2012

Conserving Montana's sagebrush highway: long distance migration in sage-grouse

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CONSERVING MONTANA'S SAGEBRUSH HIGHWAY:

LONG DISTANCE MIGRATION IN SAGE-GROUSE

By

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B.S., University of Montana, Missoula, MT, 2010

Thesis

presented in partial fulfillment of the
requirements for the degree of:

Master of Science
in Wildlife Biology

The University of Montana
Missoula, MT

January 2013

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ACKNOWLEDGMENTS

Funding for this work came from the Montana/Dakotas Bureau of Land Management (BLM) state office, Grasslands National Park of Canada, and the World Wildlife Fund. Additional support came from the Charles M. Russell National Wildlife Refuge office of the U.S. Fish and Wildlife Service and Montana Fish, Wildlife and Parks. Randy Matchett was a saving grace when a new component of this project arose late in the game. Without his generosity of time and resources, we would not have been able to explore an unexpected outcome of a truly severe winter. There are many BLM folks who provided guidance and support throughout this project, but there are three I especially want to thank. Vinita Shea was my first BLM mentor and my whole-hearted advocate when it came time to explore graduate research opportunities with BLM. Gayle Sitter was instrumental in generating ideas and providing funding to get this project off the ground. Finally, John Carlson became my mentor, advocate, committee member, and most importantly, my friend as I worked on this project. His patience and wisdom, not to mention his expertise as a wildlife biologist and passion for his career inspired me and carried me through some of the most challenging parts of graduate school.

This project would have fallen flat without help from some outstanding technicians and volunteers. Jason Tack, Orrin Duvuvuie, Chris Binchus, Brandon Sandau, Heather Nenninger, Matt Tribby, and Cody Fulk were fantastic field assistants through trying conditions. A list of volunteers includes Chris Reed, Mark Hockett, Erin Clark, Matt Ocko, Emily Hutchins, Ashley Wruth, and an enthusiastic crew of Parks Canada interns. Mike Gregg and James Rebholz provided professional assistance during a challenging fall trapping endeavor.

One of the most valuable aspects of graduate school is the relationships formed therein; Marisa Lipsey, Marketa Zimova, Nick Sharp, and many others have become good friends and valuable colleagues. I have been fortunate to work with exceptional colleagues in my lab. Marisa, Joe Smith, and Michel Kohl ensured that I didn't work too hard but were ready with ideas and assistance when they were needed. Darin Newton stood by me through the ups and downs of graduate school as a friend and a partner, and I am greatly indebted to him for his love, support, and patience. Above all, my family has always shown unwavering support for my interests and pursuits; without them, none of this would have been possible.

Finally, I want to thank my committee members. Mark Hebblewhite and Mike Mitchell each challenged me to think critically and creatively about my research. John Carlson kept me thinking about the importance of research to practical wildlife management and periodically checked in on my emotional well-being during the long pushes of fieldwork and writing. And last, but certainly far from least, I thank Dave Naugle for taking me on as his student based primarily on the good word of Dan Pletcher and Gayle Sitter. From Dave I learned that when it comes to application of research, the method of delivery is as important as the science behind the message. His focus and dedication to implementing wildlife conservation while keeping human interests in mind are humbling, and I am honored to be a part of his conservation legacy.

Smith, Rebecca, M.S., January 2013 Fish and Wildlife Biology

Conserving Montana's sagebrush highway: long distance migration in sage-grouse

Chairperson: Dr. David E. Naugle

Landscape conservation is the mechanism for conserving migratory wildlife in sagebrush ecosystems. We study further a greater sage-grouse (*Centrocercus urophasianus*; hereafter 'sage-grouse') population with the longest-known annual migration, a 240-km journey between summer range in north central Montana, USA, and Saskatchewan, Canada, to winter range north of the Missouri River. We learned more about grouse migration by asking: Do birds fly quickly through a corridor, or do they use stopover habitats within a larger migratory pathway? New GPS-tracking technology revealed that migrating grouse frequent stopover habitats along multiple routes that coalesce to form an integrated pathway. A month-long fall migration in November was in contrast to a punctuated spring migration that lasted on average 2 weeks in late March/early April. Individual birds typically spent ~1 day at nine different stopovers, migrating 71-91 km in 11-15 days. Grouse migrated through gently rolling sagebrush flats (<5% slope), using native sagebrush rangeland in proportion to its availability, and avoiding cropland and badlands where food was scarce. Birds responded to record-breaking snowfall in winter 2011 (>274 cm) by extending their migration another ≤50 km south onto windswept ridge tops where sagebrush remained above snow. Grouse secured food resources by selecting the most similar habitat available on Charles M. Russell National Wildlife Refuge, and doing so was without consequence to winter survival; such was not the case for a nearby resident population. In spring, they made a mass exodus back north, and returned to summer range after migrating ~160 km in 18 days. Previously identified ranges remain important in most years but newly identified winter range suggests that high site fidelity is tempered by an ability to adapt quickly when resources become scarce. Ranching is a compatible land use that maintains this migratory population. We recommend a public land policy that provides grazing opportunities while precluding large-scale energy development or the whole scale removal of sagebrush to increase forage production. Management actions that maintain sagebrush as an emergency food source in newly identified sage-grouse wintering grounds will help to conserve this migratory population. Conservation easements provide a mechanism for maintaining privately-owned working ranches as a compatible and desirable alternative to sodbusting or subdivision along a sage-grouse migration pathway.

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Chapter 1: Introduction

Humans have long been intrigued by the seasonal movements of wild animals, have followed migrating herds for food, and speculated on the sudden disappearance and reappearance of songbirds. Researchers are still learning the who's, how's, and why's of migratory species, and wildlife managers are faced with the challenges of conserving highly mobile migrants. Migration arises as a behavior to which organisms are driven because of spatially and temporally variable resources (Dingle 1996). Most migrants exhibit telling characteristics, such as persistent movements greater than normal daily movements, relatively straight trajectory, temporary suppression of response to resources, restlessness before start of migration, and reallocation of energy resources in preparation for long movements (Dingle 1996). Migration for these organisms occurs regardless of the state of resources at their present location and is cued by things like change in photoperiod (Dingle 1996). Migration for others is an immediate response to changes in availability of resources or to social interactions (Dingle 1996, Chetkiewicz et al. 2006, Dingle and Drake 2007, White et al. 2007).

Migratory strategies and patterns vary widely between organisms and even within populations. A number of waterfowl and mammals like mule deer (*Odocoileus hemionus*) migrate in a stepping-stone fashion, with periods of movement interspersed with periods of rest and refueling at stopover sites (Dingle 1996, Sawyer et al. 2009). Many species move along complex networks of routes (Dingle 1996, Chetkiewicz et al. 2006) that coalesce into a broad pathway rather than following one distinctive route. From a conservation

standpoint, this means that no one formula will serve to protect every species (Chetkeiwicz et al. 2006). Fractured landscapes can cut off populations from moving between important seasonal habitats (Chetkiewicz et al. 2006, Leu et al. 2008, Sawyer et al. 2009) and decrease biodiversity (Kiesecker et al. 2009, 2010, Jeffery Evans, The Nature Conservancy, unpublished data) by preventing seasonal migrations and gene flow. It will be important to understand the movement patterns and needs of migrating wildlife in order to prevent severing migration pathways which would likely soon be followed by extirpation of migratory populations.

Greater sage-grouse (*Centrocercus urophasianus*; hereafter 'sage-grouse') are a sagebrush obligate species native to North America's northern Great Plains that is known to have migratory populations (Connelly et al. 1988, Connelly et al. 2000). Resident sage-grouse populations use overlapping seasonal ranges to carry out their life histories while migratory populations travel >10 km between distinct summer, winter, or breeding ranges (Connelly et al. 2000). Sage-grouse have experienced range constriction of around 44% (Schroeder et al. 2004) since Europeans arrived in the west. This iconic prairie species has suffered declines of between 45 and 80% range-wide (Connelly and Braun 1997, Braun 1998, Connelly et al. 2000, Aldridge and Brigham 2003), with local declines of up to 92% (Carpenter et al. 2010). Only 13 males were counted on leks in Alberta, Canada, in spring 2011 and decline to extirpation seems imminent. Extirpation of sage-grouse in Canada would make the species purely a U.S. issue rather than a joint international concern. Sage-grouse carry endangered status in Canada and will receive a final listing decision from the U.S. Fish and Wildlife Service in 2015.

Thesis format and co-authorship

I formatted my thesis for submission to the *Journal of Wildlife Management*. I use the collective term 'we' throughout my thesis to reflect co-authorship. My Master's thesis was a collaborative effort in which D. Naugle and J. Carlson contributed substantially at each step along the way. I included P. Fargey and M.R. Matchett as co-authors for their specific and substantive contributions. The views in these articles are those of the authors and do not necessarily reflect those of their employers.

This thesis focuses on further study of a sage-grouse population with the longest-known annual migration, a 240-km journey between summer range in north central Montana, USA, and Saskatchewan, Canada, to winter range north of the Missouri River (Tack et al. 2011). Co-authors first discovered this annual migration through repeated and expensive aerial searches for lost birds marked with traditional VHF transmitters (Tack et al. 2011). We use global positioning system (GPS) technology to further our knowledge of sage-grouse migration. The body of this thesis investigates sage-grouse movements and habitat use during migration, and bird response to a rare winter event that presented itself as a natural experiment. We learned more about grouse migration by evaluating whether birds flew quickly through a corridor, or if they use stopover habitats within a larger migratory pathway. GPS-tracking technology shows that migrating grouse frequent stopovers along multiple routes that coalesce to form an integrated pathway.

Record snowfall (>274 cm) on traditional wintering grounds in 2011 buried sagebrush, their primary food source in winter. The ensuing winter migration provided a rare opportunity to monitor how this population adapts to extreme winter conditions. Grouse responded to winter severity by migrating another 50 km south, moving out of

sagebrush flats and into the more rugged and patchily forested 'breaks' country inside of Charles M. Russell National Wildlife Refuge (CMR). Findings characterize timing and duration of stopovers, and identify a migratory pathway and seasonal habitats for conservation of this migratory population. We identify additional wintering grounds, characterize winter habitat on CMR, and provide recommendations for maintaining winter refugia habitat for this population during extreme winters.

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15 January, 2013

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Intact pathway successfully buffers sage-grouse migration

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Abstract: Landscape conservation is the mechanism for conserving migratory wildlife in sagebrush ecosystems. We studied a greater sage-grouse (*Centrocercus urophasianus*; hereafter 'sage-grouse') population with the longest-known annual migration, a 240-km journey between summer range in north central Montana, USA, and Saskatchewan, Canada, to winter range north of the Missouri River. We learned more about grouse migration by asking: Do grouse migrate in a single flight or do they use stopover habitats within a larger migratory pathway? GPS-tracking technology revealed that migrating

grouse frequent stopover habitats along multiple routes that coalesce to form an integrated pathway. A month-long fall migration in November contrasted with a punctuated spring migration that lasted on average 2 weeks in late March/early April. Individual birds typically spent ~1 day at nine different stopovers, migrating 71-91 km in 11-15 days. Grouse migrated through gently rolling sagebrush flats (<5% slope), using native sagebrush rangeland in proportion to its availability, and avoiding cropland and badlands where food was scarce. Birds responded to record-breaking snowfall in winter 2011 (>274 cm) by extending their migration another ≤50 km south onto windswept ridge tops where sagebrush remained above snow. In spring, they made a mass exodus back north, and returned to summer range after migrating ~160 km in 18 days. Previously identified summer and winter ranges remain important in most years but newly identified winter range suggests that high site fidelity is tempered by an ability to adapt quickly when resources become scarce. Ranching is a compatible land use that maintains this migratory population. We recommend a public land policy that provides grazing opportunities while precluding large-scale energy development or the whole scale removal of sagebrush to increase forage production. Conservation easements provide a mechanism for maintaining privately-owned working ranches as a compatible and desirable alternative to sodbusting or subdivision along a sage-grouse migration pathway.

Key words: *Centrocercus urophasianus*, habitat selection, migration, plasticity, sagebrush, stopover, winter

The Journal of Wildlife Management 00(0):000-000, 20XX

Migration can be an essential component of an organisms' life history by connecting multiple areas containing discrete resources that are important for distinct life functions.

For most familiar terrestrial and aerial vertebrates, migration is seasonal travel between two or more disparate locations that each supports a need such as secure winter, summer, or breeding habitat. Here habitat is defined as the multi-dimensional space, comprised of abiotic and biotic characteristics, which influence use of that space by a given organism (Beyer et al. 2010). Often migrations are predictable in timing, routes, and destinations. While some species are hard-wired to photoperiod or other internal and external cues that regulate movements, weather events and natural forces are capable of disrupting or altering normal migration behaviors (Bauer et al. 2011).

The factors that drive whether a population or sub unit of a population migrates may depend on such things as sex, age class, variability in local conditions, and latitude (Cagnacci et al. 2011). Differences in foraging behavior or population densities can result in different migration patterns in similar species that have overlapping ranges and otherwise share habitat types (Mysterud et al. 2012). In Sweden, moose (*Alces alces*) exhibit variable movement patterns related to latitudinal differences in snow depth, road density, and by age class (Singh et al. 2012), and European roe deer (*Capreolus capreolus*) are highly variable within and across populations throughout their range (Cagnacci et al. 2011, Mysterud et al. 2012). The complex nature of migrations, what drives them, and what they look like in time and space present challenges to conserving migratory species.

Many animals do not readily adapt to anthropogenic disturbances and development but instead respond with avoidance behaviors, higher stress levels, lower fitness and lower survival. Winter tourism in the Swiss Alps has brought increased human presence as people flock to ski resorts, and snowshoe or cross country ski into otherwise little-trammeled montane conifer forests. While good for the economy, winter sports are a point

of concern for capercaillie (*Tetrao urogallus*), the world's largest grouse species and one that has been extirpated from much of its historic range in western Europe (Thiel et al. 2008). A combination of stress caused by human presence, energy spent actively avoiding humans, and low-quality winter forage reduces body condition of birds coming out of winter and entering courtship and breeding in the spring (Thiel et al. 2008). Similarly, greater sage-grouse (*Centrocercus urophasianus*; hereafter 'sage-grouse') in western North America fair poorly in the path of anthropogenic disturbance. Sage-grouse rely heavily on a single food source, sagebrush, through winter and depend heavily on sagebrush for nesting cover and forage the rest of the year (Doherty et al. 2008). Sage-grouse are North America's largest grouse species and inhabit the sagebrush steppe and prairies of the west. Where winter tourism and tree plantations are detrimental to capercaillie in Europe (Thiel et al. 2008), a suite of anthropogenic development resulting ultimately in habitat loss are the big stressors to sage-grouse, as well as other North American prairie species. Anthropogenic development and disturbances in western North America includes urban expansion, energy development and related infrastructure, sod-busting, altered fire regimes, and expansion of woody and exotic plant species (Knick et al. 2003, Brennan and Kuvlesky 2005, Leu et al. 2008). Such alterations to land not only remove habitat but can also inhibit important seasonal movements of species and populations.

Grassland and sagebrush steppe ecosystems are rich in biodiversity, are good carbon sinks, and are important producers of grain and meat products; yet these collective rangeland systems are poorly conserved, and their loss poses serious threat to global biodiversity (Samson and Knopf 1994, Brennan and Kuvlesky 2005). Grassland birds are in perilous decline as patches of native rangelands shrink (Samson and Knopf 1994,

Brennan and Kuvlesky 2005), and fragmentation by various forms of development threatens dispersal and migratory movements of multiple wildlife species (Tack et al. 2011). Movement corridors facilitate gene flow which maintains viable populations, help build disease resistance among populations, and connect important seasonal ranges (Simberloff et al. 1992). Yet, what corridors remain are at risk of severance characteristic of fragmented systems, and their loss has great ramifications for the species that rely on corridors. Pronghorn antelope (*Antilocapra americana*) are but one example of an endemic species whose long-distance movements have been truncated or severed by habitat alteration, providing evidence that fragmented systems are unable to sustain migratory populations (Berger 2004, Berger et al. 2006).

A number of waterfowl and mammals, such as mule deer (*Odocoileus hemionus*), migrate in a stepping-stone fashion, with periods of movement interspersed with periods of rest and refueling at stopover sites (Dingle 1996, Sawyer et al. 2009). Many species move along a complex network of routes (Dingle 1996, Chetkiewicz et al. 2006) that coalesce into a broad pathway rather than following one distinctive route. Small reserves support sedentary species, but only large and intact systems provide the stepping stones necessary to maintain migratory species. Wildlife and land managers can make more effective decisions for conserving migratory species when migration routes, habitat requirements enroute, and destinations are known.

Sage-grouse are a sagebrush steppe species that require large intact landscapes and that are known to migrate seasonally (Berry and Eng 1985, Connelly et al. 2000, Fedy et al. 2012). Driven by endogenous and exogenous cues (Fischer et al. 1996), sage-grouse may follow traditional routes, taking several days or even months to meander from one seasonal

habitat to another (Connelly et al. 1988). Most sage-grouse that migrate travel <60 km in a season, and typical movements in a migratory Idaho population are 11-15 km in length (Connelly et al. 1988, Fedy et al. 2012). We chose to further study the sage-grouse population with the longest-known annual migration, a population known to travel 120 km one-way from north central Montana, USA, and Saskatchewan, Canada, to wintering grounds north of the Missouri River (Tack et al. 2011). We first documented their wintering grounds by chance and through repeated and expensive aerial searches for lost birds marked with VHF-style transmitters. Efforts are ongoing to maintain this migratory pathway but conservation is incomplete because little is known about how birds move through the 'sagebrush highway'. Global positioning system (GPS) technology we deployed in this study enabled us to document their migratory behavior at a finer resolution as birds move from summer to winter range than attainable with traditional radio telemetry.

The goal of this study was to inform implementation of conservation actions pertaining to migratory populations of a sagebrush steppe native. Our objective was to figure out what makes migration work in a system that has not already suffered extensive alteration and fragmentation. Understanding a healthy working system ought to be the first step before diagnosing symptoms of stressors. Given what is known about migration in prairie steppe systems, we proposed a series of hypotheses to guide a characterization of sage-grouse migration in a landscape still dominated by native sagebrush rangelands: 1) We predicted that sage-grouse migrate in a similar fashion to prairie ungulates by using a series of pathways punctuated with multiple stopover sites, in contrast to classic long-distance bird migrants that make long direct flights with a few communal stopovers. 2) We predicted that the migratory pathway would best be characterized by presence of silver

sagebrush for forage and by gentle terrain. 3) We predicted that sage-grouse exhibit annual fidelity to the same seasonal ranges, much as hens show annual fidelity to areas they nested the previous year. 4) Finally, an additional migration witnessed in response to a winter of unusually high snow fall provided a rare opportunity to characterize the plasticity of this population to respond to extreme conditions. We predicted that sage-grouse would avoid starvation by migrating south in search of food, a highly adaptive behavior, that enables this population to persist. A more complete understanding of sage-grouse migration can speed conservation success, and the answers cannot come quickly enough. This population is one of the last sage-grouse strongholds in Canada, and its persistence depends largely on the effectiveness of conservation actions implemented along Montana's 'sagebrush highway'.

Study area

Our study area includes the East Block of GNP, Saskatchewan, extending south through Valley County, MT, and into the Charles M. Russell National Wildlife Refuge (CMR) along the Missouri River (Figure 1). East Block of GNP is 399 km², with 208 km² in-holdings of private ownership. Cattle are grazed on private lands inside the park and in pastures as part of a biodiversity and grazing study, and agricultural cropland adjoins most of the park boundary (Parks Canada 2010). The Bureau of Land Management (BLM) is the primary land manager in Valley County, and they lease federal rangelands for livestock grazing. BLM also administers the Bitter Creek Wilderness Study Area as a 240 km² parcel in which motorized vehicle use is restricted to established trails and roadways. Cattle are

grazed within Bitter Creek but rangeland improvements and other infrastructure are limited.

Sage-grouse summer range in north Valley County and GNP is typified by mixed short grass prairie and silver sagebrush. Grouse in north Valley County and GNP migrate each year because sparse stands of silver sagebrush (*Artemisia cana*), the predominant shrub on summer range (Aldridge and Brigham 2001, 2002, 2003; Figure 2, panels A and C), are buried under snow and inaccessible to birds in most winters (Tack et al. 2011). Sage-grouse migrate to winter range where dense stands of big sagebrush (*Artmisia tridentata*) provide forage (Figure 2, panels B and D). Birds move between seasonal ranges by flying over a 10-km swath of the Milk River, U.S. Highway 2, and agricultural croplands. The Vandalia gas field lies in the northwest portion of their winter range south of Hinsdale, MT. Summer and winter ranges inside high abundance sage-grouse 'core areas' have been prioritized for conservation by Montana Fish, Wildlife and Parks.

South Valley County lies between the Milk River and Ft. Peck Reservoir, and CMR is nested in Valley and Phillips Counties along the reservoir and Missouri River. Most of south Valley County is gently rolling big sagebrush flats intermixed with greasewood (*Sarcobatus vermiculatus*) and native grasses. Sagebrush flats transition into steep and rugged 'breaks' country in the CMR where ravines and draws are populated with juniper (*Juniperus* spp.) and ponderosa pine (*Pinus ponderosa*). Ownership on traditional wintering grounds is a mix of privately owned sagebrush grazing lands and public lands administered largely by BLM.

Precipitation varied greatly between years of study from wet and snowy in 2010-2011 to warm and dry in 2011-2012. Year 1 (fall 2010-spring 2011) brought above average

precipitation in both rain and snow, and Year 2 (fall 2011-spring 2012) was warmer and drier than average. The first winter brought record-breaking snowfall, with 275.8 cm recorded by the National Weather Service Station in Glasgow. Average annual precipitation is 28.5 cm, and average snowfall across the region is 76.2-101.6 cm. In contrast, December 2011 through March 2012 was a consecutive string of warmer-than-average months (National Weather Service Forecast Office, Glasgow, MT).

Methods

Trapping and handling

We trapped male and female sage-grouse on leks (The University of Montana Institutional Animal Care and Use Committee approval 065-09DNWB-010810) during the breeding season (15 March-20 April) in 2010. We used rocket nets (Giesen et al. 1982) to trap birds on leks in Montana. We captured birds on Fireguard Lek in GNP using walk-in traps (Schroeder and Braun 1991). Inclement weather in spring 2011 precluded trapping on leks. We spotlighted for sage-grouse (Wakkinen et al. 1992) in September and October 2010, and in late September 2011. Sage-grouse trapped in fall 2010 served as replacements for grouse that died between spring trapping and fall movements in Year 1. We attached 24, 30-gram (<3% total body weight) solar-powered backpack-style GPS transmitters to 5 males and 19 females in spring 2010. We deployed 8 new and 3 refurbished GPS transmitters in fall 2011. We used standard methods of aging and sexing grouse by examining primary feather development, checking under tail covert pattern, and measuring head and tarsus length (Eng 1955, Crunden 1963).

GPS transmitters were designed and constructed by North Star Science and Technology LLC (King George, VA) with a guaranteed battery life of 2 years; some lasted up to 3. Transmitters were programmed to collect 4 points per day and transmit collected locations to the Argos Data Collection System once every 5 days. Transmitters rendered inactive by way of bird mortality or detachment were collected from the field.

We camouflaged GPS units by painting them to match the cryptic markings on sage-grouse feathers (Figure 3). Painting units lowers visibility to predators by reducing reflected light and by breaking up the solid form through patterning and natural colors. GPS transmitters were designed to ride on the rump of grouse. Methods follow those of Brett Walker (Colorado Parks and Wildlife, unpublished data) who has successfully marked and monitored GPS-fitted birds for >2 years.

Treatment of GPS locations

Raw data were processed from text format with free decoding software available from North-Star Science and Technology LLC. Location data were collected as sensor data, Doppler data, and GPS data. GPS data are the most reliable, so we removed from analysis points that were not GPS fixes and that had >26 m location precision. We retained for analyses locations with fix precision of <26 m. We screened for inaccurate locations and deleted any that would have required a severe departure from normal movements as characterized by step length, turn angle, and relative location from consecutive locations (Frair et al. 2010). Average GPS fix success was 70% across individuals and seasons. Sparse canopy cover in our system did not impede transmission, and terrain used by sage-grouse did not detract from GPS fix success. Missed fixes or inaccurate locations likely were related to transmitter make and model or fix reduction due to movement rather than

canopy obscuration, topographic complexity, or grouse behavior (Frair et al 2010). We tested for differences between age and sex classes for duration of migration, number of stopovers made, and cumulative distance moved. We tested for these within seasons, and between fall and spring migrations. Age classes did not differ, and sexes differed only in duration of stopover in fall 2011. Therefore, we grouped sex and age classes due to small sample size and similarity in migratory behavior.

Identifying routes along the migration pathway

Data were brought into a geographic information system (GIS) for visual interpretation. We used Geospatial Modeling Environment to calculate step lengths of individual sage-grouse by migration season (Beyer 2012). We defined step length as the straight-line distance measured between 2 GPS locations. We defined the start of a migration as the day of the first directional movement towards the appropriate seasonal destination that was followed by a sequence of locations trending that direction.

We define a stopover as ≥2 consecutive GPS locations ≤1 km from one or more other consecutive locations. Most movements were >1 km between GPS fixes, so a step length of <1 km can reasonably be considered within a stopover location rather than a migration step. We did not consider locations with only one GPS fix to be a stopover because that fix could have occurred while a bird was moving. Any location that was missing a consecutive location 6 hours prior to or after it was not treated as a stopover because we were unable to determine if the bird had moved ≥1 km between when fixes should have occurred. Two consecutive fixes meant that a bird was in a specific location for ≥6 hours. We assumed straight line travel between consecutive fixes; thus, movement distances are conservative estimates of actual cumulative distances moved.

Characterizing habitat use along fall migration routes

Used and available points. We used Geospatial Modeling Environment (Beyer 2012) to calculate step length, turn angle, and bearing of migrating sage-grouse in fall. Step length is the straight line measurement between two consecutive locations, and turn angle is the change in trajectory from steps 1 and 2 to steps 2 and 3. Available locations were conditional based a distribution of step lengths and turn angles for each individual (Forester et al. 2009, Beyer 2012). We generated 2 available locations per used location for GIS land use analyses (n = 1,848). We generated a 1:1 set of available per used location for local slope and vegetative analysis (n = 162). For our winter analysis we used points from both winters. Used winter points were buffered by 10 km, the average step length for all birds in winter 2011. We used average step length from winter 2011 to depict distances that sage-grouse are capable of moving to meet resource demands under extreme rather than normal winter conditions. Available points were randomly selected within a polygon around buffered locations for both years. For winter 2011 the polygon included the southern-most extent of used locations and excluded late migration points north of the Milk River. We used a GIS to generate random points (1:1 used to available ratio) within the polygon for both winters. Number of used and available points for both winters was 8,056 (2011, n = 4,503; 2012, n = 3,553 used and available locations).

Winter survival of GPS-marked birds. We remotely monitored survival of GPS-marked sage-grouse. Movement between multiple daily fixes indicated survival of marked individuals. We visually confirmed survival each spring when marked birds returned to breeding grounds. We did not conduct a formal survival analysis, but no marked birds died in either winter.

Analysis

GIS land use categories for fall migration. We used a GIS to compile a land use layer (Montana Natural Heritage Program 2010). Land use types were native sagebrush rangeland, crop/pasture, and badlands. We did not include a layer for sagebrush cover because none are available that classify accurately sparse silver sagebrush. We overlaid land use types with used and available fall migration points. We used a Pearson's χ^2 test to evaluate differences in proportional land use (Johnson 1980). We used post-hoc pairwise comparisons with Bonferroni adjustments to identify any differences in land use.

GIS terrain variables for winter habitat selection. At winter locations we used a GIS to calculate slope and a measure of vector ruggedness (hereafter 'ruggedness') from a digital elevation model (Sappington et al. 2007). Ruggedness is measured between 0 and 1, where 0 is flat and 1 is a vertical surface. We considered slope and ruggedness as individual covariates in our models because these have been shown to be individually important variables in other studies (Sappington et al. 2007). We joined raster values of slope, aspect, and ruggedness to used and available locations in a GIS and combined the used and available points by winter into a single dataset. We removed all locations with aspect value of -1.

Local vegetation metrics. In summer 2011 we visited a subset of fall 2010 migration locations and a matched set of available points in Valley County and GNP. Heavy rains that rendered unpaved roads impassable for most of summer limited number of points visited. We generated a second set of used (n = 37) and available (n = 27) points to evaluate local vegetation metrics for winter 2011. Points fell inside the same polygon employed for measuring landscape metrics. Vegetation data was collected the following summer because

winter severity and human safety precluded visiting sites when birds were present. We measured characteristics of shrub density and height (Wambolt et al. 2006), slope, and aspect. We did not measure shrub inflorescences because these were new years' growth. We broke measurements of slope into three categories (0-5, 6-10, and >11%).

Fall migration and winter habitat resource selection. We used conditional logistic regression in R (R Core Team 2012) to evaluate differences in local vegetation metrics at used and available points. Metrics included slope, aspect, percent composition of all shrubs, percent composition of sagebrush relative to all shrubs measured, percent composition of combined *Artemisia* spp., number of shrub species, and average shrub height between used and available points. We evaluated model strength using an information theoretic approach (Burnham and Anderson 1998) and used Akaike's Information Criterion (AIC) corrected for small sample size (AIC_c) to determine best model rank. We used a Spearman rank-order correlation matrix to test for correlation between variables for all datasets. We used a GLM to evaluate the importance of GIS landscape covariates in habitat selection. We also used GLM to evaluate the role of local vegetation measures in winter habitat selection on CMR. Lastly, we characterized habitat selection by comparing proportional use between used and available points in 2011. We evaluated model rank using an information theoretic approach (Burnham and Anderson 1998). We used Spearman rank to test for correlation between variables in each dataset. We excluded highly correlated variables ($r_s \geq |0.7|$) in multivariate models, but we retained moderately correlated variables ($|0.3| < r_s < |0.7|$) in analyses.

Results

Migration characteristics

All GPS-marked sage-grouse migrated seasonally each year. Birds did not make long over-flights within a singular corridor. Rather, individual routes varied to form a diffuse pathway along which birds frequented stopover habitats as they migrated back and forth between seasons (Figure 4). This population exhibited high fidelity to seasonal habitats under normal and drought conditions. Seasonal habitats occupied in summer 2011 and 2012, and in winter 2012 are similar to those previously identified (Tack et al. 2011). On average, birds spent 11-15 days and migrated 71-91 km (range = 37-143) to reach these destinations (Table 1). Duration varied (3-37 days) and did not always correspond with total distance traveled (17 days to travel 37 km versus 127 km in 12 days; Table 1). Migrating birds averaged 7-9 stopovers (range = 2-15) apiece, with each lasting about a half-day in fall ($\bar{x}$ = 15.5 hrs) to one full day in spring ($\bar{x}$ = 20.5 hrs; Table 1). In November 2011, one bird completed a 20-day, ~140-km loop that took it south towards the Milk River and then swung back north to spend the rest of winter 11 km south of the Canadian border (Figure 4; panel C).

Fall migration was a protracted month-long event (23-45 days) in November. In comparison, spring migration was punctuated, lasting 2 weeks in late March and early April (mean departure dates: 2011 = 29 March, 2012 = 10 March; mean arrival dates: 2011 = 15 April, 2012 = 20 March). Spring arrival in 2011 coincided with the long-term average in peak male lek attendance (10 April) for GNP and north Valley County. Grouse undertook an extension of their fall migration in early to mid January in response to

record-breaking snowfall. Winter severity in 2011 delayed spring migration by 3 weeks (15 April versus 20 March).

Habitat selection in fall migration

Native sagebrush rangeland was the most common land type used by migrating sage-grouse in fall (93.4% used versus 81.7% available). Proportional use differed between land type ($\chi^2 = 44.08$, df = 2, $P \leq 0.01$; Figure 5). Sage-grouse avoided crop/pasture and badlands ($P \leq 0.01$ for both tests). Local-scale analyses at a sub-set of points indicated that sage-grouse used silver sagebrush flats with ≤5% slope ($\Delta AIC_c = 0$ and weight = 0.41). Silver sagebrush was the most common shrub found along fall migration routes. Big sagebrush was rarely encountered (<5% of points), and no other shrubs were present without silver sagebrush. Densities of shrubs and of sagebrush were highly correlated ($r_s = 0.82$), but shrub density did not differ ($P_{\text{shrub density}} = 0.62$; $P_{\text{sage density}} = 0.02$). Models including silver sagebrush performed better than those with total sagebrush density**.** Average shrub height was correlated ($r_s = 0.74$) with sagebrush density and was moderately correlated ($r_s = 0.66$) with shrub diversity. Top ranking GIS models indicated that sage-grouse selected flat slopes (≤5%) regardless of whether they were on traditional wintering grounds in 2012 or inside of CMR during the extreme winter of 2011. Evaluated in separate models to reduce collinearity, slope explained more variation than ruggedness in habitat use in 2012. A moderately supported model indicated that southwest facing aspects may increase bird use of flat wind-blown ridge tops inside of CMR ($\Delta AIC_c < 1$ and weight = 0.45). Birds also selected for southwest facing aspects in flat to rolling terrain in 2012 ($\Delta AIC_c = 0$).

Extended migration and habitat selection in winter 2011

Birds responded to record-breaking snowfall in winter 2011 (>274 cm) by extending their migration another ~50 km south (Table 1), moving out of their usual sagebrush flats and onto windswept ridge tops inside CMR where sagebrush remained above snow (Figure 6). After surviving the harsh winter, birds made a mass exodus back north, and returned to normal summer range after migrating 159 km in 18 days (Table 1). In spring 2012, migrating birds averaged 12 stopovers (range = 10-16) apiece, each lasting 14-23 hrs (Table 1). The new round-trip total for the longest migratory population of sage-grouse ever is 290 km (Table 1).

At winter locations inside the CMR, our on-site analysis reconfirmed that sage-grouse selected flat slopes (≤%5) in 2011 ($\Delta AIC_c = 0$ and weight = 0.94). The same top ranking model also indicated that habitat use was inversely related to shrub diversity. Shrub diversity was higher on steep slopes (>5%) but sage-grouse selected flat slopes with monotypic stands of big sagebrush (Figure 7). Monotypic stands were sagebrush 72.7% of the time at used points; no available points were monotypic stands of sagebrush. More used (83.8%) than available (37.0%) points had ≤2 shrub species. Where present, density of sagebrush was similar between used (4.8%) and available (4.7%) points. Juniper spp. or ponderosa pine occurred within 37.5% of available points; trees were absent in all used points.

Landscape perspective of sage-grouse migration

A majority of fall stopovers (65%) and wintering locations (58%) occurred on BLM-owned lands. Privately-owned lands provided 31% of stopover habitat and 23% of winter habitat, of which <10% is under conservation easement. Privately-owned lands enrolled in The

Nature Conservancy's Grassbank Program comprised 30% of total private land use by grouse in winter and 6% in fall. The CMR 'breaks' country provided winter habitat in 2011; a rugged and patchily forested landscape, CMR was not even formerly considered to be grouse habitat. Other lands providing stopover or winter habitat included State Trust lands in Montana (2-4%) and GNP (~1%).

Discussion

GPS-based movement data indicate that migrating sage-grouse use a network of routes rather than a single distinct route or corridor. Multiple routes coalesce to form an integrated migratory pathway. We found that grouse move slowly down the pathway, making frequent use of stopover sites, presumably stopping to forage and rest, before continuing on. We presume that grouse foraged at stopovers because 93% of sites visited during fall migration were within native sagebrush rangeland, and birds avoided other land types that provided little food or cover (e.g., badlands and cultivated lands).

We extend to grouse from other avian species the well-known concept of stopover habitat as an adaptive mechanism for replenishing lost energy during migration (Warnock 2010, O'Neal et al. 2012). Similar advances in ungulate migration show that mule deer routes contain a series of stopover sites where deer spend most of their time, connected by corridors through which they move quickly (Sawyer et al. 2009). Both examples are consistent with foraging theory whereby stopovers help individuals maintain body condition during migration.

Five years of tracking this population confirms that their migration is an obligate event that occurs annually regardless of winter severity. Previously identified ranges (Tack

et al. 2011) remain important in most years, but newly identified winter range 50 km south greatly expands our understanding of the size of landscapes necessary to support migratory populations. New insights gained from an additional migration in winter 2011 also suggest that high site fidelity to seasonal ranges is tempered by an inherent flexibility to adapt quickly when resources become scarce. Such behavior is highly adaptive, and in stark contrast to more sedentary galliformes (e.g., pheasants [*Phasianus colchicus*]) that succumb to extreme conditions (Gabbert et al. 1999). We do not speculate whether the resident sage-grouse population in south Valley County undertook a similar emergency migration in winter 2011.

Barriers to sage-grouse migration are poorly understood; many are suspected, but few have been documented, and little historical data exists. Sage-grouse in this study moved up and down the migratory pathway using gently rolling (<5% slope) sagebrush flats along the way. Our GPS-tracking data show that grouse are can travel >15 km in <6 hours, and are capable of crossing the Missouri River and Highway 2, a 10-km-wide corridor lined by cultivated lands. Migrating sage-grouse selected the same features along the migratory pathway as characterizes their summer and winter ranges, a behavior also observed in dispersing mountain lions (*Puma concolor*; Newby 2011). We were unable to test the effects of energy development on sage-grouse migration habitat because there is no development along the pathway we studied; however, numerous studies have repeatedly demonstrated the incompatibility of sage-grouse and development (e.g. Walker et al. 2007, Doherty et al. 2008, Doherty et al. 2011, and others). We find it reasonable to infer that mineral extraction or any other major human development (e.g. sodbusting) that removes native

sagebrush rangeland would be detrimental to sage-grouse migration just as it is to sage-grouse summer and winter range.

Fragmentation isolates sage-grouse populations (Oyler-McCance 2005), so least-cost paths are being identified (Spear et al. 2005, Storfer et al. 2007) to maintain gene flow across landscapes. Insights into migratory behavior may provide a surrogate for what is needed to maintain gene flow through dispersal, a rare but important event that is almost impossible to observe. Anecdotal evidence suggests that sage-grouse in Alberta migrated down to Montana in winter, but any historic pathway has long been replaced by sod busting for wheat production. Genetic analyses revealed that sage-grouse populations in Canada and eastern Montana are closely related, indicating recent genetic exchange between the relatively isolated Alberta population with Saskatchewan and Montana grouse (Bush et al. 2011). While the Alberta dispersers contribute their genetic signatures to other populations, it does not necessarily follow that dispersers from Saskatchewan and Montana are contributing to Alberta. The relative recentness of development and ability of grouse to disperse long distances confounds the ability to determine which forms of disturbance are most detrimental to gene flow in the long term (Bush et al. 2011). Combining genetics with tracking studies and identifying migratory status of populations may provide greater insights on this topic in the future.

We generally agree with others that sage-grouse habitat use in winter is best characterized as expansive sagebrush flats (Table 3; Doherty et al. 2008, Carpenter et al. 2009). Forced from their sagebrush flats in 2011, our population adapted its search image to include as habitat the flat and windswept sagebrush ridge tops inside CMR, a rugged and patchily forested landscape that until now was not even considered to be grouse

habitat. Bird use of ridge tops in CMR surprised many people but analyses show that grouse selected the most similar habitat available to secure food resources critical to winter survival. More importantly, relaxing constraints on winter habitat selection was without consequence to over winter survival (100%); such was not the case for a nearby resident sage-grouse population (58%; Moynahan et al. 2006). Still, a well-replicated study comparing survival of VHF- versus GPS-marked grouse has yet to be conducted (Fedy et al. 2012). Additional insights into the migratory behavior and plasticity of this species may be revealed when GPS technology is fully integrated into sage-grouse research. Our discovery of CMR as winter refugia precludes a complete understanding of source-sink dynamics (Pulliam 1988) that may influence survival in future years.

Management recommendations

Ranching is the common thread that maintains this migratory pathway across a tapestry of comingled land ownerships. Grazing is a compatible and highly desirable land use alternative to the fragmenting effects of energy development, sod busting, and subdivision. Historically, grazing by native ungulates was a widespread and natural occurrence in rangeland ecosystems. Today, grazing by cattle has largely replaced native grazers but still provides similar ecosystem services in absence of overgrazing (Crawford et al. 2004). Privately-owned ranch operations depend heavily on access to federal and state public lands for grazing. We recommend BLM policy that continues to provide grazing opportunities while precluding large-scale energy development or the whole scale removal of sagebrush to increase forage production. Nearly a third of sage-grouse stopover sites and winter habitat locations fall within privately-owned lands, of which >90% are at risk of

conversion. Conservation easements provide a mechanism by which landowners may receive economic incentives for voluntarily maintaining working ranches in grazing lands dominated by sagebrush. We encourage the continued success of The Nature Conservancy's pioneering Grassbank in south Phillips County. Under this program, local ranchers pay discounted fees to graze their cattle on the Matador Ranch in exchange for implementing wildlife-friendly practices including sage-grouse conservation on their own private lands.

Conserving this migratory spectacle depends in part on safeguarding the wintering grounds on which birds depend for food and cover. We recommend that BLM refrain from burning in big sagebrush habitats on winter ranges that support this population. Silver sagebrush on summer range north of Highway 2 responds favorably when burned, re-sprouting after a fire. In contrast, fires in big sagebrush habitats reduce food and cover for birds when fire management programs exceed the natural return intervals (50-80 years; Rhodes et al. 2010, Baker et al. 2012, Beck et al. 2012). We recommend BLM policy that precludes the fragmenting effects of energy development and the whole scale removal of sagebrush to increase forage production. Sustainably grazing privately-owned lands is a compatible and highly desirable alternative to row crop agriculture and subdivision. Conservation easements provide a mechanism by which landowners may receive economic incentives for voluntarily maintaining working ranches in sagebrush grazing lands. We also recommend that FWS refrain from burning ridge tops on CMR that provide refugia for birds in severe winters and which may facilitate invasion by cheatgrass (*Bromus tectorum*) or other exotics (Blomberg et al. 2012). Periodically hand-felling and removing encroaching trees will maintain openings where sagebrush provides requisite food

resources. Sage-grouse avoid conifer-encroached habitats where invading trees reduce sagebrush food and cover (e.g., Miller and Eddleman 2000).

Acknowledgments

We thank BLM for funding this project. The BLM, Parks Canada, and World Wildlife Fund helped purchase transmitters. We thank S. Klessens and staff from the BLM Glasgow Field Office for providing helpful advice, logistical support and field equipment for this study. M. Tribby, J.C. Fulk, H. Nenninger, J. Lamp, M. Hockett, M. Ocko, and E. Clark were invaluable field technicians and volunteers who collected data for this project. J. Tack, O. Duvuvuei, C. Sandy, C. Binschus, J. Carlo, L. Burke, B. Sandau, H. Nenninger, K. Minkley, V. Shea, G. Delves, A. Wruth and volunteers from Parks Canada provided outstanding trapping assistance. M. Gregg and J. Rebholz with FWS provided professional trapping assistance. Additional advice and support came from Montana Fish, Wildlife, and Parks.

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Associate editor:

Tables

Table 1. Distance, duration and number of stopovers used by migratory sage-grouse, north central MT, USA, 2011-2012. We denoted December 2010 through February 2011 as winter 2011 because the majority of winter movements occurred after the first of the year.

		No. stopovers			Hours/stopover			Distance (km)			Duration (days)		
Season	Year	Mean	Range	SE	Mean	Range	SE	Mean	Range	SE	Mean	Range	SE
Fall (1 Oct -30 Nov)	2010	8	3 - 15	1	15	9 - 22	2	80	51 - 124	8	12	4 - 28	2
	2011[a]	9	2 - 15	2	16	11 - 29	2	91	58 - 143	11	15	5 - 37	4
Spring (1 Mar -30 Apr)	2011	12	10 - 16	1	20	15 - 30	3	159	146 - 171	4	18	14 - 23	1
	2012	7	5 - 10	1	21	8 - 39	6	71	37 - 127	15	11	3 - 17	2
Winter (1 Dec - 28 Feb)	2011	4	1 - 11	2	14	6 - 28	3	49	15 - 98	11	8	2 - 16	2

[a]All means for fall 2011 include data from the individual that traveled the >140 km loop. The 2 short migration distances were excluded because we lacked movement data for those individuals between departure and arrival locations.

Table 2. Coefficients and p-values for covariates from the highest ranking landscape model (ΔAIC_c) at used and available winter locations from 2011 and 2012.

Model	Covariate	Coefficient	SE	z value	Pr(>|z|)
Slope+Aspect	(Intercept)	0.71	0.05	13.58	<0.001
	SLOPE	-0.21	0.01	-23.33	<0.001
	ASPECT	0.00	0.00	2.42	0.0155
Slope	(Intercept)	0.80	0.04	21.94	<0.001
	SLOPE	-0.21	0.01	-23.29	<0.001

Table 3. Top five ranking models (ΔAIC_c) for slope and vegetative variables at used and available locations inside CMR.

Models	K	AIC_c	ΔAIC_c	AICc weight	Log-likelihood
Slope+No. species	4	61.25	0	0.94	-26.28
No. species	2	67.97	6.73	0.03	-31.89
Slope+big sage	4	69.4	8.16	0.02	-30.36
Slope+shrub density	4	72.52	11.27	0	-31.92
Slope	3	74.13	12.88	0	-33.86

Figures

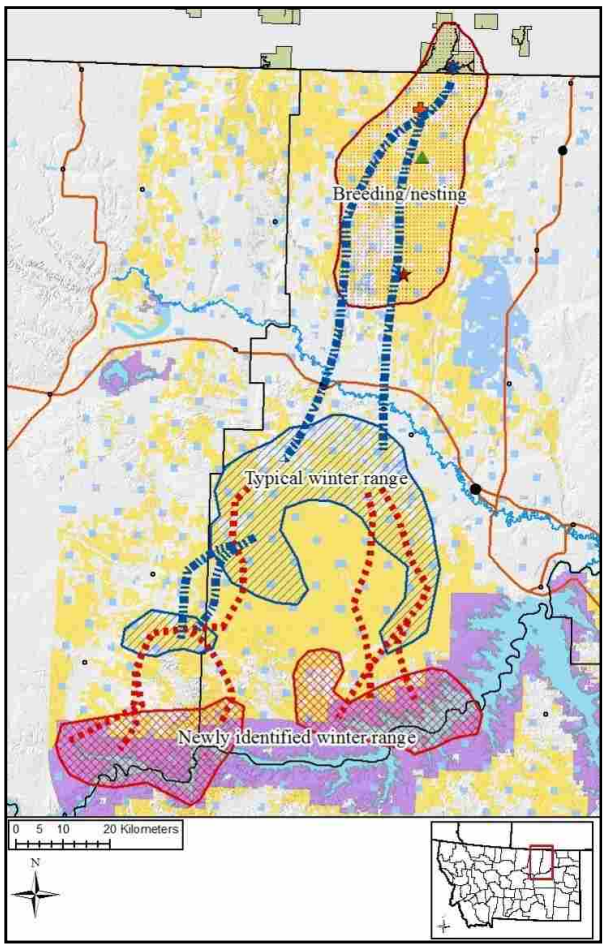

Figure 1. Study area in Valley County, MT, USA and GNP, Saskatchewan, Canada. The blue asterisk, orange cross, green triangle, and red star represent the four leks where we captured sage-grouse. Red stippling indicates summer range, blue hatch marks show typical winter range, and red cross-hatch shows newly identified winter range used in years of high snowfall. Blue dashed lines are a generalization of typical migration pathways while red dashed lines show migration routes to extreme winter refugia. Colors depict land ownerships by BLM (yellow), Montana State Trust Lands (blue), CMR (purple), and Parks Canada (green). The Milk River and U.S. Highway 2 run east-west between sage-grouse summer and winter ranges.

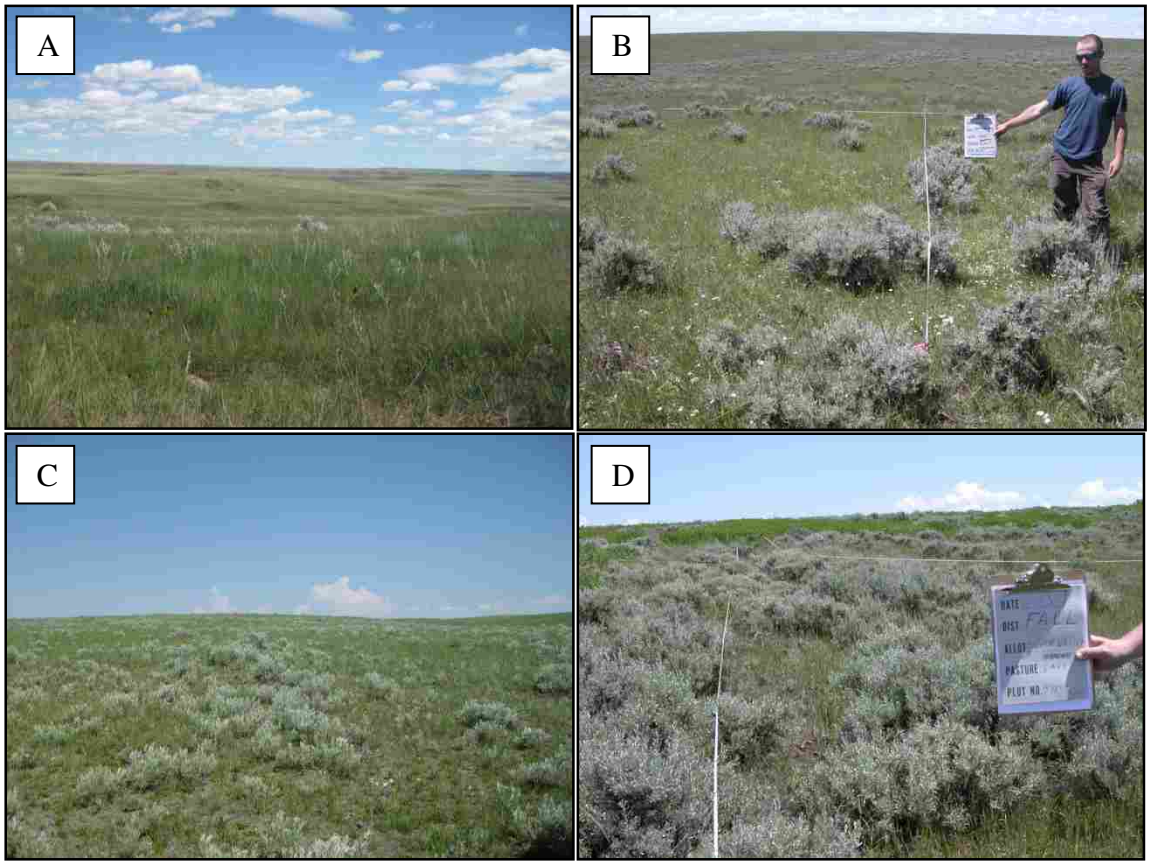

Figure 2. Sage-grouse summer range in north Valley County, MT, characterized by sparse silver sagebrush (panels A and C). Big sagebrush in south Valley County where sage-grouse typically winter (panels B and D) is more abundant and is typically found in higher density across the land than silver sagebrush.

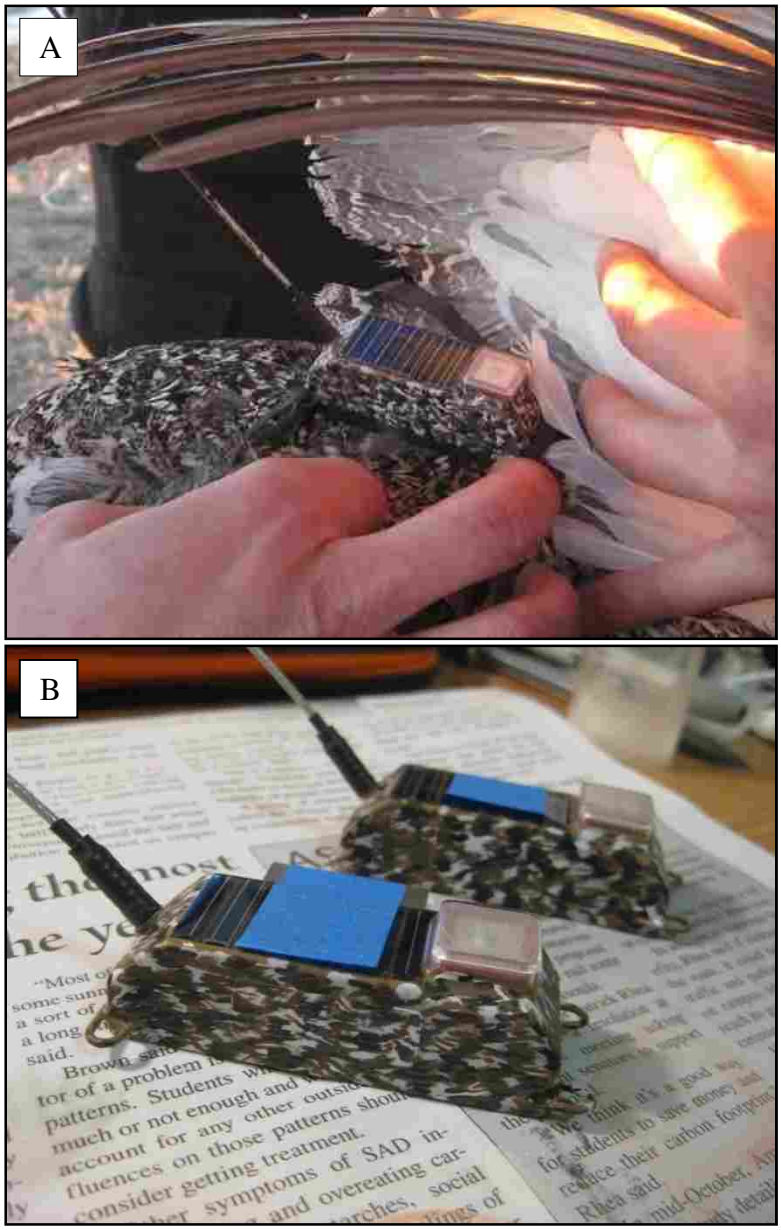

Figure 3. Camouflaged GPS transmitter attached to the rump of a sage-grouse (panel A). Close view of camouflage painting on transmitters (panel B). Painting done by R.E. Smith.

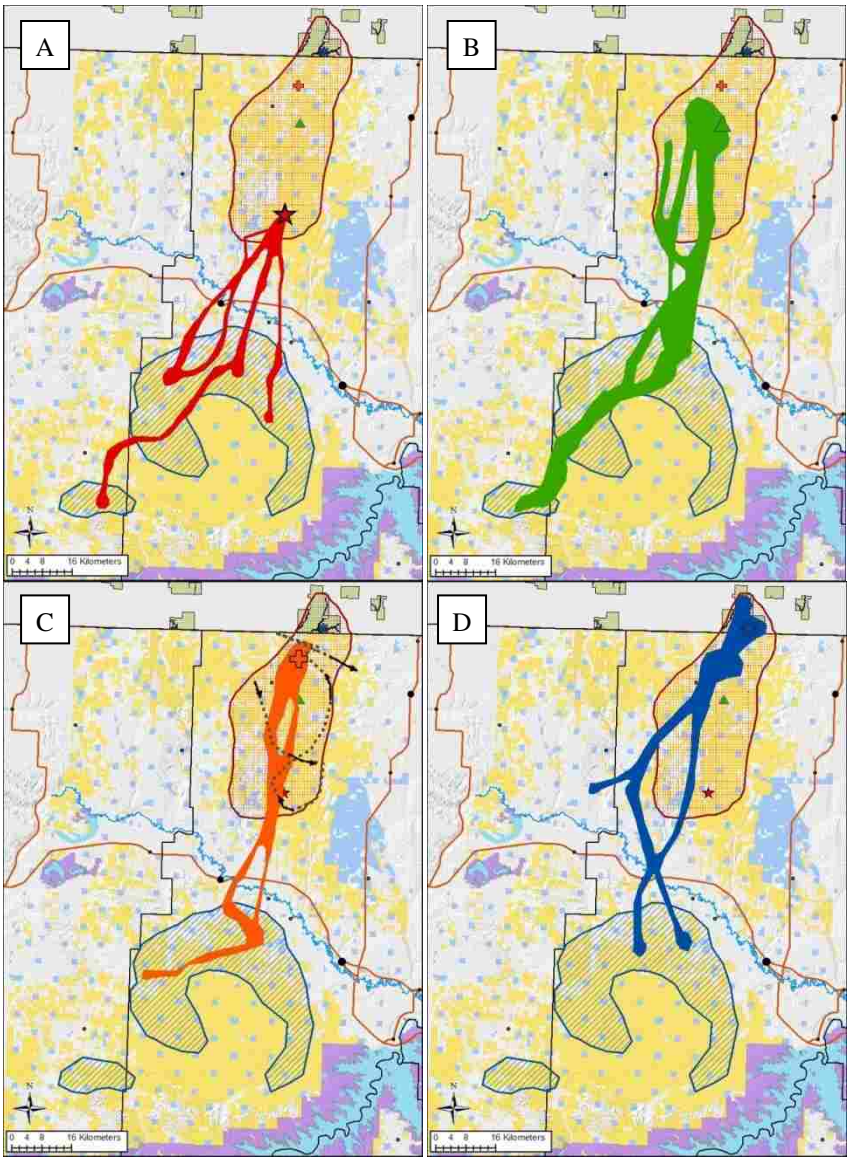

Figure 4. Sage-grouse migration routes in fall by lek of capture. Symbols depict lek of capture for Lek 101 (star; panel A), Lek 102 (triangle; panel B), Lek 57 (cross; panel C), and Fireguard Lek (asterisk; panel D). Fall migration routes are pictured north to south. The dashed grey line (panel C) depicts the loop made by grouse 606 in fall 2011. Arrows show direction of travel. The red stippled area marks summer range, and the blue hatching denotes typical winter range.

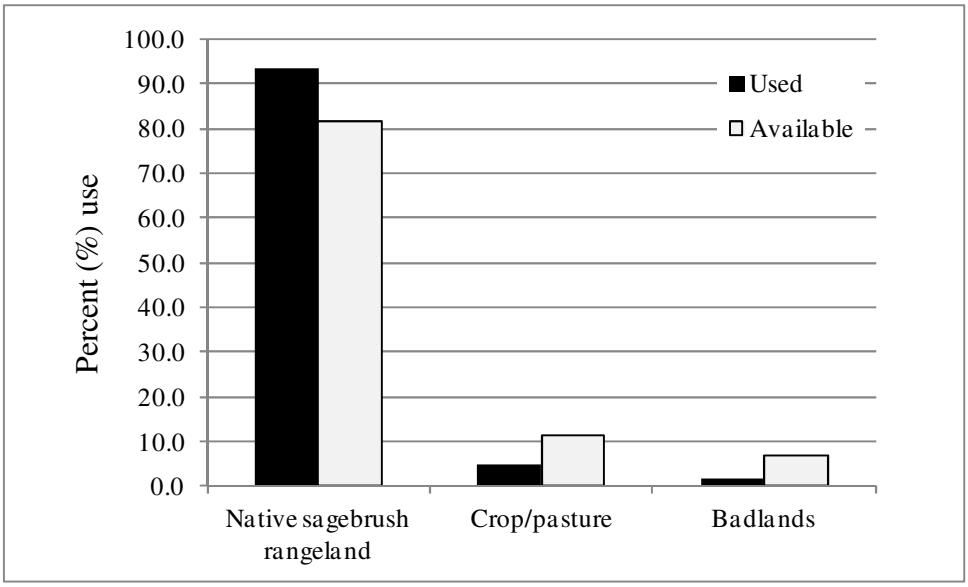

Figure 5. Proportions of used and available points during sage-grouse migration in fall 2010 and 2011.

Figure 6. Snow depth in early March 2011 in Valley County, MT (panel A) and in CMR (panel B) in early January. Photos courtesy of M. Kohl (A) and M.R. Matchett (B).

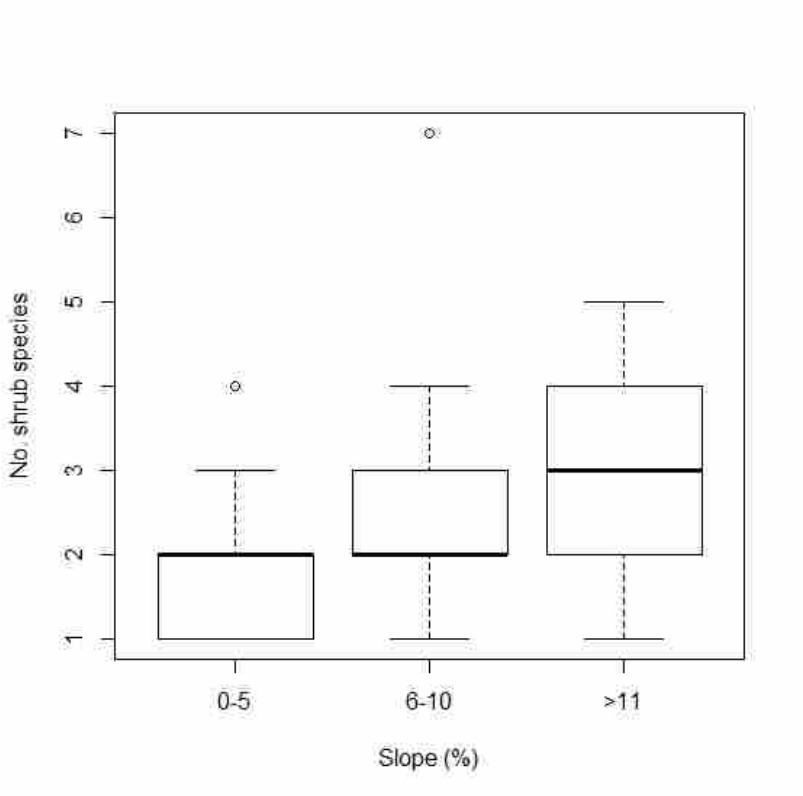

Figure 7. Number of shrub species by percent slope for used and available locations inside the CMR in winter 2011.