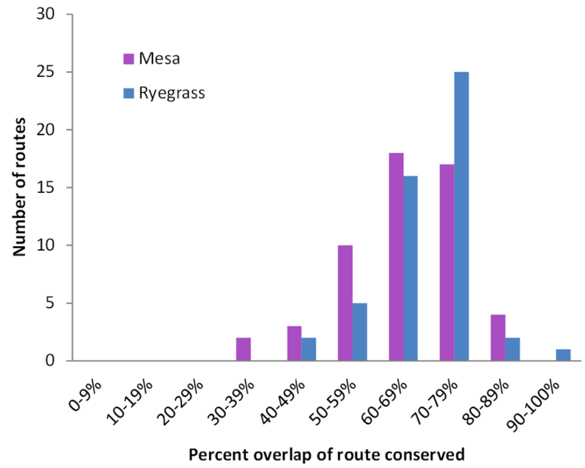

Fig. 3. Histogram of percentage of individual migration routes of adult female mule deer in the Mesa and Ryegrass subpopulations that overlapped lands with some form of conservation restrictions including, US Forest Service lands, conservation easements, and sage-grouse core area.

for the Ryegrass subpopulations (Fig. 4). The total proportion of overlap resulting from sage-grouse conservation was 34% for the Mesa and 40% for the Ryegrass. Conservation easements overlapped with high-priority movement corridors about 5% for both subpopulations, but only 1% was attributable to sage-grouse efforts for Ryegrass and 4% for Mesa.

For stopover areas, 74% for the Mesa and 75% for the Ryegrass overlapped with conserved lands (Fig. 4). The proportion of overlap resulting from sage-grouse efforts was approximately half, or 33% for the Mesa and 41% for the Ryegrass, with the majority resulting from sage-grouse core areas (Mesa = 32%; Ryegrass = 39%) and the remainder (Mesa = 1%; Ryegrass = 1.8%) from sage-grouse funded easements.

For winter ranges, 52% for the Mesa and 91% for the Ryegrass overlapped with conserved lands. In both winter ranges, the majority of overlap (Mesa = 51%; Ryegrass = 83%) was from the WCAP restrictions and only a small percentage from conservation easements (Mesa = 1%; Ryegrass = 8%).

Prioritizing migration route segments for conservation

We analyzed risk of residential development to segments of individual migration routes that did not overlap with lands already protected by conservation easements. For the Mesa subpopulation, the mean relative risk of residential development was 57 (SD = 15, min = 19, max = 88) and the Ryegrass subpopulation, was lower at 46 (SD = 22, min = 4, max = 89; Fig. 5). Within these segments of lands at relatively high risk (i.e., >50) of residential development, there were 26,975 hectares of private lands that overlapped with segments of migration routes of high

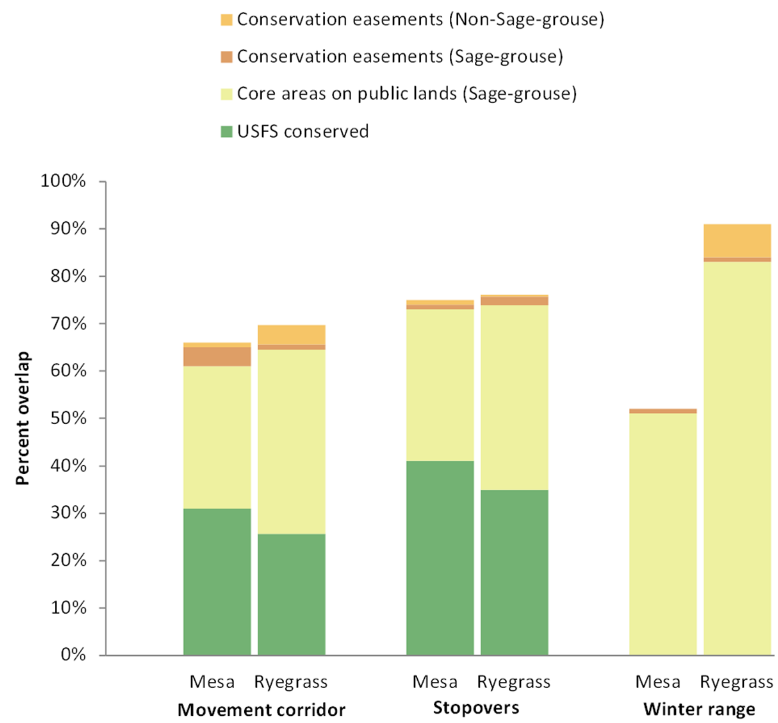

Fig. 4. Proportion of stopovers, high-priority migration corridors, and winter ranges of mule deer that overlap with lands offering some level of conservation protection including conservation easements, sage-grouse core area on public land, and US Forest Service lands, in the upper Green River Basin, Wyoming, USA.

development potential. We estimated it would cost approximately $52 million to place voluntary conservation easements on these lands (Fig. 6). Of these high-priority at-risk private lands, 77% also were within a sage-grouse core area; therefore, placing conservation easements on these lands within core areas would also likely benefit sage-grouse, potentially increasing the return on conservation investment.

WCAP project analysis

For the intensively developed site examined by Sawyer et al. (2013), average disruption was 3.83 per km^2 (SD = 1.28, min = 1.27, max = 7.64) and surface disturbance was 5.87% (SD = 1.50%, min = 2.64%, max = 10.02%), which we used as a disturbance threshold for comparison to development projects under WCAP. Within the 10,000 randomly sampled plots of the reviewed development area in the WCAP database, average disruption was 0.12 per km^2 (SD = 1.11, min = 0, max = 53.48) and average surface disturbance was 1.62% (SD = 5.74%, min = 0%, max = 100%). Based on the aforementioned thresholds known to elicit a response in mule deer, percent disturbance exceeded thresholds in 5% of all sample plots (N = 10,000) for disturbance and 0.43% for disruption. When considering sample plots within each reviewed development project (N = 233), 10 projects contained 20% or more in sample plots that exceeded disturbance thresholds within the project (Fig. 7). Of the 516 (5%) sample plots that exceeded thresholds, 499 of these were developed before the WCAP was in place. Only 17 sample plots in four distinct project locations added more than 5% new surface disturbance.

Discussion

Populations of long-distance, terrestrial migrants continue to decline in the face of ever-increasing anthropogenic land use that has the potential to alter or sever important migration routes (Berger 2004, Bolger et al. 2008, Sawyer et al. 2013). We sought to explore how conservation

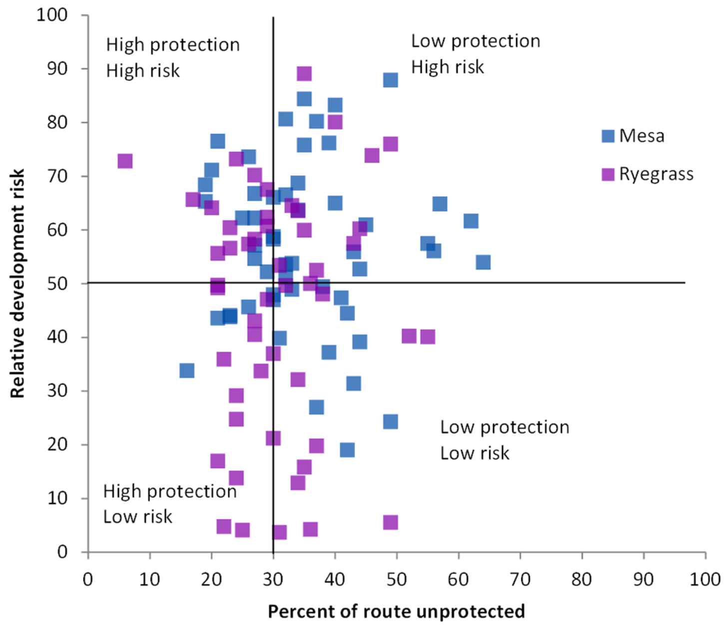

Fig. 5. Relative risk of residential development for generalized migration routes of adult female mule deer relative to the percentage of the route that does not overlaps with lands that have some form of conservation protection in place, including US Forest Service lands, conservation easements, and sage-grouse core area, for the Mesa and Ryegrass subpopulations, upper Green River Basin, Wyoming, USA.

actions targeted at a species of conservation concern, the Greater Sage-Grouse, might in turn offer ancillary benefits to migratory mule deer in western Wyoming. Our findings suggest that through the WCAP and private conservation easements, sage-grouse confer meaningful conservation to mule deer winter ranges and migration routes, including stopover habitat and high-use movement corridors in our study area (Fig. 4). Overall, spatial overlap from combined conservation measures that would benefit mule deer, which included sage-grouse policy, conservation easements, and US Forest Service lands were 66–70% for migration corridors, 74–75% for stopovers, and 52–91% for winter ranges. Of those proportions, conservation actions targeted specifically towards sage-grouse accounted for approximately half of the overlap in migration corridors and stopover areas, and nearly all of the overlap on winter ranges. Therefore, sage-grouse policy effectively doubled the amount of conservation afforded to migration routes for deer in this region.

Although these measured benefits represent an important step towards the conservation of migratory mule deer, two key aspects warrant careful consideration as efforts to conserve migratory populations move forward. First, provisions of allowed surface disturbance within sage-grouse core areas according to WCAP do not fully prohibit disturbance levels that can impact mule deer migration. Second, not all winter ranges and migration routes of mule deer overlap with sage-grouse core areas, which could create "sacrifice areas" when lands adjacent to sage-grouse core areas are developed in lieu of lands inside core areas. Thus, the potential benefits to migration routes inside sage-grouse core areas may be negated by increased levels of disturbance on migration route segments outside core areas.

Disturbance thresholds set within the WCAP must be biologically tolerable to mule deer for conservation efforts of sage-grouse to provide concomitant protection to mule deer migration. Intensive development within a portion of the project area could potentially exceed disturbance thresholds for migrating mule deer, while maintaining an allowable level of development according to WCAP when averaged across the

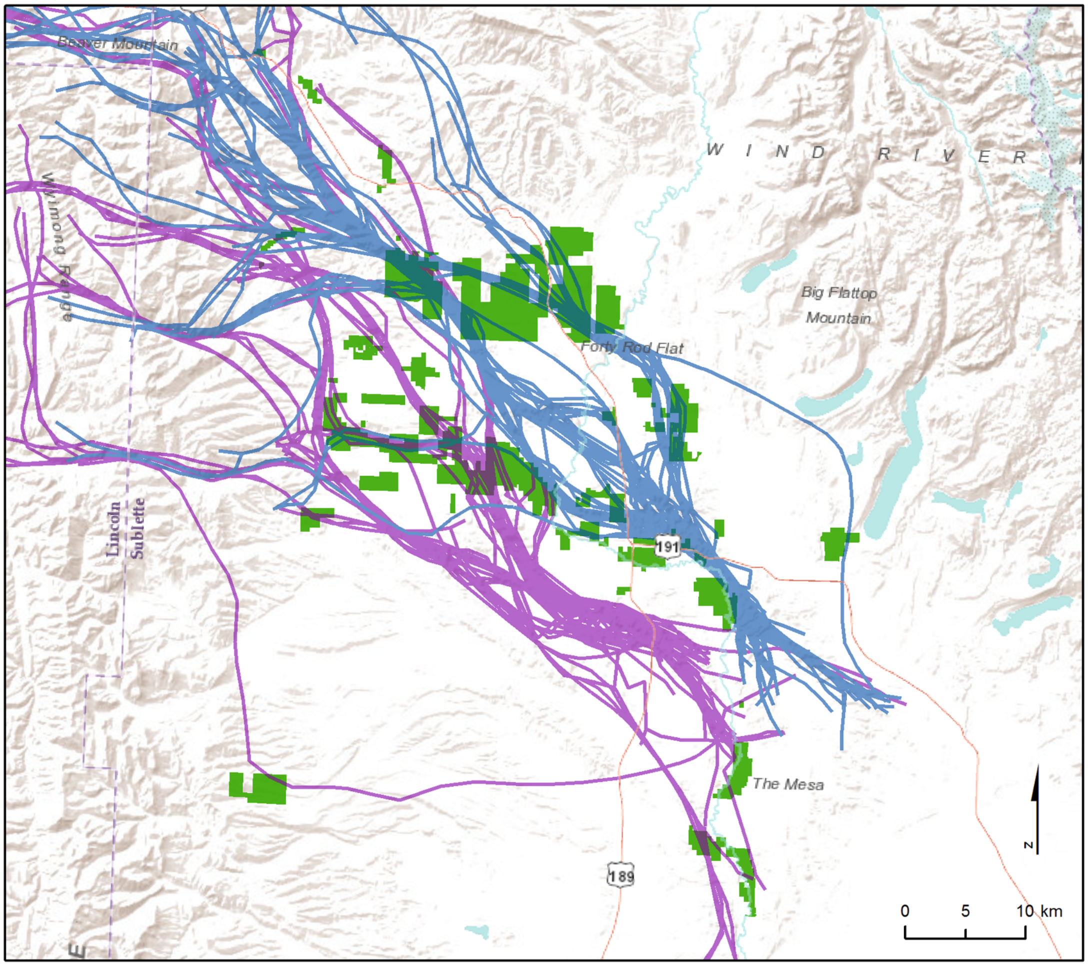

Fig. 6. Conservation opportunities on private land (green) with individual migration routes for Mesa (blue) and Ryegrass (purple) mule deer subpopulations.

project area. To evaluate this potential, we conducted an analysis to calculate this probability and found that within the reviewed development area, 95% of all sample plots ($N = 10{,}000$) were below thresholds known to elicit a response to mule deer migration. When evaluated on a summary project basis, 10 of 233 projects had more than 20% of sample plots exceeding disturbance thresholds (Fig. 7). Nevertheless, 97% of the sample plots that exceeded disturbance thresholds were developed before the WCAP was in place, with only 17 sample plots in four distinct project areas adding more than 5% new surface disturbance. Therefore, the majority of surface disturbance within our sample plots existed before WCAP.

Conservation policies and actions aimed at protecting sage-grouse will reduce disturbance for a high proportion of routes and stopovers for migrating mule deer in our study area. Conservation of migratory species presents unique challenges because although overlap with conserved lands may be high, connectivity of the entire route must be maintained and barriers to connectivity within the corridor could render it not viable. In light of these challenges, we view our umbrella analysis as an important planning tool that highlights potential gaps in conservation, especially where conservation efforts on private land can bridge and connect lands with other protections. To help guide future conservation action for mule deer, we identified areas that

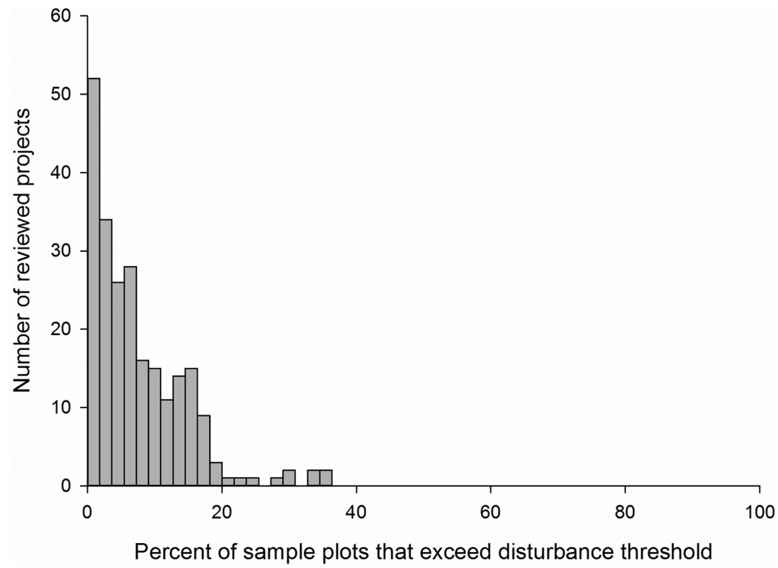

Fig. 7. Histogram of the number of completed development projects ($N = 233$) within Wyoming Core Area Policy relative to the proportion of 1-km buffers randomly placed within those projects that exceeded disturbance thresholds of percent surface disturbance (5.87%) for migrating mule deer, upper Green River Basin, Wyoming, USA.

were at high risk for development and intersect critical stopover, migration, and winter ranges (Fig. 6). In addition, the conservation of sagebrush ecosystems through the umbrella of sage-grouse has the potential to benefit many species in addition to migratory mule deer, especially sagebrush obligate species that depend on these habitats during the breeding season or year-round such as pronghorn (*Antilocapra americana*), pygmy rabbit (*Brachylagus idahoensis*), Brewer's Sparrow (*Spizella breweri*), and Sage Thrasher (*Oreoscoptes montanus*).

Lasting conservation benefits also will depend upon state and federal agency decision-makers to stay steadfast to the WCAP, regardless of future ESA listing decisions. The WCAP was an effort to proactively conserve sage-grouse and avert an ESA listing. Since sage-grouse core areas do not always overlap mule deer range, many important mule deer habitats are outside of core area boundaries. This presents a challenge because state policy in turn encourages development outside of core, which could place additional stress on mule deer populations that do not overlap with core areas. The Mesa winter range is one example of an important area for mule deer outside of a sage-grouse core area that has been subjected to a major natural gas development; mule deer populations in this area have declined by an estimated 42% since development began (Sawyer and Nielson 2012). In addition, critical winter range for the Wyoming Range mule deer herd, one of the largest mule deer populations in the West, lies immediately to the southwest of the Mesa and Ryegrass subpopulations, but is entirely outside of a core area. Increased exposure to development for deer populations outside of sage-grouse core areas could offset conservation benefits gained from the WCAP.

Conservation easements that address risk of development on private lands have played a small but important role in conserving high-priority movement corridors and stopover areas for mule deer. Conservation easements protected a relatively small percentage of areas that corresponded directly to migration of mule deer in the GRB (1–8%); although, when calculated as a proportion of private lands, easements represented a much larger fraction (13–18% of high-priority migration corridors). Unlike most other administrative protections associated with migration routes, easements are protected in perpetuity and provide long-term assurance of habitat protection. Conservation easements provide a unique opportunity to protect important areas on a site-specific basis—a valuable tool because mule deer exhibit high fidelity to migration corridors and stopovers (Sawyer and Kauffman 2011). For example, conservation easements northwest of Pinedale, Wyoming protect habitats used by >1,000 mule deer to access summer range in the Bridger Teton National Forest. Other privately led efforts have played an important conservation role. A bipartisan sportsman-led coalition spearheaded an effort to establish the Wyoming Range Legacy Act in 2009, a policy that withdrew 490,000 ha of oil and gas leases within mule deer summer range on the Bridger Teton National Forest. A coalition of conservation groups then bought remaining leases to conserve 26–41% of high-priority stopovers and migration pathways on these lands (Fig. 4).

The upper GRB contains an especially large sage-grouse core area with large populations of migrating mule deer. Therefore, it is likely that our analysis represents a best-case scenario, as the overlap between core areas and mule deer migration may be smaller, more fragmented, or nonexistent in other areas of Wyoming. Given the widespread overlap between sage-grouse and mule deer range, a larger study examining these intersections in Wyoming appears warranted, especially given current commitment to sage-grouse conservation efforts. A challenge in applying our approach more broadly is a lack of fine-scale movement and stopover data for other migratory populations. Nonetheless, our results indicate that where mule deer ranges overlap with sage-grouse core areas, increased level of protection is afforded to winter ranges and migration routes within the umbrella of sage-grouse conservation, so long as concentrated developments within core areas do not intersect with high-priority stopovers or corridors and ranges outside of core areas are not sacrificed in lieu of development within core area.

Managing landscapes for both energy development and abundant wildlife sustainably into the future represents an enormous challenge (Bolger et al. 2008, Berger et al. 2014). Mule deer face many challenges, whether from energy or residential development or from decreased habitat quality related to climate change. Our results indicate that conservation efforts on behalf of sage-grouse may translate more broadly to migrating wildlife that also inhabit those systems. We measured important benefits to deer from the WCAP and private conservation efforts that are an important first step in a broader, ecosystem-based approach to multiple species benefit through efforts focused on one species. We caution, however, that WCAP does not fully protect lands inhabited by mule deer because of the provisions on limits to disturbance and that an unintended consequence of WCAP may be to expedite oil and gas development on public lands outside of core areas. These analyses highlight a key opportunity for state and federal agencies and NGOs to proactively conserve remaining migration corridors, stopovers, and winter ranges for mule deer. This can be done by actively targeting easements on private lands currently at risk of development and by limiting disturbance on federal lands both within and outside of sage-grouse core areas that deer use as migration corridors, stopover areas, and winter ranges.

Acknowledgments

We are grateful to the Knobloch Family Foundation, Kaplan Family Foundation, NRCS Sage Grouse Initiative, Mule Deer Foundation and The Nature Conservancy for financial support. We thank several individuals for help with data and fact-checking including Lisa McGee, Dan Stroud, and Tim Griffiths. We thank several anonymous reviewers for thoughtful comments and edit suggestions. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Literature Cited

Andelman, S. J., and W. F. Fagan. 2000. Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? Proceedings of the National Academy of Sciences 97:5954–5959.

Bastian, C., and T. K. Foulke. 2010. Estimating the market value of Wyoming agricultural lands as an input into lease valuation for federal programs conducted in the state. University of Wyoming, Laramie, Wyoming, USA.

Berger, J. 1997. Population constraints associated with the use of black rhinos as an umbrella species for desert herbivores. Conservation Biology 11:69–78.

Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. Conservation Biology in Practice 18:320–331.

Berger, J., S. L. Cain, E. Cheng, P. Dratch, K. Ellison, J. Francis, H. C. Frost, S. Gende, C. Groves, W. A. Karesh, E. Leslie, G. Machlis, R. A. Medellin, R. F. Noss, K. H. Redford, M. Soukup, D. Wilcove, and S. Zack. 2014. Optimism and challenge for science-based conservation of migratory species in and out of U.S. national parks. Conservation Biology 0:1–9.

Beyer, H. L. 2012. Geospatial modelling environment. Version 0.7.2.1. http://www.spatialecology.com/gme

Bishop, C. J., G. C. White, D. J. Freddy, B. E. Watkins, and T. R. Stephenson. 2009. Effect of enhanced nutrition on mule deer population rate of change. Wildlife Monographs 172:1–28.

Blickley, J., D. Blackwood, and G. Patricelli. 2012. Experimental evidence for the effects of chronic anthropogenic noise on abundance of Greater sage-grouse at leks. Conservation Biology 26:461–471.

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.

Bureau of Land Management. 2000. Record of decision: environmental impact statement for the Pinedale Anticline Oil and Gas Exploration and Development Project Sublette County, Wyoming. Bureau of Land Management, Pinedale Field Office, Pinedale, Wyoming, USA.

Bureau of Land Management. 2008. Record of decision: final supplemental environmental impact statement for the Pinedale Anticline Oil and Gas Exploration and Development Project. Bureau of Land Management, Pinedale Field Office, Pinedale, Wyoming, USA.

Bureau of Land Management. 2012. Instruction Memorandum Number WY-2012-019. Bureau of Land Management, Cheyenne, Wyoming, USA.

Caro, T. M., and G. O'Doherty. 1999. On the use of surrogate species in conservation biology. Conservation Biology 13:805–814.

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. I. M. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 155:1–61.

Copeland, H., and K. Browning. 2013. Conservation easements held by land trusts and agencies in Wyoming. http://wygl.wygisc.org/DataServer/

Copeland, H. E., A. Pocewicz, D. E. Naugle, T. Griffiths, D. Keinath, J. S. Evans, and J. Platt. 2013. Quantifying the benefits of the core area policy and conservation easements to sage-grouse in Wyoming. PLoS ONE 8:1–14.

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, Utah, USA.

Doherty, K., D. E. Naugle, H. Copeland, A. Pocewicz, and J. M. Kiesecker. 2011. Energy development and conservation tradeoffs: systematic planning for greater sage-grouse in their eastern range. Pages 505–516 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. University of California Press, Berkeley, California, USA.

Doherty, K. E., D. E. Naugle, B. L. Walker, and J. M. Graham. 2008. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187–195.

Fishburn, I. S., P. Karieva, K. J. Gaston, and P. R. Armsworth. 2009. The growth of conservation easements as a conservation tool. PLoS ONE 4 (3):e4996.

Fleishman, E., D. Murphy, and P. Brussard. 2000. A new method for selection of umbrella species for conservation planning. Ecological Applications 10:569–579.

Gamo, S., J. D. Carlisle, J. L. Beck, J. A. C. Bernard, and M. E. Herget. 2013. Greater sage-grouse in Wyoming: an umbrella species for sagebrush-dependent wildlife. The Wildlife Professional. http://news.wildlife.org/category/twp/2013-spring/

Grovenburg, T. W., J. A. Jenks, R. W. Klaver, K. L. Monteith, D. H. Galster, R. J. Schauer, W. W. Morlock, and J. A. Delger. 2008. Factors affecting road mortality of white-tailed deer in eastern South Dakota. Human-Wildlife Conflicts 2:48–59.

Gude, P. H., A. J. Hansen, R. Rasker, and B. Maxwell. 2006. Rates and drivers of rural residential development in the Greater Yellowstone. Landscape and Urban Planning 77:131–151.

Hanser, S. E., and S. T. Knick. 2011. Greater sage-grouse as an umbrella species for shrubland passerine birds: a multiscale assessment. *In* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. University of California Press, Berkeley, California, USA.

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 73:437–448.

Harrington, J. L., and M. R. Conover. 2010. Characteristics of ungulate behavior and mortality associated with wire fences. Wildlife Society Bulletin 34:1295–1305.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to gas field development in western Wyoming. Dissertation. University of Wyoming, Laramie, Wyoming, USA.

Holloran, M. J., R. C. Kaiser, and W. A. Hubert. 2010. Yearling Greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65–72.

Horne, J., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movements using brownian bridges. Ecology 88:2354–2363.

Johnson, D. H., M. J. Holloran, J. W. Connelly, S. E. Hanser, C. L. Amundson, and S. T. Knick. 2011. Influences of environmental and anthropogenic features on greater sage-grouse populations, 1997-2007. Page 646 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitat. University of California Press, Berkeley, California, USA.

Kaiser, R. C. 2006. Recruitment by greater sage-grouse in association with natural gas development in western Wyoming. University of Wyoming, Laramie, Wyoming, USA.

Kiesecker, J. M., T. Comendant, T. Grandmason, E. Gray, C. Hall, R. Hilsenbeck, P. Karieva, P. Lozier, P. Naehu, A. Rissman, M. R. Shaw, and M. Zankel. 2007. Conservation easements in context: a quantitative analysis of their use by The Nature Conservancy. Frontiers in Ecology and the Environment 5:125–130.

Knick, S. T., S. E. Hanser, and K. L. Preston. 2013. Modeling ecological minimum requirements for distribution of Greater sage-grouse leks: implications for population connectivity across their western range, U.S.A. Ecology and Evolution 3:1539–1551.

Lendrum, P. E., C. R. Anderson, 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 3:1–19.

Lendrum, P. E., C. R. Anderson, Jr., K. L. Monteith, J. A. Jenks, and R. T. Bowyer. 2013. Migrating mule deer: effects of anthropogenically altered landscapes. PLoS ONE 8:e64548.

Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage-grouse nest initiation and movement. Wildlife Society Bulletin 31:486–491.

Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, J. G. Kie, and R. T. Bowyer. 2014. Life-history characteristics of mule deer: effects of nutrition in a variable environment. Wildlife Monographs 186:1–62.

Naugle, D. E., K. Doherty, B. L. Walker, H. E. Copeland, and J. D. Tack. 2011. Sage-grouse and cumulative impacts of energy development. Page 274 *in* P. R. Krausman and L. K. Harris, editors. Cumulative effects in wildlife management. CRC Press, Boca Raton, Florida, USA.

Ozaki, K., M. Isono, T. Kawahara, S. Iida, T. Kudo, and K. Fukuyama. 2006. A mechanistic approach to evaluation of umbrella species as conservation surrogates. Conservation Biology 20:1507–1515.

Pocewicz, A., J. M. Kiesecker, G. P. Jones, H. E. Copeland, J. Daline, and B. A. Mealor. 2011. Effectiveness of conservation easements for reducing development and maintaining biodiversity in sagebrush ecosystems. Biological Conservation 144:567–574.

Roberge, J., and P. Angelstam. 2004. Usefulness of the umbrella species concept as a conservation tool. Conservation Biology 18:76–85.

Rowland, M. M., M. J. Wisdom, L. H. Suring, and C. W. Meinke. 2006. Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. Biological Conservation 129:323–335.

Sawyer, H., and M. J. Kauffman. 2011. Stopover ecology of a migratory ungulate. Journal of Animal Ecology 80:1078–1087.

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, R. M. Nielson, and J. S. Horne. 2009. Identifying and prioritizing ungulate migration routes for landscape-level conservation. Ecological Applications 19:2016–2025.

Sawyer, H., C. Lebeau, and T. Hart. 2012. Mitigating roadway impacts to migratory mule deer—a case study with underpasses and continuous fencing. Wildlife Society Bulletin 36:492–498.

Sawyer, H., F. Lindzey, and D. McWhirter. 2005. Mule deer and pronghorn migration in western Wyoming. Wildlife Society Bulletin 33:1266–1273.

Sawyer, H., and R. M. Nielson. 2012. Mule deer monitoring in the Pinedale Anticline project area. Western EcoSystems Technology, Laramie, Wyoming, USA.

Sawyer, H., R. M. Nielson, F. Lindzey, and 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.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. Condor 106:363–376.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passe in the landscape era? Biological Conservation 83:247–257.

Sorensen, T., P. D. McLoughlin, D. Hervieux, E. Dzus, J. Nolan, J. Wynes, and S. Boutin. 2008. Determining sustainable levels of cumulative effects for boreal caribou. Journal of Wildlife Management 72:900–905.

State of Wyoming Executive Department. 2008. Greater sage-grouse core area protection executive order 2008-2. Cheyenne, Wyoming, USA.

Sublette County. 2012. Sublette County ownership data. http://www.sublettewyo.com/

Taylor, R. L., J. D. Tack, D. E. Naugle, and L. S. Mills. 2013. Combined effects of energy development and disease on greater sage-grouse. PLoS ONE 8:e71256.

Tollefson, T. N., L. A. Shipley, W. L. Myers, D. H. Keisler, and N. Dasgupta. 2010. Influence of summer and autumn nutrition on body condition and reproduction in lactating mule deer. Journal of Wildlife Management 74:974–986.

Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644–2654.

Wisdom, M. J., M. M. Rowland, and L. H. Suring, editors. 2005. Habitat threats in the sagebrush ecosystem: methods of regional assessment and applications in the Great Basin. Alliance Communications Group, Lawrence, Kansas, USA.

Wyoming Game and Fish Department. 2012. Mule deer crucial winter ranges. http://wgfd.wyo.gov/web2011/WILDLIFE-1000811.aspx