To the University of Wyoming:

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Increased levels of energy development across the Intermountain West have

created a variety of wildlife and habitat management concerns. Because many of the

energy resources in the region occur in shrub-dominated basins (e.g., Powder River,

Piceance, Great Divide, and Green River basins), management concerns have focused on

native shrub communities and associated species, including mule deer (*Odocoileus*

hemionus). Two of the more pressing concerns are how mule deer respond when critical

habitats (e.g., winter range) are impacted by development and how their migration routes

can be identified and prioritized for conservation. To address the first, I examined how

three types of natural gas well pads with varying levels of vehicle traffic influenced the

winter habitat selection patterns of mule deer in western Wyoming. My results showed

that mule deer avoided all types of well pads and selected areas further from well pads

that received high levels of traffic. Accordingly, impacts to mule deer could likely be

reduced through technology and planning that minimizes the number of well pads and

amount of human activity associated with them. To address the migration concerns, I

developed a quantitative framework that uses global positioning system (GPS) data and

the Brownian bridge movement model (BBMM) to: 1) provide a probabilistic estimate of

the migration routes of a sampled population, 2) distinguish between route segments that

function as stopover sites versus those used primarily as movement corridors, and 3)

prioritize routes for conservation based upon the proportion of the sampled population

that uses them. Mule deer migration routes were characterized by a series of stopover

sites where deer spent most of their time, connected by movement corridors through

which deer moved quickly. These findings suggest management strategies that differentiate between stopover sites and movement corridors may be warranted. Because some migration routes were used by more mule deer than others, proportional level of use may provide a reasonable metric by which routes can be prioritized for conservation. Although stopovers appeared to be a prominent feature of mule deer migration routes, the explicit study of stopovers (i.e., stopover ecology) has been limited to avian species. To assess whether stopover ecology was relevant to mule deer, I again used fine-scale GPS data and BBMMs to quantify a suite of stopover characteristics and examine the ecological role of stopovers in the seasonal migrations of mule deer. Mule deer utilized a series of stopover sites in both spring and fall migrations, across a range of migration distances (18-144 km). Overall, mule deer used 1.9 and 1.5 stopovers for every 10 km increase in migration distance during spring and fall migrations, respectively. Stopovers had higher quality forage compared to movement corridors, and forage quality increased with elevation, presumably because of delayed phenology along the altitudinal migration route. Stopovers likely play a key role in the migration strategy of mule deer by allowing them to migrate in concert with vegetative phenology and optimize their foraging during migration. My results suggest stopovers were a critical component in the altitudinal migrations of mule deer and that conservation of stopover sites may improve efforts aimed at sustaining migratory mule deer populations.

HABITAT USE AND MIGRATION ECOLOGY OF MULE DEER IN

DEVELOPING GAS FIELDS OF WESTERN WYOMING

By

Hall Sawyer

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CHAPTER ONE

Introduction

The influence of human-related disturbances on wildlife energetics, demography, and habitat selection is particularly important among temperate ungulates whose survival depends on minimizing energy expenditures during winter (Parker et al. 1984, Hobbs 1989). As natural gas development expands across the Intermountain West (Bureau of Land Management [BLM] 2005), identifying mitigation measures that reduce human disturbance and associated indirect habitat losses will become increasingly important, as will our ability to understand and predict animal responses to disturbance. Levels of human activity vary across most developing gas fields, with higher levels of activity at well pads with drilling operations and lower levels of activity at well pads with producing wells. The objective of Chapter 2 was to determine if mule deer (*Odocoileus hemionus*) habitat selection was influenced by well pads with varying levels of traffic in a developing gas field in western Wyoming. My intent was to provide a quantitative assessment of how wintering mule deer respond to active drilling operations versus producing well pads with different traffic regimes, such that future development and mitigation strategies may be improved. This chapter was published in the *Journal of Wildlife Management (73:1052-1061)*, with co-authors Matthew J. Kauffman and Ryan M. Nielson. Matthew Kauffman provided editorial assistance and outlined the importance of studying wildlife response to disturbance in the context of predation risk. Ryan Nielson provided statistical consultation and programming expertise.

The conservation of ungulate migration routes has received considerable attention across the globe (Fryxell and Sinclair 1988, Berger 2004, Thirgood et al. 2004, Bolger et

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al. 2008), in large part because the landscapes necessary to maintain them are becoming increasingly fragmented (Leu et al. 2008). Across the Intermountain West, mule deer, elk (*Cervus elaphus*), pronghorn (*Antilocapra americana*), moose (*Alces alces*), and bighorn sheep (*Ovis canadensis*) commonly migrate 50-100 km between seasonal ranges. The traditional migration routes of these ungulates are threatened by unprecedented levels of energy development, amplifying the need to identify and prioritize migration routes for conservation (Sawyer et al. 2009). Unfortunately, the quantitative tools needed to achieve this have not kept pace with technological advances (e.g., global positioning system [GPS] telemetry) that facilitate collection of fine-scale movement data. In Chapter 3, I attempt to bridge this methodological gap by developing an analytical framework that: 1) identifies the network of migration routes for a sampled population, 2) identifies route segments used as stopover sites versus those used for movement, and 3) prioritizes routes based upon their proportional levels of use. My approach combined fine-scale movement data with an innovative application of the Brownian bridge movement model (BBMM; Horne et al. 2007), to identify and prioritize population-level migration routes for conservation. I applied these methods to a mule deer population in Wyoming whose range is undergoing rapid energy development. This chapter was published in the *Ecological Applications (19:2016-2025)*, with co-authors Matthew J. Kauffman, Ryan M. Nielson, and Jon S. Horne. Matthew Kauffman provided advice and editorial assistance. Ryan Nielson and Jon Horne provided statistical consultation and programming expertise.

Among the key findings from Chapter 3 was that ungulate migration routes are composed of a network of stopover sites, where animals move slowly and spend most of

their time, connected by movement corridors through which animals move quickly and spend little time (Sawyer et al. 2009). The study of stopovers, termed "stopover ecology", has become an area of intense research in avian ecology and has played a vital role in developing a rigorous theory of bird migration and designing effective conservation strategies (Moore 2000). Yet, stopover ecology and its potential benefits have not been examined for non-avian migratory taxa. My goal in Chapter 4 was to assess whether stopover ecology has broad relevance to mule deer and other temperate ungulates that migrate long distances along traditional routes. Specifically, I used the methods outlined in Chapter 3 to examine a suite of stopover characteristics (number, size, spacing, forage quality, etc.) for >100 mule deer migrations in western Wyoming and evaluate what role stopovers play in the migration ecology of mule deer. This chapter was submitted to *Ecology*, with co-author Matthew J. Kauffman, who provided guidance and editorial assistance.

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CHAPTER TWO

Influence of Well Pad Activity on Winter Habitat Selection Patterns of Mule Deer

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Abstract: Conversion of native winter range into producing gas fields can affect the
habitat selection and distribution patterns of mule deer (*Odocoileus hemionus*).
Understanding how levels of human activity influence mule deer is necessary to evaluate
mitigation measures and reduce indirect habitat loss to mule deer on winter ranges with
natural gas development. We examined how 3 types of well pads with varying levels of
vehicle traffic influenced mule deer habitat selection in western Wyoming during the
winters of 2005-2006 and 2006-2007. Well pad types included producing wells without a
liquids gathering system (LGS), producing wells with a LGS, and well pads with active
directional drilling. We used 36,699 Global Positioning System (GPS) locations collected

from a sample ($n = 31$) of adult (>1.5 yr) female mule deer to model probability of use as a function of traffic level and other habitat covariates. We treated each deer as the experimental unit and developed a population-level resource selection function (RSF) for each winter by averaging coefficients among models for individual deer. Model coefficients and predictive maps for both winters suggested that mule deer avoided all types of well pads and selected areas further from well pads with high levels of traffic. Accordingly, impacts to mule deer could likely be reduced through technology and planning that minimizes the number of well pads and amount of human activity associated with them. Our results suggested that indirect habitat loss may be reduced by approximately 38-63% when condensate and produced water are collected in LGS pipelines rather than stored at well pads and removed via tanker trucks. The LGS appeared to reduce long-term (i.e., production phase) indirect habitat loss to wintering mule deer, whereas drilling in crucial winter range created a short-term (i.e., drilling phase) increase in deer disturbance and indirect habitat loss. Recognizing how mule deer respond to different types of well pads and traffic regimes may improve the ability of agencies and industry to estimate cumulative effects and quantify indirect habitat losses associated with different development scenarios.

*Key word*s: gas development, habitat selection, liquids gathering systems (LGS), mule deer, *Odocoileus hemionus*, predation risk, resource selection function (RSF), Wyoming

INTRODUCTION

Increased energy development on public lands has generated concern because of potential impacts to wildlife populations and their habitats (Lyon and Anderson 2003,

Sawyer et al. 2006, Bergquist et al. 2007, Walker et al. 2007). Because many of the largest natural gas reserves in the Intermountain West occur in shrub-dominated basins (e.g., Powder River Basin, Piceance Basin, Green River Basin), management concerns have focused on native shrub communities and associated species, including mule deer (*Odocoileus hemionus*; Sawyer et al. 2006). Changes to mule deer habitat are often obvious and direct, such as replacement of native vegetation with well pads, access roads, and pipelines. More difficult to quantify, however, are indirect habitat losses that occur when animals avoid areas around infrastructure due to increased human activity.

Understanding effects of human activity on wildlife is key to successful management and conservation (Knight and Gutzwiller 1995, Gill et al. 1996, Taylor and Knight 2003). The influence of human-related disturbances on wildlife energetics, demography, and habitat selection is particularly important among temperate ungulates whose survival depends on minimizing energy expenditures during winter (Parker et al. 1984, Hobbs 1989). Across western North America, restricting human activity in crucial ungulate winter ranges has been a common management practice for decades (Lyon and Christensen 2002). However, limiting human activity on many native winter ranges has become complicated, as the dominant land use has shifted from agriculture to energy extraction (Bureau of Land Management [BLM] 2005) and recreation (Knight and Gutzwiller 1995). Although many wintering ungulate herds are exposed to human activities, our understanding of how ungulates react to such disturbances is limited.

It has been demonstrated that wintering mule deer respond to natural gas well pads by selecting habitats ≥3 km away (Sawyer et al. 2006), but we do not know how mule deer behavior changes with levels of human activity. For example, do well pads

receiving 2 vehicle trips per day elicit a different behavioral response than those with 10 vehicle trips per day? Ungulates tend to avoid human disturbances such as roads (Rowland et al. 2000, Nellemann et al. 2001, Dyer et al. 2002), energy development (Nellemann and Cameron 1996, Bradshaw et al. 1997, Dyer et al. 2001, Nellemann et al. 2003), bicyclists (Taylor and Knight 2003), hikers (Miller et al. 2001, Papouchis et al. 2001), and snowmobiles (Freddy et al. 1986, Seip et al. 2007). However, it remains unclear how behavioral responses scale with the level of human activity.

As gas development expands across the Intermountain West (BLM 2005), identifying mitigation measures that reduce human disturbance and associated indirect habitat loss will become increasingly important, as will our ability to understand and predict animal responses to disturbance. Levels of human activity vary across most developing gas fields, with higher levels of activity at well pads with active drilling operations and lower levels of activity at well pads with producing wells. This development scenario provides an excellent opportunity to quantify how behavioral responses of ungulates vary as a function of disturbance level. Our objective was to determine if mule deer habitat selection in winter was influenced by well pads with varying levels of traffic in a developing gas field in western Wyoming. Our intent was to provide a quantitative assessment of how wintering mule deer respond to active drilling operations versus producing well pads with different traffic regimes, such that future development and mitigation strategies may be improved.

STUDY AREA

The Pinedale Anticline Project Area (PAPA) is located in the upper Green River Basin, approximately 5 km southwest of Pinedale, Wyoming. The PAPA consisted

primarily of federal lands (80%) administered by the BLM with elevations of 2,070-2,400 m (BLM 2000). The PAPA supported livestock grazing and provided crucial winter range for 4,000 to 5,000 migratory mule deer that summer in portions of 4 mountain ranges 80-160 km away (Sawyer et al. 2005). Although the PAPA covered 799 km^2, most mule deer spend winter in the northern third, an area locally known as the Mesa. The 260-km^2 Mesa is bounded by the Green River on the west and the New Fork River on the north, south, and east, and is vegetated primarily by Wyoming big sagebrush (*Artemisia tridentata*) and sagebrush-grassland communities. Our study was restricted to the Mesa portion of the PAPA, where we previously modeled predevelopment distribution patterns of mule deer during the winters of 1998-1999 and 1999-2000 (Fig. 1; Sawyer et al. 2006).

The PAPA also contains some of the largest natural gas reserves in the region, which the BLM approved for development in 2000 (BLM 2000). Due to a series of regulatory decisions (BLM 2000, 2004*a*, *b*), the PAPA contained 3 basic types of well pads during 2005 and 2006, including: 1) active drilling pads, 2) producing well pads with liquid gathering systems (LGS), and 3) producing well pads without LGS. All active drilling pads implemented directional drilling, where multiple wells were drilled and completed from one pad. Most human activity in gas fields is vehicle traffic on unpaved roads and is highest at active drilling pads. However, once drilling is completed and wells are in production phase, traffic levels decline at well pads. Among producing well pads, those with LGS have the lowest levels of traffic because water and condensate by-products are collected in pipelines rather than by tanker trucks. During the 2005-2006 winter, our study area contained 6 active drilling pads and approximately 60 and 66 LGS

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and non-LGS well pads, respectively. During the 2006-2007 winter, our study area contained 5 active drilling pads and approximately 71 and 72 LGS and non-LGS well pads, respectively.

METHODS

We captured adult (≥1.5 yr) female mule deer using helicopter net-gunning in the northern portion of the PAPA, where deer congregate in early winter before moving to their individual winter ranges throughout the Mesa (Sawyer and Lindzey 2001). Previous work showed that capturing deer in this area during early winter provides the best opportunity to obtain a representative sample of the wintering population (Sawyer et al. 2006). We fitted deer with store-on-board Global Positioning System (GPS) radiocollars (Telonics, Inc., Mesa, AZ) equipped with remote-release mechanisms and programmed to attempt a location fix every 2 hours. Potential fix-rate bias (Frair et al. 2004, Nielson et al. 2009) was not a concern because of the high (99%) fix-rate success of the GPS collars in the open terrain of our study area.

We used active infrared sensors (Trailmaster® TM 1550 sensor, Lenexa, KS) to monitor vehicle traffic at a sample of 18 well pads during 13 January – 27 March 2006 and 10 January – 17 March 2007. We placed monitors approximately 1.2 m off the ground and set them at a sensitivity level that required the infrared beam to be broken for 0.30 seconds. We designed this configuration to minimize the sensor recording multiple hits for trucks pulling trailers. We estimated mean daily traffic volume for the 3 well pad types: those with LGS, those without LGS, and active drilling pads. We also observed 235 traffic (175 pickup trucks, 38 utility trucks, 18 tractor-trailers, 8 cars) crossings across the 18 sites to assess accuracy of the monitoring system. Of the 235 vehicle

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observations, 229 (97%) were accurately recorded. We used analysis of variance (ANOVA) to test for differences in mean daily traffic volume among well pad types.

Resource Selection

Whereas traditional resource selection function (RSF) methods (Manly et al. 2002) commonly use logistic regression to compare a discrete set of used units with a set of unused or available units (Thomas and Taylor 2006), our approach used multiple regression to model probability of use as a continuous variable (Marzluff et al. 2004; Sawyer et al. 2006, 2007). Our approach consisted of 5 basic steps in which we: 1) measured predictor variables at 4,500 randomly selected circular sampling units, 2) estimated relative frequency of use in the sampling units for each radiocollared deer, 3) used relative frequency as the response variable in a generalized linear model (GLM) to estimate probability of use for each deer as a function of predictor variables, 4) averaged coefficients from models of each individual deer to develop a population-level model, and then 5) mapped predictions of the population-level model.

This method treats the marked animal as the experimental unit, thereby eliminating 2 of the most common problems with resource selection analyses: pooling data across individuals and ignoring spatial or temporal correlation in animal locations (Thomas and Taylor 2006). An additional benefit of treating each animal as the experimental unit is that inter-animal variation can be examined (Thomas and Taylor 2006), while still providing population-level inference via averaging coefficients (Marzluff et al. 2004, Millspaugh et al. 2006, Sawyer et al. 2006). Finally, by modeling use as a continuous variable, we considered resource use in a probabilistic manner that

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relies on actual time spent by an animal in a sampling unit, rather than presence or absence of the animal (Marzluff et al. 2004, Millspaugh et al. 2006).

We used the study area of Sawyer et al. (2006), which was based on the distribution (i.e., min. convex polygon) of 39,641 locations from 77 mule deer over 6 years (1998- 2003). Based on 7 years of previous modeling efforts, we identified 3 variables as potentially important predictors of winter mule deer distribution, including elevation, slope, and distance to well pad type (Sawyer et al. 2006). We did not include vegetation as a variable because the sagebrush-grassland was homogeneous across the study area, and vegetation maps that divide this habitat into finer classes did not exist. We used ArcView to calculate slope from a 26×26-m digital elevation model (U.S. Geologic Survey [USGS] 1999). We digitized roads and well pads from high-resolution (10-m) satellite images provided by Spot Image Corporation (Chantilly, VA). Images were collected in September 2005 and 2006, after most annual construction activities (e.g., well pad and road building) were complete, but prior to snow accumulation. Images were geo-processed by SkyTruth (Sheperdstown, WV). We categorized well pads as active drilling, LGS, or non-LGS.

Our sampling units for measuring habitat variables consisted of 4,500 circular units with 100-m radii randomly distributed across the study area. Ideally the sampling unit should be small enough to detect changes in animal movement or habitat selection (Millspaugh et al. 2006, Sawyer et al. 2006) but large enough to ensure the number of locations within the sampling units approximates a known error distribution (e.g., Poisson or negative binomial). Size of the sampling units may vary depending on mobility of the animal, frequency of GPS locations, and heterogeneity of the landscape. Previously, we

evaluated units with 75-, 100-, and 150-m radii and found units with 100-m radii worked well for mule deer data collected at 2-hr intervals in the PAPA study area (Sawyer et al. 2006). Alternatively, we could have used square sampling units, but regardless of the shape or number, the sampling units cannot cover the entire study area because our modeling approach requires the total number of locations for each animal occurring in the sampling units be treated as a random variable. We took a simple random sample with replacement to ensure independence of sampling units. We counted the number of deer locations within each sampling unit and measured elevation, slope, and distance to well pad type at the center of each sampling unit.

Before modeling resource selection, we conducted a Pearson's pairwise correlation analysis to identify possible multi-collinearity issues and to determine whether we should exclude any variables from our modeling ($|r| > 0.60$). Among the well pad variables, distance to active drilling and non-LGS pads were correlated ($r = 0.72$) during the 2005-2006 winter. However, we retained both covariates because this made the models more interpretable, and the correlation did not appear to influence model stability (i.e., regression coeff did not switch signs and SEs did not increase substantially as we added variables). During the 2006-2007 winter, distance to active drilling and non-LGS pads were highly correlated ($r = 0.90$); thus, we excluded distance to active drilling well pad as a covariate from the 2006-2007 model.

The relative frequency of locations from each radiocollared deer found in each sampling unit was an empirical estimate of probability of use by that deer and we used it as a continuous response variable in a GLM. We used an offset term (McCullagh and Nelder 1989) in the GLM to estimate probability of use for each radiocollared deer as a

function of a linear combination of predictor variables, plus or minus an error term assumed to have a negative binomial distribution. We preferred the negative binomial distribution over the Poisson because the negative binomial allows for overdispersion (White and Bennetts 1996), which in this application, is due to many sampling units with zero locations. We began our modeling by first estimating coefficients for each radiocollared deer with:

$$\ln(E[l_i]) = \ln(total) + \beta_0 + \beta_1 X_1 + \ldots + \beta_p X_p, \tag{1}$$

which is equivalent to:

$$\ln(E[l_i/total]) = \ln(E[\text{Relative Frequency}_i]) = \beta_0 + \beta_1 X_1 + \ldots + \beta_p X_p, \tag{2}$$

where l_i is number of locations for a radiocollared deer within sampling unit i ($i = 1, 2, \ldots, 4500$), $total$ is total number of locations for the deer within the study area, β_0 is an intercept term, $\beta_1, \ldots, \beta_p$ are unknown coefficients for habitat variables $X_1, \ldots, X_p$, and $E[.]$ denotes the expected value. The offset term, $\ln(total)$, converts the response variable from an integer count (e.g., 0, 1, 2) to a frequency (e.g., 0, 0.003, 0.005) by dividing the number of deer locations in each sampling unit (l_i) by the total number of locations for the individual deer ($total$; Fig. 2). At the level of an individual animal, this approach estimates true probability of use for each sampling unit as a function of predictor variables and is referred to as a resource selection probability function (RSPF; Manly et al. 2002). However, it is important to note that if we average coefficients from individual deer RSPFs to obtain a population-level model, the predictions reflect geometric means of individual probabilities rather than true probabilities. Also, because our sampling units may overlap, they are not mutually exclusive and thus predictions from equation 1 are not subject to a unit-sum constraint.

We followed the Marzluff et al. (2004) approach by fitting one model with all variables to each animal. Next, we treated the estimated coefficients as random variables, because they represent independent, replicated measures of resource use (Marzluff et al. 2004, Millspaugh et al. 2006). This approach quantifies the resource selection of individuals and provides a valid method of assessing population-level use by averaging coefficients among marked individuals (Marzluff et al. 2004, Millspaugh et al. 2006). We considered quadratic terms for distance to well pad and slope variables (Sawyer et al. 2006), and following convention, we also included the linear form of each variable. We did not use an information theoretic approach such as Akaike's Information Criteria (AIC; Burnham and Anderson 2002) for model selection because there is no standard method by which AIC can be properly applied to retain the animal as the experimental unit and build a population-level model with a common set of predictor variables. To evaluate population-level resource selection we assumed GLM coefficients for predictor variable t for each deer were a random sample from an approximate normal distribution (Seber 1984), with the mean of the distribution representing the population-level effect of predictor variable t on probability of use (Marzluff et al. 2004; Millspaugh et al. 2006; Sawyer et al. 2006, 2007). This approach implicitly assumes that population-level effects are accurately reflected by averaging coefficients among animals, which yields predictions that are equivalent to the geometric mean of predictions made from individual RSPFs. Importantly, the geometric mean of a set of numbers is always less than or equal to the arithmetic mean, with the difference between the two increasing with increasing variance in the numbers being averaged (Morris and Doak 2002). We recognize that an alternative approach for estimating population-level effects is to calculate the arithmetic

mean, cell by cell, from the mapped predictions of individual RSPFs, however this

approach only produces a population-level predictive map, not a population-level model.

Given that predictions from both approaches were highly correlated ($r_s = 0.65$ in 2005-

2006 and $r_s = 0.80$ in 2006-2007) and our goal was to produce a population-level model,

we averaged coefficients of the s individual deer RSPFs, using

$$\hat{\bar{\beta}}_t = \frac{1}{n} \sum_{s=1}^{n} \hat{\beta}_{ts}, \qquad (3)$$

where $\hat{\beta}_{ts}$ was the estimate of coefficient t ($t = 1, 2, …, p$) for individual s ($s = 1, 2, …, n$).

We estimated the variance of each coefficient in the population-level model using the

variation among individual deer and the equation

$$\mathrm{var}\left(\hat{\bar{\beta}}_t\right) = \frac{1}{n-1} \sum_{s=1}^{n} \left(\hat{\beta}_{ts} - \hat{\beta}_t\right)^2 \qquad (4)$$

Population-level inferences using equations 3 and 4 are unaffected by biases in

estimated coefficients caused by potential spatial autocorrelation because we selected

sampling units at random with replacement (Thompson 1992). Similarly, temporal

autocorrelation is not an issue in this analysis because the response variable is the count

of relocations within each sampling unit and does not have an associated time stamp

other than the study period. To evaluate significance of explanatory variables, we used

univariate analyses (i.e., t-tests) with each coefficient as the response variable (Marzluff

et al. 2004, Millspaugh et al. 2006, Sawyer et al. 2006). This approach to evaluating

ecological significance is considered conservative because the inter-animal variation is

included in the calculation of variance, thereby making rejection of the null hypothesis (

$\hat{\bar{\beta}}_t = 0$) less likely (Marzluff et al. 2004). Nevertheless, ecological significance of

explanatory variables is based on the consistency of selection coefficients among collared deer; our sample size was the number of marked mule deer, not sampling units or GPS locations.

We mapped predictions of population-level models for each winter on a 104×104-m grid that covered the study area. We checked predictions to ensure all values were in the interval [0,1], to verify that we would not extrapolate outside the range of model data (Neter et al. 1996). We then assigned the model prediction for each grid cell a value of 1 to 4 based on the quartiles of the distribution of predictions for each map, and we classified areas as high use, medium-high use, medium-low use, or low use. We calculated the mean value of model variables for each of the 4 categories and used high-use values as a reference for assessing how mule deer responded to different well pad types. As a predevelopment reference, we developed a map depicting predicted levels of mule deer use prior to gas development, as presented by Sawyer et al. (2006).

To evaluate predictive ability of the population-level models we developed for 2005-2006 and 2006-2007 we applied each of them to the 2007-2008 winter landscape. We then used 7,578 GPS locations collected from an independent sample ($n = 9$) of mule deer during the 2007-2008 winter to calculate a Spearman-rank correlation (r_s) characterizing the number of GPS locations that occurred in 10 equal-sized prediction bins based on each of the population-level models (Boyce et al. 2002). We performed all statistical analyses in R language and environment for statistical computing (R Development Core Team 2006).

RESULTS

In winter 2005-2006 traffic levels varied from 2-5 vehicle passes per day at LGS well pads, 4-9 at non-LGS well pads, and 86-145 at active drill pads. Mean daily traffic volumes at LGS, non-LGS, and active drill pads were 3.3 (SE = 0.30, n = 9), 7.3 (SE = 0.62, n = 6), and 112.4 (SE = 17.3, n = 3) vehicle passes per day, respectively. Mean daily traffic volumes differed across well pad types (F_2 = 119.38, $P \leq 0.001$) and 95% confidence intervals did not overlap.

In winter 2006-2007 traffic levels varied from 2-6 vehicle passes per day at LGS well pads, 6-12 at non-LGS well pads, and 86-90 at active drill pads. Mean daily traffic volumes at LGS, non-LGS, and active drill pads were 3.6 (SE = 0.50, n = 8), 8.4 (SE = 1.16, n = 7), and 85.3 (SE = 2.91, n = 3) detections per day, respectively. Mean daily traffic volumes differed across well pad types (F_2 = 981.31, $P \leq 0.001$) and 95% confidence intervals did not overlap.

Resource Selection

We used 24,955 locations from 20 GPS-collared mule deer to estimate individual models during the 2005-2006 winter (1 Dec – 15 Apr). Most deer (17 of 20) had positive coefficients for elevation, indicating a preference for higher elevations. Based on the relationship between linear and quadratic terms for slope, distance to LGS pad, distance to non-LGS pad, and distance to active drill pad, most deer selected for areas with moderate slopes (14 of 20), away from non-LGS well pads (16 of 20), away from LGS well pads (13 of 20), and away from active drill pads (13 of 20).

Coefficients from the population-level model and associated P-values suggested that most deer selected for areas with higher elevations, moderate slopes, and away from all well pad types (Table 1). Areas with the highest predicted level of use had an average

elevation of 2,239 m, slope of 4.98°, and were 2.61 km from LGS well pads, 4.30 km

from non-LGS well pads, and 7.49 km from active drill pads (Table 2). In contrast, areas

with the lowest predicted level of use had an average elevation of 2,183 m, slope of

3.07°, and were 4.03 km, 1.44 km , and 2.78 km from LGS, non-LGS, and active drill

well pads, respectively (Table 2). The predictive map indicated that deer use was lowest

in areas at low elevation and near clusters of non-LGS and active drill pads (Fig. 3).

Predicted levels of mule deer use were noticeably different than those observed prior to

development (Fig. 1).

Using the predicted high-use areas as a reference, mule deer distanced themselves

from all types of well pads and tended to select areas progressively further from well

pads with higher levels of traffic. Specifically, areas with the highest predicted deer use

were 2.61 km, 4.30 km, and 7.49 km away from LGS, non-LGS, and active drill pads,

respectively. We used these avoidance distances as a metric to assess indirect habitat loss

associated with well pad types. Using a straight line distance, mule deer avoidance of

LGS pads was approximately 40% less than that of non-LGS pads (i.e., 1-[2.6/4.3] =

0.40; Fig. 4). However, assuming a circular area of behavioral response from the point of

disturbance (well pad), the indirect habitat loss was reduced by 63% (i.e., 1-[21/58] =

0.63; Fig. 4) relative to non-LGS pads. Conversely, the straight line distance mule deer

selected away from active drill pads was approximately 2.8 times greater than LGS pads

and 1.7 times greater than non-LGS pads. Assuming a circular area of behavioral

response, indirect habitat loss associated with active drill pads was about 3.0 times more

than non-LGS pads and 8.4 times more than LGS pads.

We used 11,744 locations collected from 11 GPS-collared mule deer to estimate individual models during the 2006-2007 winter. Most deer (9 of 11) had positive coefficients for elevation, indicating a preference for higher elevations. All deer selected for areas with moderate slopes and most selected for areas away from non-LGS well pads (9 of 11) and LGS well pads (9 of 11). We did not include distance to active drill pad as a variable during this winter because it was strongly correlated with distance to non-LGS well pads.

Coefficients from the population-level model and associated *P*-values suggested that deer selected for areas with higher elevations, moderate slopes, and away from LGS and non-LGS well pads (Table 1). Areas with the highest predicted level of use had an average elevation of 2,243 m, slope of 4.55°, and were 3.46 km and 4.35 km from LGS and non-LGS well pads, respectively (Table 2). In contrast, areas with the lowest predicted level of use had an average elevation of 2,206 m, slope of 3.27°, and were 2.12 km and 0.69 km from LGS and non-LGS well pads, respectively (Table 2). Within high use habitats, deer used areas closer to LGS pads compared to non-LGS. The predictive map indicated that deer use was lowest in areas with low elevations and clusters of non-LGS well pads (Fig. 5). Predicted levels of mule deer use were noticeably different than those observed prior to development (Fig. 1).

Mule deer distanced themselves from LGS and non-LGS well pads and tended to select areas progressively further from well pads that received higher levels of traffic. Areas with the highest predicted deer use were 3.46 km and 4.35 km away from LGS and non-LGS well pads, respectively. Mule deer avoidance of LGS pads was approximately 21% less than that of non-LGS pads. However, assuming a circular area of avoidance

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from the point of disturbance (well pad), the indirect habitat loss was reduced by 38% relative to non-LGS pads.

When the 2005-2006 and 2006-2007 population-level models were applied to the 2007-2008 landscape, which included new well pad development, their predictions produced Spearman-rank correlations (r_s) of 0.903 and 0.939, respectively. The high r_s values indicated that both models effectively predicted the distribution of an independent set of locations ($l = 7,578$) collected from 9 mule deer.

DISCUSSION

Consistent with our previous work on this mule deer population, we found that deer habitat selection was influenced by well pads (Sawyer et al. 2006). Mule deer avoided all types of well pads but tended to select areas farther from well pads with higher levels of traffic. The reduced response of mule deer to low traffic levels suggests that impacts of gas development on mule deer may be reduced by minimizing traffic. Avoidance distances calculated from predicted high-use areas provided a useful metric to estimate indirect habitat loss associated with different types of well pads. Indirect habitat loss associated with LGS well pads was 38-63% less than with non-LGS well pads, which is noteworthy given that the expected production life of gas wells in the PAPA is 40 years (BLM 2006). Indirect habitat loss associated with active drilling pads was much higher than that at producing well pads; however, all active drill pads in our study were used for directional drilling, which is generally a short-term (6 months-2 yr) disturbance, whereas producing well pads represent a long-term (i.e., decades) disturbance. Recognizing how mule deer respond to different types of well pads and traffic regimes may improve the ability of agencies and industry to estimate cumulative effects and

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quantify indirect habitat losses associated with different development scenarios (e.g.,

clustered development; Theobald et al. 1997).

Evaluating wildlife responses to disturbance is conceptually similar to how

ecologists have evaluated prey response to predation risk (Lima and Dill 1990, Lima

1998). Like predation risk, human-related disturbances can divert time and energy away

from foraging, resting, and other activities that improve fitness (Gill et al. 1996, Frid and

Dill 2002), which could be important to wintering ungulates whose nutritional condition

is closely linked to survival. Similar to Gavin and Komers (2006) and Haskell and

Ballard (2008), we found it useful to evaluate our findings in relation to predation risk

theory. Predation risk (Lima and Dill 1990) predicts that antipredator behavior has a cost

to other activities (e.g., foraging, resting) and that the trade-off is optimized when the

antipredator behavior (e.g., fleeing, vigilance, habitat selection) tracks short-term changes

in predation risk (Frid and Dill 2002). Given that risk of predation can vary across

seasons, days, or even hours, antipredator behaviors of prey species should be sensitive to

the current risk of predation (Lima and Dill 1990) or level of disturbance. Our results

suggested that reducing traffic from 7 to 8 (non-LGS well pads) vehicle passes per day to

3 (LGS well pads) was sufficient for mule deer to perceive less risk and alter their habitat

selection behavior such that LGS well pads were avoided less than non-LGS well pads,

effectively reducing indirect habitat loss associated with producing well pads.

The tradeoffs associated with maximizing foraging opportunities and minimizing

predation have been well-studied (e.g., Lima and Dill 1990, Bleich et al. 1997, Brown

and Kotler 2004). Importantly however, tradeoffs can only occur if foraging benefits and

predation risks are positively correlated (Bower et al. 1998, Pierce et al. 2004). If the

most energetically profitable foraging areas are not perceived as the most dangerous, then there is no tradeoff between maximizing foraging and minimizing predation (Lima 1998). Because many of the well pads were constructed in habitats identified as highly preferred by mule deer prior to development (Fig. 1; Sawyer et al. 2006), we believe that tangible tradeoffs existed and that mule deer reduced foraging opportunities by avoiding well pads. High levels of predation risk may indirectly affect survival and reproduction by reducing the amount of time, energy, and resources needed to maintain healthy body condition (Frid and Dill 2002). Further, animals displaced from disturbed sites may experience greater intraspecific competition or density-dependent effects when congregating into smaller areas of undisturbed or suboptimal habitat (Gill and Sutherland 2000). However, the link between antipredator behavior and reduced population performance is difficult to demonstrate (Lima 1998) and has not yet been documented for mule deer and energy development.

Drilling during winter (15 Nov- 30 Apr) in areas designated as crucial winter range is a recent phenomenon. Traditionally, seasonal timing restrictions have limited development activities (e.g., construction, drilling, well completion) to non-winter months and represent the most common, and sometimes the only, mitigation measure required by the BLM for reducing disturbance to wintering ungulates on federal lands. Because of seasonal timing restrictions, the energy industry typically was not allowed to drill during the winter in crucial winter ranges. However, winter drilling will likely become a more common practice across the Intermountain West, as evidenced by recent National Environmental Policy Act decisions in western Wyoming, where stakeholders identified year-round directional drilling as the preferred method to develop the necessary

number of wells to recover natural gas reserves, regardless of winter range designation

(BLM 2004*a*, *b,* 2006). Wildlife managers have expressed concerns about year-round

drilling in crucial winter range because seasonal timing restrictions would be waived and

levels of human disturbance would increase substantially during winter (BLM 2004*a*),

when mule deer are most vulnerable (Parker et al. 1984, Hobbs 1989). Although

significant indirect habitat loss may occur with seasonal timing restrictions in place

(Sawyer et al. 2006), our results suggest that wintering mule deer are sensitive to varying

levels of disturbance and that indirect habitat loss may increase by a factor of >2 when

seasonal restrictions are waived.

Both directional drilling and construction of the LGS were large-scale, multi-

million dollar decisions that involved an assortment of local, state, and national

stakeholders (BLM 2004*a*). Although Wyoming currently produces the most natural gas

in the contiguous United States, the scale and intensity of gas development is predicted to

increase elsewhere in the Intermountain West, especially in Colorado, Utah, New

Mexico, and Montana (BLM 2005). As gas development becomes more widespread,

wildlife and development conflicts will be inevitable. Although the wildlife species of

concern (e.g., mule deer, greater sage-grouse (*Centrocercus urophasianus*), pronghorn

(*Antilocapra americana*)) may differ across states or regions, the available development

strategies (e.g., directional drilling, LGS) will likely be similar. If human disturbances

such as vehicle traffic are analogous to predation risk (Gill et al. 1996, Frid and Dill

2002, Gavin and Komers 2006), then mule deer responses to directional drilling and LGS

development strategies should be qualitatively similar in other areas across the

Intermountain West.

The conceptual framework of predation risk provides a useful context for interpreting responses of ungulates to human disturbances (e.g., Rowland et al. 2000, Nellemann et al. 2003, Taylor and Knight 2003, Gavin and Komers 2006). However, given the rapid and widespread energy exploration and development across the Intermountain West (BLM 2005), manipulative studies will be necessary to advance our understanding of wildlife responses to human disturbance and habitat perturbations. Unfortunately, many of the systems we study are too large or too expensive to manipulate (Macnab 1983). Additionally, when experiments are conducted at large spatial scales, such as the 799-km^2 PAPA, replication and randomization are rarely options (Nichols 1991, Sinclair 1991). When the treatment or manipulation is commodity driven, such as mineral extraction or gas development, randomization becomes especially difficult to achieve. Recognizing the constraints that limit our ability to conduct large-scale manipulative studies, researchers have been encouraged to treat management prescriptions, such as fire or harvest regimes, as a form of experimentation (Macnab 1983, Nichols 1991, Sinclair 1991) and as an opportunity for adaptive management (Walters and Holling 1990). Gas development will likely continue to be a dominant activity on federal lands across the Intermountain West. As such, we encourage researchers to consider energy development strategies and mitigation measures as large-scale experimentation that, if properly monitored, can improve our knowledge of energy development impacts to wildlife.

MANAGEMENT IMPLICATIONS

Because mule deer selected for habitats progressively further from well pads with higher levels of traffic, our results suggest that potential impacts of gas development on

mule deer may be reduced by technology and planning that minimizes the number of well pads (e.g., directional drilling) and the level of human activity associated with them (e.g., LGS). Our results suggest indirect habitat loss to mule deer could potentially be reduced by 38-63% when condensate products are collected in LGS pipelines rather than being stored at well pads and removed via tanker trucks. Additionally, because a LGS can be installed underground and usually in existing roadway or pipeline corridors, associated direct habitat losses are minimal. The LGS appeared to be an effective means for reducing long-term (i.e., production phase) indirect habitat loss to wintering mule deer, whereas drilling in crucial winter range created a short-term (i.e., drilling phase) increase in deer disturbance and indirect habitat loss.

ACKNOWLEDGMENTS

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Table 1. Coefficients for population-level models of radiocollared mule deer during winters of 2005-2006 and 2006-2007 in western Wyoming.

Predictor variable	Winter 2005-2006			Winter 2006-2007		
	$\hat{\bar{\beta}}$	SE	P	$\hat{\bar{\beta}}$	SE	P
Intercept	-60.089	12.640	<0.001	-73.969	15.364	<0.001
Elevation (m)	0.012	0.004	0.010	0.020	0.007	0.012
Slope (°)	0.168	0.052	0.004	0.359	0.052	<0.001
Slope^2 (°)	-0.013	0.003	0.001	-0.024	0.003	<0.001
Non- LGS well pad (m)	3.060	0.003	0.001	5.748	1.545	0.004
Non-LGS well pad^2 (m)	-0.182	0.109	0.110	-0.653	0.156	0.001
LGS well pad (m)	1.316	0.880	0.151	3.397	1.013	0.007
LGS well pad^2 (m)	-0.437	0.109	<0.001	-0.421	0.126	0.007
Active drilling pad (m)	3.121	1.204	0.178	na		
Active drilling pad^2 (m)	-0.197	0.073	0.014	na		

[na] Not applicable

Table 2. Average values of population-level model variables in low, medium-low, medium-high, and high use mule deer categories during winters of 2005-2006 and 2006-2007 in western Wyoming.

|	Predicted mule deer use							
	High		Medium-high		Medium-low		Low	
Model variables	2005-2006	2006-2007	2005-2006	2006-2007	2005-2006	2006-2007	2005-2006	2006-2007
Elevation (m)	2,239	2,243	2,224	2,203	2,238	2,233	2,183	2,206
Slope (°)	4.98	4.55	3.64	3.61	3.26	3.52	3.07	3.27
Distance to LGS pad (km)	2.61	3.46	3.33	3.43	2.87	2.53	4.03	2.12
Distance to non-LGS pad (km)	4.30	4.35	3.53	3.97	2.50	2.83	1.44	0.69
Distance to active drill pad (km)	7.49	na	5.47	na	3.93	na	2.78	na

[na] Not applicable
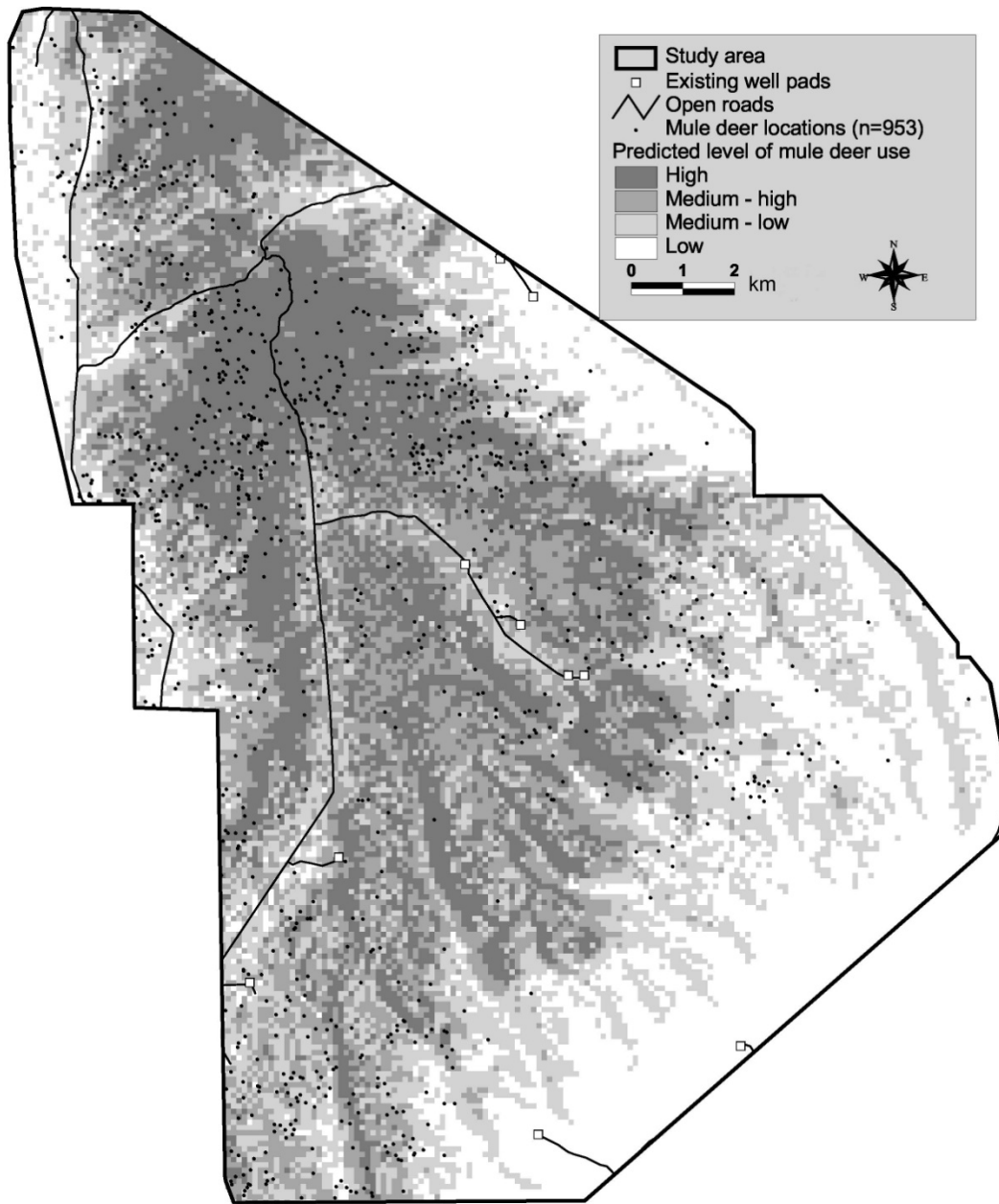
Figure 1. Population-level model predictions and associated categories of mule deer habitat use prior to gas development, during winters of 1998-1999 and 1999-2000 in western Wyoming (from Sawyer et al. 2006).
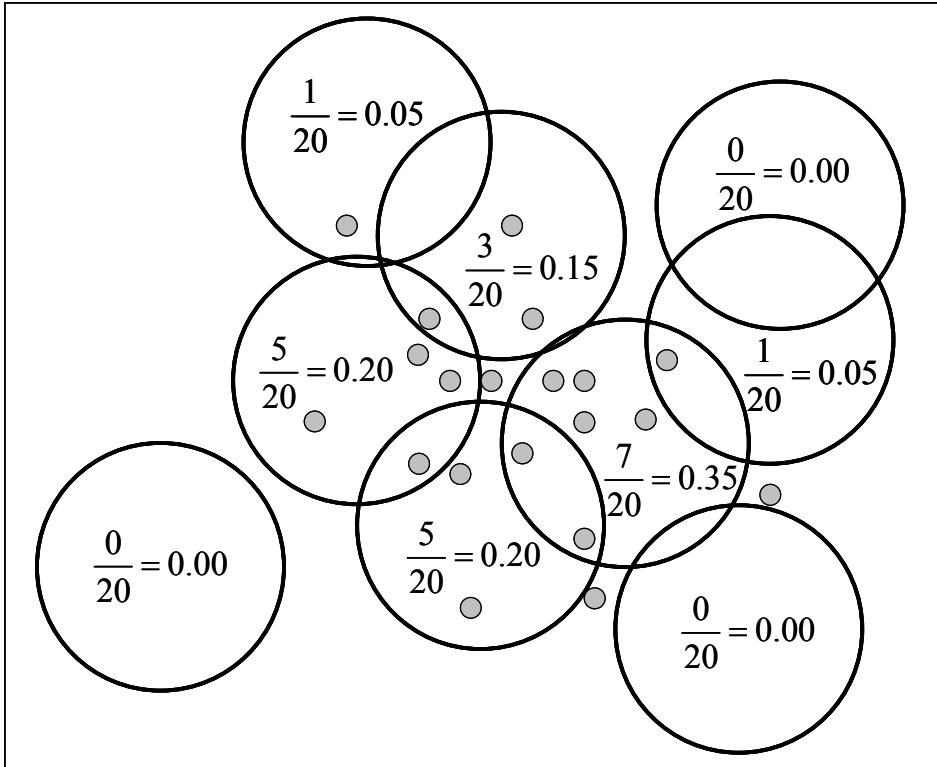
Figure 2. Dividing the number of deer locations in each circular sampling unit by total number of locations converts the response variable to relative frequency of use (e.g., 0.05, 0.15, 0.20), rather than integer counts (e.g., 1, 3, 5). This hypothetical example uses a random sample of circular sampling units and a total of 20 deer locations. Note that 3 locations occurred outside of the sampling units.
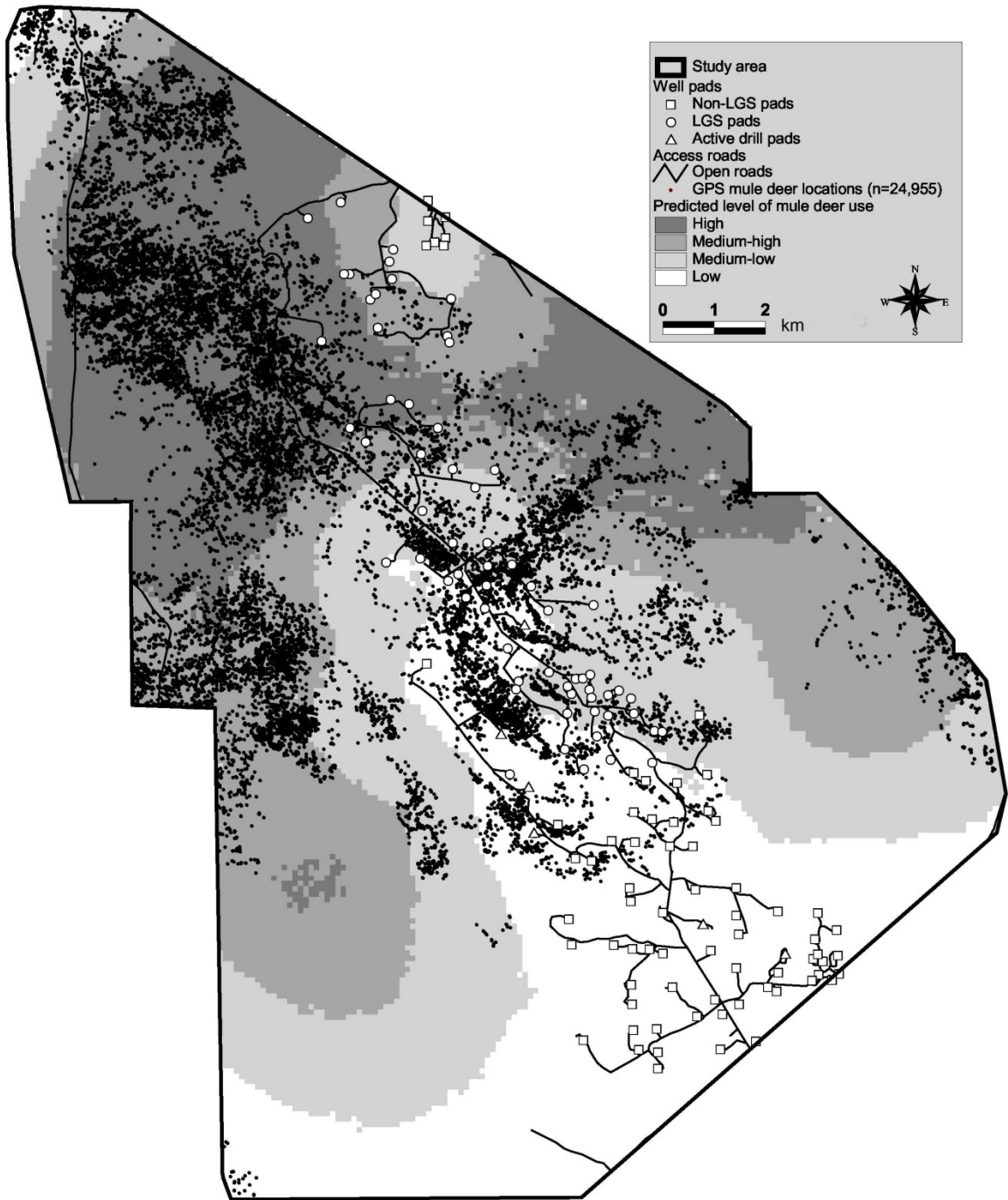
Figure 3. Population-level model predictions and associated categories of mule deer habitat use during winter of 2005-2006 in western Wyoming.
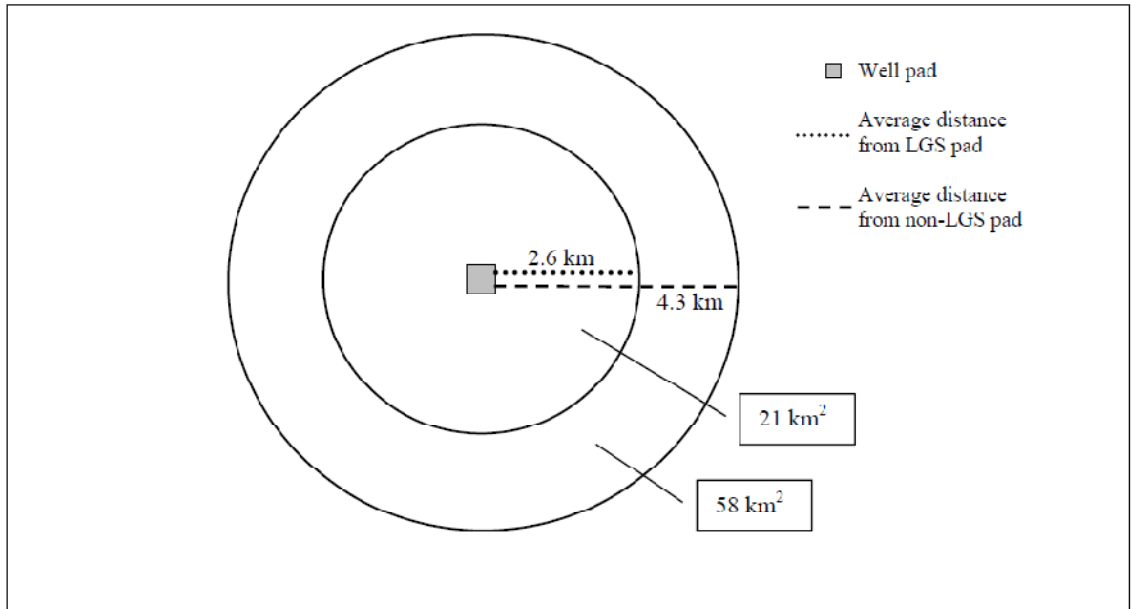
Figure 4. The relationship between straight-line avoidance distances and circular area of impact as a measure of indirect mule deer habitat loss associated with LGS and non-LGS well pads during the 2005-2006 winter in western Wyoming.
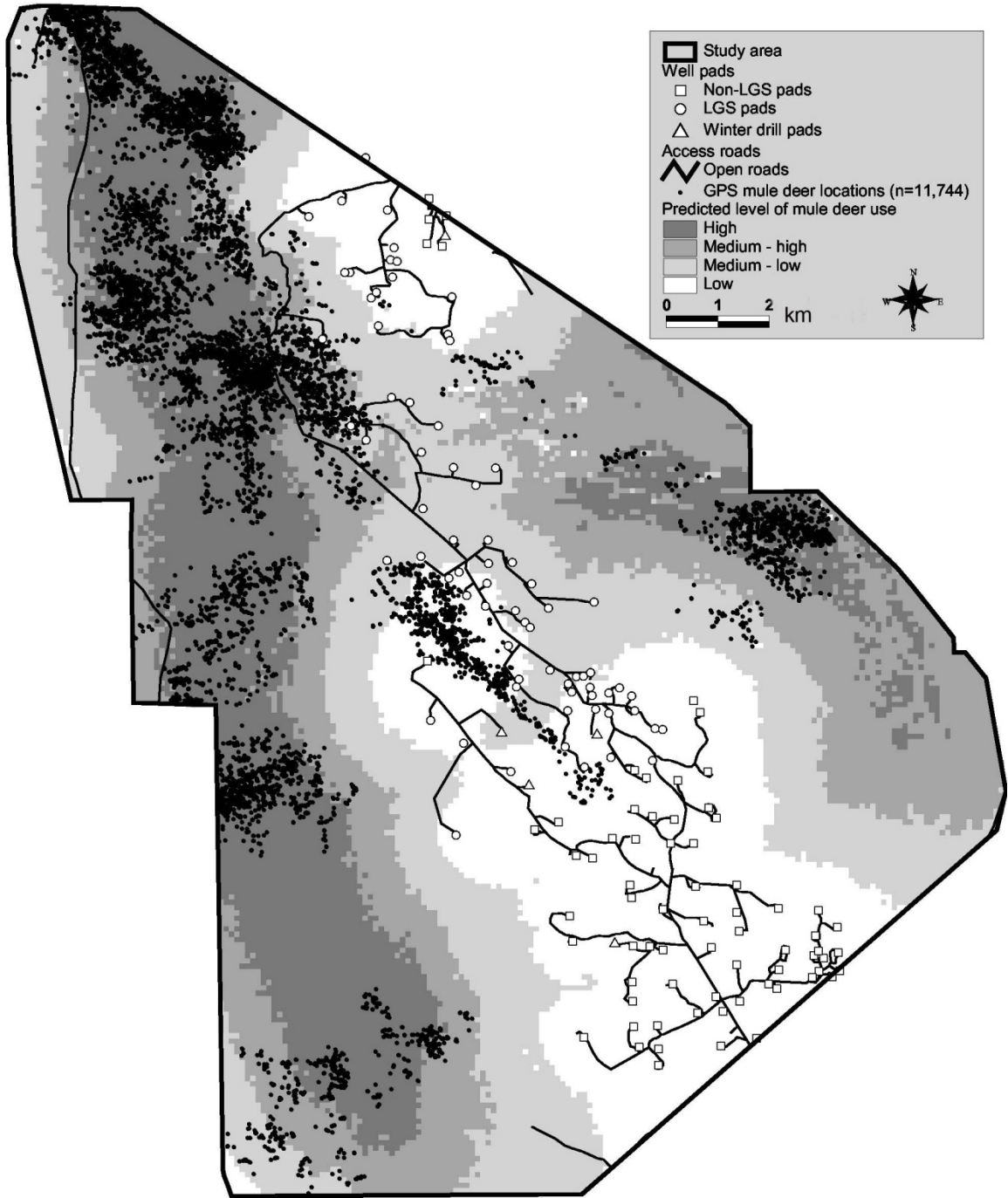
Figure 5. Population-level model predictions and associated categories of mule deer habitat use during winter of 2006-2007 in western Wyoming.

CHAPTER THREE

Identifying and prioritizing ungulate migration routes for conservation

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Abstract: As habitat loss and fragmentation increase across ungulate ranges, identifying

and prioritizing migration routes for conservation has taken on new urgency. Here we

present a general framework using the Brownian bridge movement model (BBMM) that:

1) provides a probabilistic estimate of the migration routes of a sampled population, 2)

distinguishes between route segments that function as stopover sites versus those used

primarily as movement corridors, and 3) prioritizes routes for conservation based upon

the proportion of the sampled population that uses them. We applied this approach to a

migratory mule deer (*Odocoileus hemionus*) population in a pristine area of southwest Wyoming, where 2,000 gas wells and 1,609 km of pipelines and roads have been proposed for development. Our analysis clearly delineated where migration routes occurred relative to proposed development and provided guidance for on-the-ground conservation efforts. Mule deer migration routes were characterized by a series of stopover sites where deer spent most of their time, connected by movement corridors through which deer moved quickly. Our findings suggest management strategies that differentiate between stopover sites and movement corridors may be warranted. Because some migration routes were used by more mule deer than others, proportional level of use may provide a reasonable metric by which routes can be prioritized for conservation. The methods we outline should be applicable to a wide range of species that inhabit regions where migration routes are threatened or poorly understood.

*Key word*s*:* Brownian bridge movement model (BBMM), Global Positioning System (GPS), migration, movement corridors, mule deer, *Odocoileus hemionus*, stopover site, utilization distribution (UD), Wyoming.

INTRODUCTION

The conservation of ungulate migration routes has received considerable attention across the globe (Fryxell and Sinclair 1988, Berger 2004, Thirgood et al. 2004, Bolger et al. 2008), in large part because the landscapes necessary to maintain them are becoming increasingly fragmented (Leu et al. 2008). Across the Intermountain West, elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), moose (*Alces alces*), and bighorn sheep (*Ovis canadensis*) commonly migrate 50-100 km between seasonal ranges. The traditional migration routes of these ungulates are

threatened by unprecedented levels of energy development (Bureau of Land Management [BLM] 2005), amplifying the need to identify and prioritize migration routes for conservation. Unfortunately, the quantitative tools needed to achieve this have not kept pace with technological advances (e.g., global positioning system [GPS] telemetry) that facilitate collection of fine-scale movement data. Here, we present an analytical framework to: 1) identify the network of migration routes for a sampled population, 2) identify route segments used as stopover sites versus those used primarily for movement, and 3) prioritize routes for conservation based upon their proportional levels of use. Our approach combines fine-scale movement data with an innovative application of the Brownian bridge movement model (BBMM; Horne et al. 2007), to identify and prioritize migration routes for conservation. We apply these methods to a mule deer population in Wyoming whose range is undergoing rapid energy development.

Migration is an adaptive behavioral strategy that allows ungulates to avoid resource shortages (Baker 1978) and possibly reduce the risk of predation (Fryxell and Sinclair 1988, Hebblewhite and Merrill 2007). Across the Intermountain West, it is common for ungulates to seasonally migrate from low-elevation winter ranges to high-elevation summer ranges, allowing them access to high-quality forage necessary for successful breeding and recruitment of young (Albon et al. 1987, Singer et al. 1997, Cook et al. 2004). Accordingly, the loss of migration routes is expected to have population-level consequences for ungulates, including local extirpations (Bolger et al. 2008). Given that ungulate migrations generally occur along traditional routes that are learned and passed on from mother to young (McCullough 1985, Sweanor and Sandegren 1988), the protection of relatively small corridors may benefit large numbers of ungulates.

A common perception is that ungulate populations migrate between seasonal ranges along one well-defined route (Fig. 1A). Portions of a single migration route are assumed to have equal importance, and therefore, maintaining the migration requires only that we identify the route and protect it (e.g., Berger 2004). While this migratory pattern is known to occur (Berger 2004, Berger et al. 2006), it is likely restricted to populations that occupy relatively small winter and summer ranges (Fig. 1A). We suggest that it is more common for temperate ungulates to utilize a summer range that is considerably larger than their winter range, which necessitates the use of multiple routes by different parts of the populations (Fig. 1B). This migratory pattern is especially evident across the Intermountain West, where winter ranges are restricted to relatively small areas due to snow cover and limited forage availability, whereas summer ranges often consist of entire mountain ranges. In these cases, individuals share a common winter range and then migrate to distinct locales within summer range (Fig. 1B). Ideally, managers could protect all migration routes, but in regions with high energy, agricultural, or housing development potential, prioritizing specific route segments for management and conservation is necessary to minimize the impacts of development and sustain functional migration routes.

Although recent advances in GPS technology have improved our ability to study ungulate movements, identifying migration routes from discrete location data has remained problematic. Specifically, it is difficult to account for the uncertainty in animal movements between known locations (Horne et al. 2007, Patterson et al. 2007) and it has been unclear how to combine migration routes of individuals to make population-level inference. For example, the method of connecting the dots between GPS locations of

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marked animals (Sawyer et al. 2005, Berger et al. 2006, White et al. 2007) has improved our understanding of ungulate migrations, including the timing, distances traveled, and movement rates. Yet, such approaches ignore the uncertainty in both the locations and the trajectory of movement, thereby producing a line with no associated area or error (e.g., is the route 10 m or 1 km wide?) and no means of combining individual routes to characterize the population-level route network.

An alternative approach proposed by Horne et al. (2007) uses time-specific location data and the BBMM to quantify the probability of use along a route by estimating a probability density or utilization distribution (UD). Provided that movement data are collected at frequent intervals and with some measure of error (Horne et al. 2007) the BBMM provides a probabilistic estimate of a migration route by accounting for location error and the uncertainty of the movement trajectory between locations. This advancement allows the estimation of the relative amount of use along a migration route, and importantly, provides a quantitative method for combining multiple individual routes into a population-level estimate of migration corridors. Delineation of the population-level migration route provides a basis for conserving all routes or prioritizing which routes should be targeted for conservation or management.

Western Wyoming is a region where some of the world's largest mule deer populations coincide with some of the world's largest natural gas reserves. As the level of natural gas development expands across the region (BLM 2005), large areas of mule deer habitat are rapidly being converted into producing gas fields, characterized by networks of access roads, well pads, pipelines, and other infrastructure that may impede deer migration. Agencies, industry, and non-governmental organizations recognize the need to

incorporate migration routes into current planning and policy, but their efforts have been limited by the quantitative tools available to them. In this study, we provide a general framework to identify and prioritize mule deer migration routes for landscape-level conservation and management.

STUDY AREA

Our study was conducted in the 1,093 km^2 Atlantic Rim Project Area (ARPA) located in southwest Wyoming, immediately west of the Sierra Madre mountain range (BLM 2006). The ARPA is characterized by rolling topography, prominent ridges, and dry canyons dominated by sagebrush (*Artemisia sp.),* black greasewood (*Sacrobatus vermiculatus*), Utah juniper (*Juniperus osteosperma*), and other shrub species (*Purshia tridentata, Prunus virginiana, Amelanchier alnifolia, Chrysothamnus sp., Cercocarpus sp.*). Elevations range from 1,920 to 2,530 m. The ARPA supports approximately 2,000 – 3,000 mule deer and contains two distinct winter ranges, locally known as Dad (40 km^2) and Wild Horse (141 km^2). At the time of study (2005-06), there were approximately 116 natural gas wells in the ARPA, but in 2007 an additional 2,000 wells and 1,609 km of pipeline and access roads were approved for construction (BLM 2006).

MATERIALS AND METHODS

Capture, Collaring, and Data Collection

We used helicopter net-gunning to capture 31 adult female mule deer across the Wild Horse and Dad winter ranges in February 2005, with another 16 captured in December 2005. We attempted to sample deer in proportion to their abundance, as determined by pre-capture aerial surveys that indicated approximately 1/3 of deer occurred in Dad and 2/3 in Wild Horse. We fitted deer with store-on-board GPS radio-

collars (TGW 3500, Telonics, Inc., Mesa, Arizona) programmed to collect one location

every 2.5 hours. Between February 10, 2005 and November 15, 2006, we collected

116,494 GPS locations from 47 deer. Three deer did not migrate and were excluded from

analysis. We collected data for 80 migrations (56 spring, 24 fall) from 44 deer.

Estimating Migration Routes

We used the BBMM (Horne et al. 2007) to estimate a UD for each individual

migration route collected from GPS-collared mule deer. The BBMM requires: 1) the

sequence of time-specific location data, 2) the estimated error associated with the

location data, and 3) grid cell size for the output UD. We used a sequence of GPS

locations (i.e., the migration path) that occurred between winter and summer range during

a specific migration (spring or fall), including the 24-hour period prior to, and following

migration. We defined the start and end of migrations as locations occurring outside a

minimum convex polygon generated from winter and summer range locations (Saher and

Scmiegelow 2005). Missing observations or fix-rate bias (Nielson et al. 2009) were not a

concern, because 99% of our GPS fix attempts were successful. Nonetheless, we took

precautions to ensure that occasional missing observations were accounted for by

restricting the BBMM calculations to sequential locations. We used an estimated location

error of 20 m because 86% of our GPS locations were three-dimensional (3-D) fixes,

which typically have < 20 m error (Di Orio et al. 2003). We used a grid cell size of 50 x

50 m that was intended to provide high-resolution mapping, while maintaining a

reasonable processing time.

The BBMM is a continuous-time stochastic movement model, where the

probability of being in an area is conditioned on the distance and elapsed time between

successive locations, the location error, and an estimate of the animal's mobility, referred to as the Brownian motion variance (BMV; Horne et al. 2007). Assuming that odd-numbered locations are independent observations from Brownian bridges connecting even-numbered locations, the BMV can be estimated by maximizing the likelihood of observing the odd locations (Horne et al. 2007). The two assumptions associated with the BBMM are that location errors correspond to a bivariate normal distribution and that movement between successive locations is random. The assumption of normally distributed errors is appropriate for GPS-telemetry, but the assumption of conditional random movement between successive locations may become less likely as time between locations increases (Horne et al. 2007). Given our locations were only 2.5 hrs apart, and Horne et al. (2007) successfully applied the BBMM to migratory data collected at 7-hr intervals, we considered the assumption of conditional random movement to be reasonable. We programmed the BBMM calculations in the R language for statistical computing (R Development Core Team 2007).

Estimating Population-level Migration Routes

Application of the BBMM resulted in a UD for each migration route of each collared deer. For deer that had > 1 migration recorded ($n = 20$), we summed the cell values of all their UDs and then re-scaled their cumulative cell values to sum to one, such that the migratory route of each deer was represented by one UD. Next, we sought to characterize the network of migration routes used by the entire sampled population, which we refer to as a population-level migration route. We then followed this same re-scaling procedure with the UDs of all deer to estimate population-level migration routes. Because deer migrations originated from two winter ranges, we created a population-

level migration route for each winter range. Once the individual UDs were combined, the resulting surface provided an estimate of the relative amount of use across the population-level route. We categorized the UD values for each population-level migration route into 25% quartiles, such that the top 25% were classified as high-use and the lowest 25% were low-use. Estimating population-level UDs for separate seasons (spring and fall) was not necessary because individual deer showed fidelity to their migration routes.

Although the amount of time an animal spends in a particular area is the most common metric in resource use studies, it is not particularly effective at capturing rare events, such as visiting watering sites, seeking mates, or quick migration bouts (Buskirk and Millspaugh 2006). The population-level migration routes estimated by the BBMM are unique in that they reflect two metrics of migratory behavior; time spent in an area and rate of movement. We considered both metrics by recognizing that high-use areas represent areas where animals spend the most time and move slowly (e.g., stop moving or series of tortuous movements), while moderate-use areas represent areas where animals spend the least time and move quickly. Thus, we assumed that high-use areas represent stopover sites, presumably used for foraging and resting habitat, whereas moderate-use areas located between stopover sites represent movement corridors (Fig. 2). Similar to other movement models (Johnson et al. 2002, Morales et al. 2004, Frair et al. 2005, Forester et al. 2007, Barraquand and Benhamou 2008), our analysis implicitly assumed that behavioral state (i.e., stopover or migratory movement; Saher and Schmielgelow 2005) could be inferred from movement rates. The validity of this assumption depends on the frequency of the movement data, the type of behaviors to be distinguished, and how

likely those behaviors are to be associated with different movement rates. In our application, we collected movement data at frequent (2.5-hr) intervals and attempted to differentiate between two coarse-scale behavioral states (i.e., stopover versus migratory movement) that were characterized by pronounced differences in movement rates. Our analysis was not designed to distinguish between fine-scale behaviors, such as foraging and resting.

To prioritize routes, we assumed that route segments used by a larger proportion of the population had higher conservation priority than those used by a small proportion of the population. We determined the proportion of the sampled population that used each route segment by calculating how many of the individual migration routes (99% UD) occurred within each 50 x 50 m cell of the estimated population-level route. Thus, cell values ranged from one to a possible maximum value equal to the total number of marked deer in each winter range. We then considered migration routes used by >10% of the sampled population to have higher conservation priority than others. The 10% criteria was a subjective decision intended to reflect routes used by more than one marked animal. We recognize that other criteria could be used, but in the absence of a metric directly related to fitness, we found proportional use to be an intuitive metric to prioritize migration routes.

RESULTS

We estimated UDs for 80 migration routes (56 spring, 24 fall) collected from 44 radio-collared deer. Mean BMV of individual migration routes in the Dad and Wild Horse winter ranges was 3,310 m^2 ($n = 19$, SE = 685) and 2,679 m^2 ($n = 61$, SE = 280), respectively. The population-level route for the Wild Horse winter range (Fig. 3A)

included 61 migrations by 32 deer, whereas the population-level route for the Dad winter

range (Fig. 4A) included 19 migrations by 12 deer. The population-level migration routes

represent a probabilistic measure of where both spring and fall migrations occurred

during 2005 and 2006. Population-level migration routes were characterized by stopover

sites, where deer spent most of their time, connected by movement corridors through

which deer moved quickly (Figs. 3A & 4A). Stopover sites corresponded with high-use

areas that were presumably used as foraging and resting areas, whereas movement

corridors were reflected by moderate-use segments, located between stopovers, through

which deer moved quickly. Low-use areas reflected the uncertainty across the entire the

migration route and did not appear to be associated with stopovers or movement

corridors.

Marked deer from both populations used a network of migration routes to access

their respective summer ranges, however the population-level route for the Wild Horse

population (718 km^2) was nearly 3× larger than that for the Dad population (258 km^2).

Proportional use of route segments within the population-level migration routes ranged

from 3-56% in the Wild Horse population and 8-75% in the Dad population. Routes used

by >10% of the sampled populations were considered to have the highest conservation

priority and were mapped against the population-level routes. The highest priority routes

(Figs. 3B & 4B) for the Wild Horse and Dad populations covered approximately 20%

(146 km^2) and 53% (137 km^2) of their respective population-level migration routes.

Three areas proposed for gas development overlapped with the population-level

migration routes, including two in the Wild Horse and one in the Dad population (Figs. 3

and 4).

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DISCUSSION

Our application of the BBMM was successful at identifying population-level migration routes for conservation planning. Mule deer from two sub-populations in our study area used a network of migration routes, rather than one distinct route per sub-population. We suggest that for temperate ungulates a multiple-route migratory pattern is more common than a single route. This pattern is likely to occur when seasonal ranges are disproportionate in size, whether it be large summer and small winter ranges as in our study, or large winter and small summer ranges as observed in caribou (*Rangifer tarandus*; Bergman et al. 2000). Compared to a single migration route, the conservation of multiple migration routes is complicated by the increased likelihood that route segments will overlap with development projects or other anthropogenic disturbances. Additionally, because individual mule deer showed a strong fidelity to their migration routes across seasons and years, the fact that multiple routes were used by these sub-populations does not necessarily mean that individual animals can modify their migratory behavior or have alternative options available to them if their route is blocked. Estimation of a population-level migration route provides a basis from which all migration routes may either be protected, or from which a prioritization process may be initiated to identify which routes should be targeted for conservation or management.

Our work suggests that the BBMM may be a useful tool for distinguishing between areas associated with different behavioral states, as others have done with non-linear curve-fitting (Johnson et al. 2002, Saher and Schmiegelow 2005), state-space models (Forester et al. 2007), Markov models (Franke et al. 2004), random walks (Morales et al. 2004), and first-passage-time approaches (Frair et al. 2005, Bailey and

Thompson 2006). We found the migration routes of mule deer were characterized by a series of stopover sites, presumably used for foraging and resting, connected by movement corridors. Similarly, Alerstam and Hedenström (1998) characterized bird migrations as alternating between flights, when distance is covered and energy consumed, and stopover periods when energy is accumulated. Similar to migratory bird conservation (Klassen et al 2008, Newton 2008), we suggest that migratory ungulates may benefit from the identification and subsequent management of stopover sites. For ungulates, such stopover sites are typically referred to as transition range and are thought to aid individuals in meeting their nutritional requirements by providing better forage than is often available on winter ranges, allowing them to recover body condition earlier in the spring and maintain body condition later in the fall, before entering winter (Short 1981).

Migration theory suggests that the function of stopover sites is to provide animals with areas where they can accumulate energy reserves necessary to complete the migration or movement to the next stopover site, whereas the function of movement corridors is to facilitate movement between stopover sites (Alerstam and Hedonström 1998, Hedenström 2003). In general, a migration strategy that involves many stopover sites is energetically preferable to one with few stopovers because animals may travel shorter distances with lighter fuel loads (Alerstam 2001). A key consideration for land migrants is that management strategies that differentiate between the type of migratory segments (i.e., stopover site versus movement corridor) may be warranted. For instance, in our study area hundreds of kilometers of road will be constructed as part of a large-scale energy development project (BLM 2006). When a road must be built across a

migration route, is it least likely to affect mule deer migration if it bisects a stopover site or a movement corridor? Given that ungulates tend to avoid disturbances associated with energy development on their seasonal ranges (Dyer et al. 2001, Nellemann et al. 2003, Cameron et al. 2005, Sawyer et al. 2006), it is likely that human disturbance (e.g., traffic, noise) and habitat loss (e.g., road, pipeline, and well pad construction) that occur in stopover sites will reduce foraging opportunities and increase energy expenditures. In contrast, similar disturbances in movement corridors appear less likely to reduce migration route function, assuming that animals can safely cross the road and anthropogenic features (e.g., fences) do not restrict animal movement. Following this argument, we recommend stopover segments be managed to minimize habitat loss and human disturbance, while movement segments be managed to maintain connectivity (i.e., ensure animal movement is not impeded). However, given our limited understanding of how development impedes ungulate movement (Frair et al. 2008), careful consideration should be given to the potential barrier effects created by development.

Our results indicate that when multiple migration routes exist, some route segments are used by a larger proportion of the population than others. In birds, such migratory patterns are influenced by energetic and behavioral constraints (Alerstam and Hedenström 1998, Alerstam 2001) and predation risk (Lindström 1990, Pomeroy et al. 2006). The disproportionate use of migration route segments suggests that potential impacts to migratory ungulate populations may be minimized by focusing management or conservation efforts on routes used by a large proportion of the population. Unfortunately, our analysis does not allow us to evaluate the population-level consequences of targeting conservation efforts at migration routes used by >10% of the

sampled population. Further, we recognize that routes used less frequently may have higher conservation value under different climate conditions or disturbance regimes, although archaeological records suggest at least some ungulate migration routes in the region have been used for several thousand years (Sawyer et al. 2005, Berger et al. 2006). Nonetheless, when large-scale development poses a threat to migratory routes, managers must make difficult decisions, often with imperfect data. Conserving migratory routes used by a large proportion of the population should minimize the number of animals that are potentially impacted by such disturbances. We characterized high priority routes as those used by >10% of the sampled population, however, we note that prioritizing route segments based upon a fixed level of proportional use will always maintain a larger degree of connectivity in populations that utilize fewer migration routes (Fig. 3B) compared to those that utilize many (Fig. 2B).

Migration is an important, but often neglected, life-history component that should be considered in conservation planning (Saher and Schmiegelow 2005). Sustaining current numbers of migratory mule deer in our study area will likely require that migration routes be maintained during and after the construction of 2,000 gas wells and associated infrastructure. An inherent assumption of migration and migratory routes is that they are positively correlated with fitness (Fryxell et al. 1988). Yet, the empirical evidence describing the potential demographic consequences of migration routes that are blocked or converted to unusable habitat is scant (but see Bolger et al. 2008). Future research should focus on the demographic consequences of migration routes that are altered or lost due to development. We successfully identified where migration routes occurred relative to a 1,000-km^2 proposed gas development project (BLM 2006), which

provided common ground for stakeholders to assess the potential impact to migrating

mule deer. Additionally, by distinguishing between migratory segments used as stopover

sites versus those used primarily for movement, we provided a basis for modifying

development plans to minimize habitat loss and human disturbance in stopover sites,

while maintaining connectivity in movement corridors. Because complete protection of

migration route networks is unlikely in our study area, we provided stakeholders with a

means to prioritize routes (Sawyer and Kauffman, unpublished data), which they have

used to identify areas appropriate for seasonal timing restrictions and other mitigation

measures (e.g., habitat improvements, fence modifications, and conservation easements).

Together, these tools have provided agencies, industry, and conservation groups with the

information necessary to make informed land-use decisions and improve the conservation

of migratory ungulates in an area of the West experiencing unprecedented levels of

energy development.

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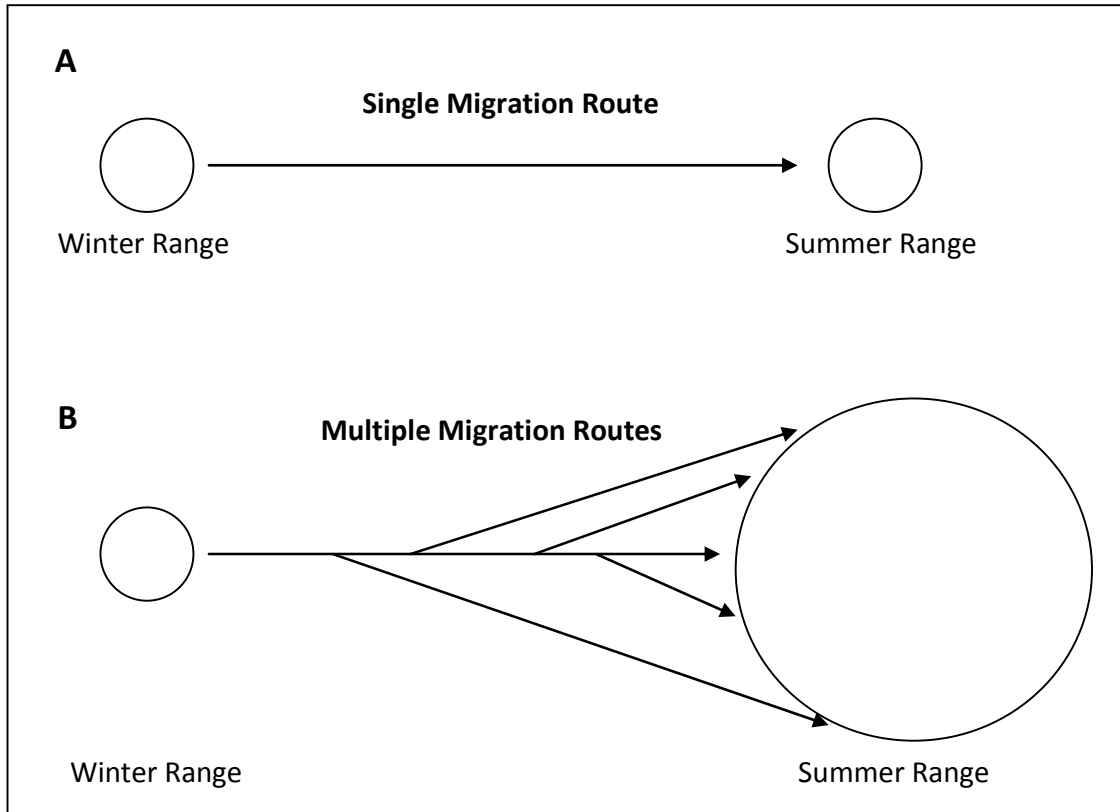
Figure 1. Conceptual model illustrating a scenario (A), where one distinct migration route occurs between two relatively small seasonal ranges, and a scenario (B), where the migration route from a small winter range splinters into multiple routes in order to access a larger summer range.
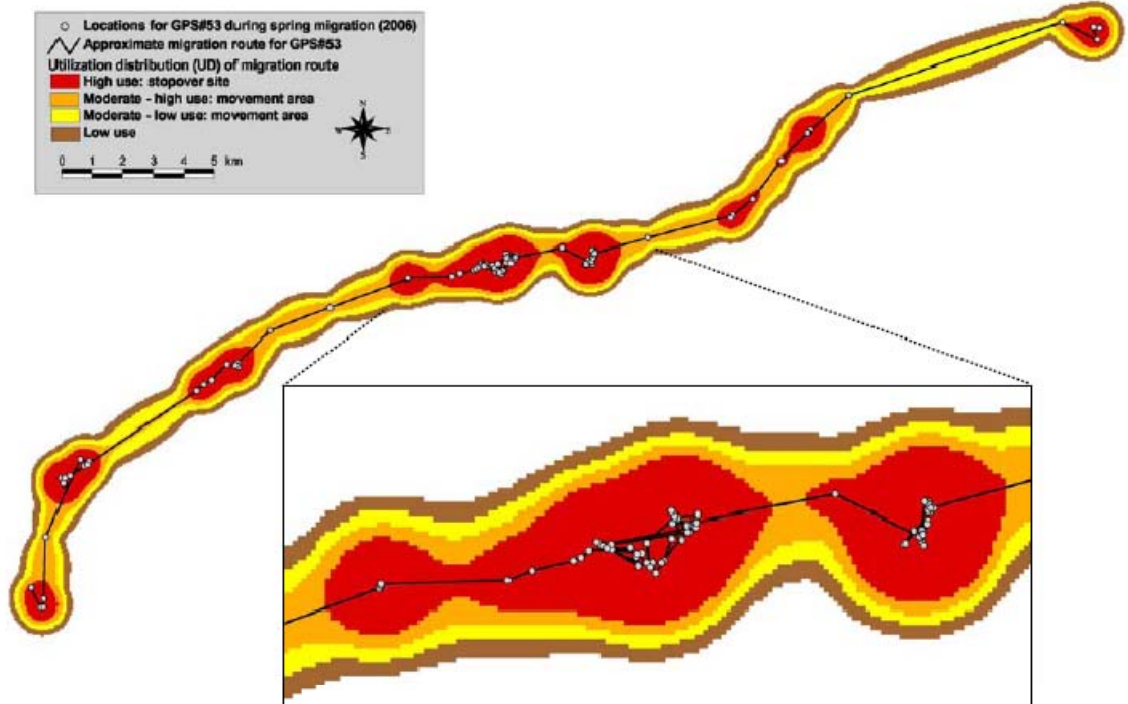
Figure 2. Utilization distribution (UD) estimated for individual deer (GPS#53) during spring migration of 2006. High-use areas corresponded with stopover sites, where the deer spent most time (i.e., tortuous movements). Moderate-use areas located between stopover sites corresponded with migratory segments through which deer moved quickly in one direction. Low-use areas reflected the uncertainty in the entire route.
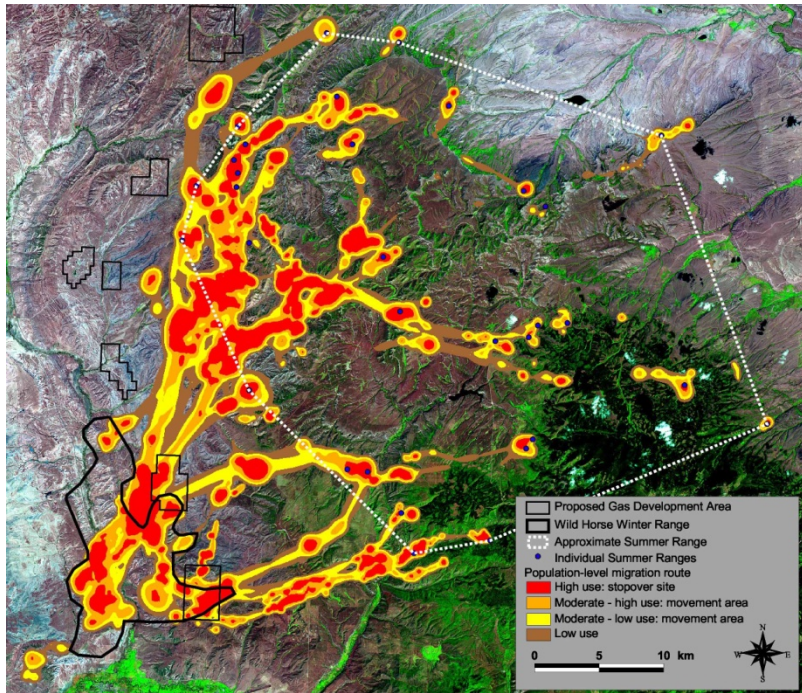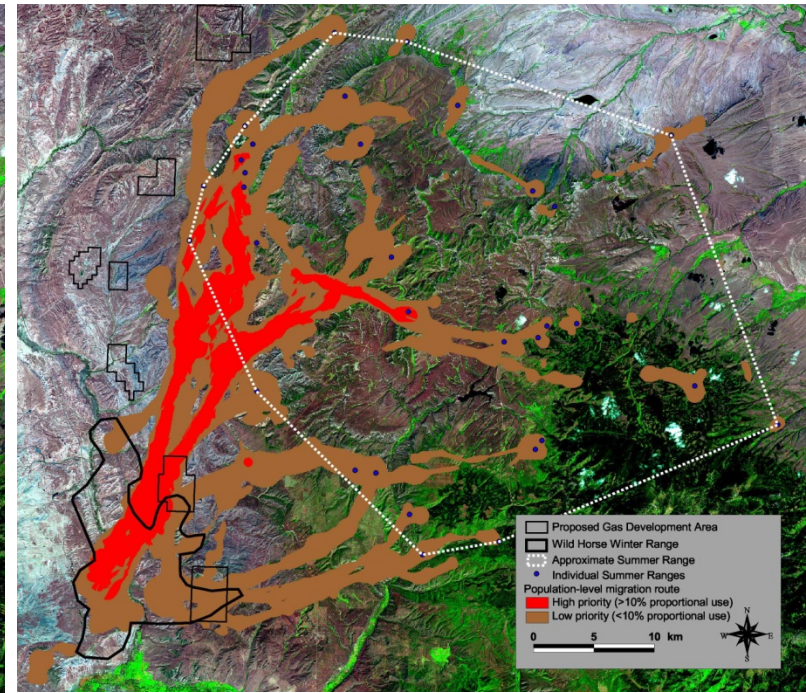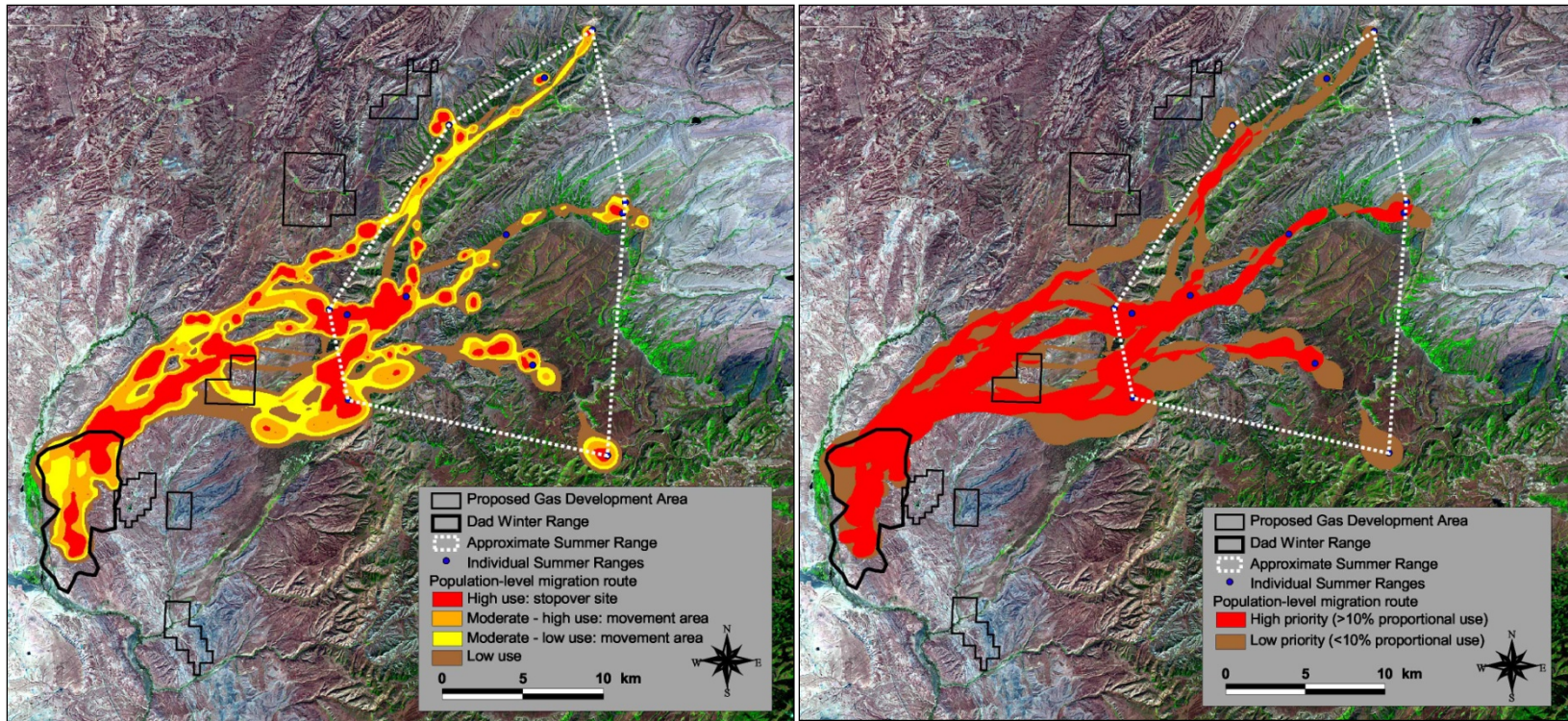
Panel A   Panel B

Figure 3. Panel A: Panel A: Estimated population-level migration route and relative amounts of use for mule deer in the Wild

Horse Winter Range, southwest Wyoming, USA. High-use areas represent stopover sites presumably used as foraging and

resting habitat, whereas moderate-use areas represent movement corridors. Panel B: Prioritization of migration routes based on

proportion of sampled mule deer population (>10%) using routes segments across the Wild Horse population-level migration

route.

65

Panel A   Panel B

Figure 4. Panel A: Estimated population-level migration route and relative amounts of use for mule deer in the Dad Winter

Range, southwest Wyoming, USA. High-use areas represent stopover sites presumably used as foraging and resting habitat,

whereas moderate-use areas represent movement corridors. Panel B: Prioritization of migration routes based on proportion of

sampled mule deer population (>10%) using routes segments across the Dad population-level migration route.

CHAPTER FOUR

Stopover ecology of a migratory ungulate

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Abstract: Stopover ecology has become an area of intense research in avian ecology and has

played a key role in developing a rigorous theory of bird migration and designing effective

conservation strategies. Although stopover behavior occurs in other migratory taxa, the explicit

study of stopovers has been limited to avian species. We suggest stopover ecology may have

broad application to other migratory taxa, particularly ungulates that annually migrate long

distances along traditional routes. We used fine-scale global positioning system (GPS)

movement data and Brownian bridge movement models (BBMM) to quantify a suite of stopover

characteristics and examine the ecological role of stopovers in the seasonal migrations of mule

deer (*Odocoileus hemionus)* in western Wyoming, USA. We found that mule deer utilized a series of stopover sites in both spring and fall migrations, across a range of migration distances (18-144 km). Overall, mule deer used 1.9 and 1.5 stopovers per 10 km of migration distance during spring and fall migrations, respectively. During migrations that lasted 3 to 92 days, mule deer spent 95% of their time in stopovers and 5% in the movement corridors that connect them. Individual deer showed high fidelity to stopover sites across seasons and years, although spatial overlap between the same seasons (e.g., spring to spring) was higher than between different seasons (e.g., spring to fall). Stopovers appeared to have higher quality forage compared to movement corridors, and forage quality increased with elevation, presumably because of delayed phenology along the altitudinal migration route. Unlike most avian taxa that employ a time-minimizing migration strategy, the most likely strategy for ungulates is one that maximizes energy intake. We hypothesize that stopovers play a key role in this migration strategy by allowing ungulates to migrate in concert with vegetative phenology and optimize their foraging during migration. Our results suggest stopovers were a critical component in the altitudinal migrations of mule deer and that conservation of stopover sites may improve efforts aimed at sustaining migratory ungulate populations.

*Key word*s*: Brownian bridge movement model (BBMM); migration routes; movement corridors; mule deer; *Odocoileus hemionus*; phenology; stopover ecology; ungulate migration.

INTRODUCTION

With the exception of orientation and navigation capacity, the ability of animals to complete long-distance migrations is largely determined by the energetic requirements needed to fuel migratory movements (Alerstram et al. 2003). Animals use a wide variety of adaptations to

meet these energetic requirements, including changes in morphology, physiology, and behavior (Ramenofsky and Wingfield 2007, Hedenström 2008). Across taxa, some species display all three of these traits (e.g., birds), while others may exhibit only behavioral changes (e.g., ungulates). A common behavioral strategy among all long-distance migrants is their use of stopover sites – habitat patches along the migration route where animals rest and renew energy reserves. The study of stopover sites, or "stopover ecology", has become an area of intense research in avian ecology (Moore 2000, Newton 2008), with particular emphasis on optimal migration strategies (Farmer and Wiens 1998, Erni et al. 2002), energetics (Weber and Houston 1997a, b), and predation risk (Lindström 1990, Pomeroy et al. 2006). To date, stopover ecology has been largely ignored in migratory taxa whose mode of locomotion is running or swimming (but see Hedenström 2003).

Avian ecologists have developed a rigorous theory of bird migration (Alerstam and Hedenström 1998), which relies heavily on stopover ecology. From such work has come the widely accepted view that the optimal migration strategy of birds is one of time-minimization (or speed-maximization), whereby birds attempt to migrate from wintering areas to breeding grounds in the shortest time possible (Hedenström 2008). With time-minimizing migration, stopover sites are considered the most important component of migration performance because the rate of fuel accumulation determines the overall migration speed (Åkesson and Hedenström 2007). Empirical evidence, based on stopover duration and the fuel loads at stopover departure, offers convincing support of the time-minimizing strategy in birds (Hedenström 2008). The ability to formulate robust predictions about migratory behavior has allowed avian ecologists to address key conservation issues, such as the consequences of habitat loss at stopovers (Weber et

al. 1999, Simons et al. 2000) and the potential effects of barriers on migration (Alerstam 2001, Delingat et al. 2008).

Our interest here is to explore whether stopover ecology has broad relevance to non-avian migratory species, particularly temperate ungulates such as mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), moose (*Alces alces*), and pronghorn (*Antilocapra americana*) that annually migrate long distances between seasonal ranges, along traditional routes. Ungulates demonstrate strong fidelity to their seasonal ranges (Garrott et al. 1987, Kufeld et al. 1989, Brown 1992) and migration routes (Sweanor and Sandegren 1988, Berger et al. 2006, Sawyer et al. 2009), but knowledge of their stopover use and the degree to which stopovers influence migratory patterns and strategies is limited. Sawyer et al. (2009) recently characterized mule deer migration routes as networks of stopover sites where deer spent most of their time, connected by movement corridors through which deer moved quickly. Others have used movement models to identify behavioral states (e.g., foraging/resting vs. movement) from time-specific location data (Bergman et al. 2000, Johnson et al. 2002, Franke et al. 2004) and to refine resource selection studies by differentiating between sites used for foraging or resting versus those used for movement (Saher and Schmiegelow 2005). Although these studies have improved our ability to characterize and delineate ungulate migration routes, basic knowledge of stopover use remains incomplete. For example, we do not know how many and what spacing of stopovers are needed to complete migrations, how large stopovers are, whether ungulates use the same stopovers year after year, and whether stopovers offer better foraging opportunities than other segments of the migration route. Given the relative ease with which fine-scale movement data can be collected

with GPS-telemetry, it is now possible to quantify stopover characteristics and examine the ecological role of stopovers in the migrations of ungulates and other land migrants.

Unlike birds, the body size and locomotor mode of ungulates allows them to carry more fuel than necessary to complete long-distance movements. The energetic costs of carrying large fuel loads are always greater than small fuel loads (Åkesson and Hedenström 2007), but for ungulates, these costs are heavily outweighed by those associated with snow depth, travel speed, and slope (Parker et al. 1984, 1996). Further, completing seasonal migrations in the shortest amount of time does not have any obvious fitness benefits to ungulates, whereas the importance of nutrition and body condition for increasing fitness is well-documented (Hobbs 1989, Cook et al. 2004, Bishop et al. 2009, Parker et al. 1996, 2009). Thus, rather than adopt a time-minimization strategy like birds, a more likely strategy for ungulates is one that involves relatively slow migration speeds while maximizing the intake of high quality forage. Maximum energy intake occurs when forage plants are less mature and highly digestible, but developed enough such that intake is not constrained by cropping time (Hebblewhite et al. 2008). Tropical ungulates achieve this by aggregating in large herds that keep forage at an immature but highly nutritious growth stage (Fryxell 1991) and migrating in response to phenology gradients created by rainfall patterns (e.g., wildebeest [*Connochaetes taurinus*] migration; Boone et al. 2006, Holdo et al. 2009). In contrast, temperate ungulates such as elk migrate along phenology gradients created by elevation and topography (Hebblewhite et al. 2008). Regardless of whether the phenology gradient is created by rainfall or elevation, existing evidence suggests that a general strategy of migratory ungulates is to follow the most nutritious vegetation in order to maximize energy intake during the growing season (Albon and Langvatn 1992, Wilmshurst et al.

1999, Fryxell et al. 2004, Holdo et al. 2009). Although previous research supports energy maximization as a general foraging strategy for ungulates, the role of stopover use in this context has yet to be explored.

For most species, migration is an adaptation for exploiting seasonal peaks of resource abundance and avoiding seasonal resource depletion (Alerstam et al. 2003). For temperate ungulates, high-elevation summer ranges provide an abundance of high-quality forage that allows animals to meet the energetic costs of lactation and accumulate fat reserves for the winter (Parker et al. 1996, Cook et al. 2004). In contrast, forage availability and quality in the lower-elevation winter ranges are limited by snowpack and plant senescence, respectively (Wallmo et al. 1977, Garrott et al. 1987). Combined with the higher energetic costs of moving through snow and maintaining homeostasis (Parker et al. 1984), these factors create a negative energy balance that may last for most of the winter months (Parker et al. 2009). To minimize over-winter mortality ungulates strive to delay the onset of this negative energy balance in the autumn and reverse it as soon as possible in the spring (Hobbs 1989, Parker et al. 2009). In altitudinal migrations, precipitation patterns and delayed phenology create a forage quality gradient that corresponds with elevation (Albon and Langvatn 1992, Hebblewhite et al. 2008). Thus, stopovers may allow ungulates to optimize their foraging patterns by migrating (and pausing) in concert with plant phenology, although such a mechanistic role for stopovers has yet to be evaluated. Similar to birds (Mehlman et al. 2005), understanding the role of stopovers in ungulate migration may lead to new, and potentially more effective, conservation strategies.

In this study, we use fine-scale movement data collected from GPS collars to examine the ecological role of stopovers for migratory mule deer in Wyoming, USA, where migration

distances range from 18 to 144 km. We determined the size and number of stopovers used during migrations and estimated the number of stopovers needed by mule deer to complete both spring and fall migrations as a function of migratory distance. We also examined stopover spacing and calculated the amount of time deer spent in stopovers compared to the movement corridors that connect them, as well as the fidelity of individual animals to stopover sites across seasons and years. Finally, we characterized the forage quality of stopovers relative to movement corridors and evaluated whether delayed phenology creates a foraging gradient along the migration route, as commonly assumed in altitudinal migrations (Albon and Langvatn 1992, Hebblewhite et al. 2008). We use these stopover metrics to evaluate the likely role of stopovers in mule deer migration and the potential benefits of stopover conservation.

METHODS

We used helicopter net-gunning to capture adult female mule deer across winter ranges in two regions of western Wyoming, USA including: 1) the upper Green River Basin (UGRB) near Pinedale, Wyoming, and 2) the lower Great Divide Basin (LGDB) near Baggs, Wyoming. We fitted deer with store-on-board GPS radio-collars (TGW 3500, Telonics, Inc., Mesa, AZ) programmed to collect one location every 2 or 2.5 hours. Collars were programmed to drop off 1-2 years after capture, at which time they were recovered from the field and downloaded. Between 1 December 2005 and 2008, we collected GPS data for 109 migrations (65 spring, 44 fall) from 68 deer. The UGRB was characterized by low elevation (2,100–2,200 m) sagebrush basins that served as winter range, surrounded by rugged mid-elevation (2,200–2,500) foothills and high-elevation (2,500–3,100 m) mountains that mule deer used as summer range. The LGDB was characterized by low elevation (1,900–2,100 m) sagebrush (*Artemisia sp.*) and mixed-shrub

basins that provided winter range, surrounded by mid-elevation (2,100–2,500 m) rolling foothills

that mule deer used as summer range. Detailed information about the vegetation and land-use

characteristics of the study areas is provided in Sawyer et al. (2006, 2009).

Stopover Delineation

We followed the approach of Sawyer et al. (2009) to identify migratory stopover sites.

First, we used the Brownian bridge movement model (BBMM; Horne et al. 2007) to estimate a

utilization distribution (UD) for each migration route collected from GPS-collared mule deer

(Fig. 1). The BBMM uses time-specific location data to estimate the probability of use along a

movement route, where the probability of being in an area is conditioned on the start and end

locations, the elapsed time between locations, and the speed of movement (Horne et al. 2007).

Calculation of the BBMM requires: 1) a sequence of time-specific location data, 2) the estimated

error associated with the location data, and 3) grid cell size for the output UD. Consistent with

Sawyer et al. (2009), we used a sequence of GPS locations (i.e., the migration path) that occurred

between winter and summer range during a specific migration (spring or fall), including the 24-

hour period prior to, and following, migration. We used an estimated location error of 20 m and

grid cell size of 50 × 50 m. Following UD estimation, stopover sites were defined as the highest

25% quartile in the UD. Such a characterization appears to accurately reflect migratory

segments where animals actually stop, rather than segments where animals move slowly (Sawyer

et al. 2009, Fig. 1). We used the BBMM code from Sawyer et al. (2009) and conducted all our

analyses in the R language for statistical computing (R Development Core Team 2008).

Seasonal stopover use

After stopover sites were delineated for each migration route, we used a paired *t* test to determine if the number of stopovers differed between spring and fall migration. To control for migration distance, we restricted this analysis to individual deer that had >1 migration route collected (*n* = 27). Key to this seasonal comparison was whether the duration (days) of migration varied between the spring and fall migrations. We again used a paired *t* test to determine whether the number of migration days differed between spring and fall. To calculate the average size of stopovers within each route, we used the entire sample of migration routes (*n* = 109). We then plotted the average stopover size against the temporal length of each migration and fit a smoothed line to assess the relationship between migratory duration and stopover size. We also estimated the amount of time each deer spent in stopover habitat as the proportion of total migratory locations that occurred in stopovers.

Stopover number and spacing

The numbers and spacing of stopovers along a migration routes provide key insights into migration strategies and conservation options (Alerstam et al. 2003). We used linear regression to examine the relationship between migration distance and the number of stopovers. Migration distance was measured along the centerline of each UD estimated for 109 migration routes from 68 individual deer. We estimated the number of stopovers used in each deer migration as a function of the total migration distance. Because stopover use was not possible unless an animal migrated, we forced the intercept of our linear model through zero. This had little or no effect on the estimated coefficients. Spring (*n* = 65) and fall (*n* = 44) migrations were analyzed separately to account for seasonal differences.

In addition to the average number of stopovers per distance travelled along a migration route, the spacing of potential and actual stopover sites may be limiting to migrating animals. To test for non-random spacing of stopovers along migration routes, we measured the sojourn distances (Taylor and Karlin 1984), defined as the distances between consecutive stopover sites, for each migration route that had 6 or more stopovers ($n = 66$). To test for non-random (e.g., resulting for a linear Poisson process) placement of stopover sites, we compared the observed variance in sojourn distances for each route to the distribution of variances of 5,000 simulated routes, upon which the same number of stopovers were randomly placed. The placement (percentile) of the observed variance within the distribution of variances from simulated routes then indicate random or non-random placement of stopovers: low percentile values (< 5%) indicate significantly uniform placement of stopovers, while high values (>95%) indicate significantly clumped stopover sites. Additionally, we characterized the entire distribution of sojourn distances observed in our migration data, as the highest sojourn distances may reflect the maximal movement range of mule deer between stopovers.

Stopover fidelity

Temperate ungulates tend to use the same migration routes across seasons and years (Sweanor and Sandegren 1988, Berger et al. 2006, Sawyer et al. 2009), but it is unknown whether they have such fidelity to their stopover sites. We examined the fidelity of stopover use across seasons (spring to fall) by calculating the proportion of stopover sites in the spring migration that overlapped with stopover sites from the subsequent fall migration. Similarly, we assessed stopover fidelity across years (spring to spring) by calculating the proportion of stopover sites in a spring migration that overlapped with those of the subsequent spring

migration. Because these comparisons required paired data, we restricted the seasonal and annual

comparisons to mule deer that had at least 2 (spring and fall; $n = 27$) and 3 (spring, fall, and

spring; $n = 14$) migration routes collected, respectively. Comparing the proportion of overlap in

stopover sites between seasons and years was intuitive and provided a reasonable metric for

consistency of use. However, this metric has no expected value associated with it. Thus,

presented alone it was unclear whether the observed degree of overlap differed from that which

would be expected from random use of stopovers along the route. Accordingly, we used an area-

based selection ratio approach (Manly et al. 2002) to determine if stopover fidelity, from spring

to fall and spring to spring, was more or less than expected by chance. Using stopovers paired

within each individual deer, we defined used units as the number of migratory deer locations in

one season (e.g., spring 2006) that occurred in the stopover sites of its previous migration (e.g.,

spring 2005). Because our stopovers were defined as the top 25% quartile of the UD, the

available or expected number of GPS locations to occur in the stopovers of a previous migration

was $0.25 \times$ the number of locations. We calculated a selection ratio for each deer as (used

locations)/(available locations), and used the 95% CI of the mean ratio across deer to assess

whether deer selected stopovers more or less than expected. A selection ratio of 1 indicates no

selection (i.e., use is proportional to availability), whereas ratios >1 indicate selection for and

ratios <1 indicate selection against (Manly et al. 2002).

Forage quality assessment

The presumed function of stopover sites is to provide foraging habitat during the

migration bout, whereas other segments of the migration route function primarily as movement

corridors (Sawyer et al. 2009). We used the Normalized Difference Vegetation Index (NDVI) as

an index of forage quality to determine if forage quality differed between stopover sites and the movement corridors that connected them. The NDVI is widely used as a measure of forage quality (Hamel et al. 2009), primary productivity (Hebblewhite et al. 2008), and plant phenology (Boone et al. 2006) in habitat assessments (Pettorelli et al. 2005). Importantly, NDVI is positively correlated with the timing of peak faecal crude protein in temperate ungulates (Hamel et al. 2009) and has been successfully used to assess how plant productivity affects ungulate body mass in temperate environments (Pettorelli 2006, 2007). We restricted our NDVI analysis to mule deer in the LGDB because the area was characterized by open habitat that could be remotely sensed, rather than closed forest canopy. We further restricted NDVI analysis to the spring migration because the fall imagery contained areas of snowpack that could have created spuriously high values (Pettorelli et al. 2005). Our intent was to obtain a snapshot of NDVI values for the end of the migration period (mid-June), with the expectation that a forage quality gradient associated with elevation should be evident by then. We acquired $30 \times 30m$ – resolution NDVI data for June 14, 2005 and May 14, 2006 from the U. S. Geological Survey (USGS) Earth Resources Observation and Science Center (EROS). Reliable imagery from June 2006 was not available because of cloud cover. We randomly selected 15 migration routes from 2005 and 2006 and calculated the average NDVI value in stopovers and movement corridors within each route. For sampling purposes, we defined the movement corridor as the most probable path between the stopovers, which was equivalent to the straight-line trajectory connecting GPS locations (Fig. 1). Thus, the average NDVI value of a movement corridor was the mean NDVI value of 30-m cells that intersected the straight lines connecting stopovers. We conducted paired t tests to determine if NDVI values differed between stopovers and movement corridors.

To assess whether forage quality varied across the elevation gradient of the migration route, we used the same random sample of 30 deer and regressed the mean NDVI value of each stopover in each year (2005 and 2006) as a function of its mean elevation. We calculated elevation from a 26 × 26 m digital elevation model (USGS 1999). In some cases, ungulates may migrate from a low-elevation basin, over a mountain range, and down to another basin destination where elevation is similar to its departure site (e.g., pronghorn; Sawyer et al. 2005, Berger et al. 2006). In this scenario, a forage quality gradient may be associated with elevation, but would not necessarily be positively related with the length of the migration route. To account for this we also used linear regression to evaluation the relationship between the mean NDVI value of each stopover and its distance from winter range. We created 3-dimensional plots to illustrate the relationship between NDVI, elevation, and distance from winter range of each stopover.

RESULTS

Mule deer used more stopovers (mean difference ± 95% CI, 2.07 ± 1.02) in spring migrations compared to fall (t_{26} = 4.03, P < 0.001), but the duration (days) of spring (mean ± 95% CI, 21.3 ± 7.6) and fall (mean ± 95% CI, 20.8 ± 8.5) migrations did not differ (t_{26} = 0.13, P = 0.896). Although the mean migration duration was not different, the variation between the duration of spring and fall migrations was noticeably larger as migration duration increased (Fig. 2). Overall, mule deer spent similar amounts of time migrating in the spring and fall, but tended to use more stopovers during the spring (Fig. 2).

Regression analysis revealed that the number of stopovers increased significantly with migration distance during both spring ($F_{1, 64}$ = 696.5, P < 0.001) and fall ($F_{1,43}$ = 280.4, P <

0.001) migrations (Fig. 3). Migration distance explained slightly more variation in the number of spring ($R^2 = 0.91$) stopovers than the fall ($R^2 = 0.86$). Estimated coefficients indicated that mule deer used 1.9 and 1.5 stopovers for every 10 km traveled during spring and fall migrations, respectively. Although the number of stopovers increased linearly with migration distance, the spacing of stopovers was not uniform along the routes. The observed variances in sojourn distances had a wide range of percentile values when compared to randomly placed stopover sites (range = 5.3 to 97.9%), but the average variance was near the center of the randomized distributions (mean $\pm$ 95% CI = $57^{th} \pm 7\%$). Sojourn distances were weakly correlated with total migration distance ($r_p = 0.13$) and rarely exceeded 10 km (min = 0.10, max = 25.86, mean = 4.33) in length (Fig 4).

The proportion of overlap in stopover sites between the same (spring to spring) and different (spring to fall) seasons was 80% ($n = 14$, SE = 0.03) and 62% ($n = 27$, SE = 0.04), respectively. Overlap of stopover sites was higher among same seasons in different years ($t_{37} = -3.43$, $P = 0.001$). Comparing the proportion of migratory locations that occurred in stopover sites delineated in the previous season to the proportion expected by random use indicated that deer had high fidelity to known stopovers. Selection ratios for spring to spring, and spring to fall, migrations were 2.34 ± 0.33 (mean $\pm$ 95% CI) and 2.05 ± 0.43, respectively. Because confidence limits did not overlap 1, this analysis indicates strong selection of stopover sites (i.e., fidelity) between seasons and across years.

The average size of stopovers within each migration route was 239 ha $\pm$ 50 (mean $\pm$ 95% CI) and no differences were detected between the size of stopovers in spring versus fall ($t_{107} = -0.50$, $P = 0.621$). The average stopover size exponentially declined as the temporal length of

migration increased (Fig. 5). Migrations that lasted < 10 days tended to include relatively large (> 200 ha) stopovers, whereas migrations of more than 10 days used smaller (< 200 ha) ones. Given the strong correlation between migratory distance and duration ($r_s = 0.72$), our results suggest short migrations were characterized by a few large stopovers, while longer migrations tended to have more stopovers of smaller size. Across all migrations, mule deer spent $95 \pm 0.4\%$ (mean $\pm$ 95% CI) of their time in stopovers and only 5% in movement corridors. Although deer tended to use more stopovers in spring compared to fall, the proportion of time deer spent in stopovers did not differ between seasons ($t_{66} = -2.50$; $P = 0.015$).

Mean NDVI values were higher in stopovers (2005; $\bar{x} = 0.21$, $n = 15$, SE = 0.01, and 2006; $\bar{x} = 0.14$, SE = 0.01) compared to movement corridors (2005; $\bar{x} = 0.18$, $n = 15$, SE = 0.01, and 2006; $\bar{x} = 0.12$, SE = 0.01) in both 2005 ($t_{29} = 3.14$, $P = 0.007$) and 2006 ($t_{29} = 3.87$, $P = 0.002$), suggesting forage quality was higher in stopovers than in movement corridors. Not surprisingly, the mean NDVI value of stopovers was higher in 2005 compared to 2006 because the imagery was obtained later in the spring. The 30-day disparity in the dates and associated phenological differences in the 2005 and 2006 imagery from which NDVI was calculated was also apparent in our assessment of whether forage quality increased with the elevation gradient along the migration route. Regression analysis revealed that NDVI values of stopovers increased with elevation (2005; $P < 0.001$, $F_{1,110} = 150.5$, and 2006; $P < 0.001$, $F_{1,115} = 72.8$) and distance from winter range (2005; $P < 0.001$, $F_{1,110} = 60.8$, and 2006; $P < 0.001$, $F_{1,115} = 10.6$) in both years, but the gradient was stronger in 2005 (Fig.6).

DISCUSSION

The theoretical and applied benefits of stopover ecology are not limited to avian taxa.

Our analysis of mule deer demonstrates that, as for birds, stopovers play a key role in the altitudinal migrations of temperate ungulates. Mule deer utilized a series of stopover sites along their seasonal migrations routes, which they appeared to use year after year. Deer spent 95% of their migration time in stopovers, and the number of stopovers increased linearly with migration distance. Interestingly, while these results indicate that a typical distance is usually traveled between stopovers, we did not find that there was a significantly uniform spacing of stopovers within each route. This suggests that while deer require roughly one stopover every 5.5 to 6.6 km of movement, they are not severely constrained by this average spacing, and both shorter and longer distances between stopovers are routinely used. Our NDVI analysis indicated that stopovers had higher forage quality compared to the movement corridors that connected them and that the forage quality of stopovers improved as elevation and distance from winter range increased. We believe these findings indicate that stopover use is a key behavioral mechanism that allows migratory ungulates to exploit nutritional gradients associated with altitudinal migrations. Here, we discuss the stopover characteristics observed in our study, evaluate the likely role that stopovers play in ungulate migration, and identify potential conservation benefits of stopover ecology to the management of migratory ungulates.

Mule deer utilized a series of stopover sites along their migrations routes, but tended to use more stopovers in spring than in fall. Unlike pronghorn in the same region that complete their fall migrations in less time than in spring (Sawyer et al. 2005), mule deer showed no such differences in the duration of seasonal migrations. Thus, seasonal differences in stopover use did not result from variable migratory rates, but they may have been influenced by mule deer shifting their diets from primarily herbaceous forage in the spring to browse in the fall. We hypothesize

that differential use of stopovers between seasons allow mule deer to accommodate different environmental conditions and optimize their foraging patterns without having to navigate different migration routes in the spring and fall. Birds, for example, often encounter different environmental conditions (e.g., prevailing winds) during spring and fall migrations (Alerstam et al. 2006), which they sometimes adapt to by completing loop migrations – a migratory pattern where the fall migration route is markedly different from the spring (Newton 2008).

Across a wide range of migratory distances (18-144 km), the number of stopovers increased linearly with migration distance. On average, mule deer used 1.9 and 1.5 stopovers for every 10 km increase in migration distance during spring and fall, respectively. Thus, a 100-km migration appears to require 15-19 stopovers. Interestingly, the size of stopovers declined exponentially as the duration of migration increased, such that short migrations (< 10 days) were characterized by a few large stopovers, whereas longer migrations (> 10 days) had many small stopovers. The mean distance between stopovers was 4.33 km and rarely exceeded 10 km, regardless of the total migration distance. However, we found no evidence of uniform or clumped patterns in stopover spacing. A possible explanation for this lack of spacing pattern is the wide variation in stopover sizes and durations, which could add variation into the subsequent distances that animals are willing to travel.

In general, a migration strategy that involves many stopovers is energetically preferable to one with few stopovers because animals may travel shorter distances with lighter fuel loads (Alerstam 2001). This is especially true for animals that fly because of the energetic constraints associated with carrying excessive weight. For ungulates and other land migrants, migratory locomotion is not likely to be constrained by heavy fuel loads, because the associated energetic

costs are small compared to those of other variables such as snow depth, topography, and travel speed (Parker et al. 1984, 1996). Thus, unlike birds that utilize stopovers to minimize their fuel loads and maximum migration speed, ungulates may use stopovers to maximize energy intake and maintain a relatively slow migration speed. We suspect that the range (i.e., 0–10 km) and random spacing of sojourn distances is a result of mule deer optimizing their stopover use in a landscape of heterogeneous foraging opportunities. The degree to which variable sojourn distances allow animals to establish and maintain migration routes in heterogeneous (and changing) landscapes is unknown.

An implicit assumption of stopovers is that they provide better foraging opportunities than other segments of the migration route. Ideally, this assumption could be tested with direct measures of nutritional quality, such as digestible energy or crude protein (e.g., Hebblewhite et al. 2008). In lieu of a direct nutritional measure, the NDVI is often used as an index of forage quality (Pettorelli et al. 2005). Our analysis provided a snapshot of NDVI values during spring migration and indicated that forage quality was higher in stopovers compared to movement corridors. This finding suggests that deer selectively choose stopovers based on their forage quality. Determining the habitat characteristics and nutritional value of stopovers will be an important next step in the development of ungulate stopover ecology. Although other factors such as predation risk may affect stopover selection (Lindström 1990, Pomeroy et al. 2006), our results suggest NDVI or other measures of forage quality may provide a reasonable starting point for distinguishing stopover habitat from other migratory segments or the surrounding matrix.

A second assumption of altitudinal migration is that delayed phenology associated with elevation creates a nutritional gradient, where vegetation phenology is delayed at higher

elevations and provides higher forage quality compared to lower elevations (Albon and Langvatn 1992). In a recent study of a partially-migratory elk herd, Hebblewhite et al. (2008) estimated that phenology was delayed by 50 days for every 1000-m increase in elevation, and that compared to resident elk, migratory animals improved their forage quality 6.5% by accessing vegetation at higher elevations. Similarly, Albon and Langvatn (1992) found that crude protein was positively correlated with elevation and that body weights of red deer *(Cervus elaphus)* that migrated to higher elevations were higher than those that did not. We found the forage quality of stopovers was positively correlated with elevation and distance from winter range. Temporally, forage quality for such altitudinal migrations may best be viewed as a phenological wave that advances from lower to higher elevation (and from winter to summer range). Indeed, the ability of migratory ungulates to exploit such gradients in forage quality is a key benefit to the migratory life history (Fryxell and Sinclair 1988, Albon and Langvatn 1992, Holdo et al. 2009). Recent studies have documented cases of historically migratory ungulate populations abandoning their migrations in favor of year-around residency (Hebblewhite et al. 2006). Decreased migrant:resident ratios are presumed to occur when the fitness benefits of migration no longer exceed those of non-migratory behavior, which could possibly occur if the nutritional gradient deteriorated along the migration route.

Improved forage quality associated with delayed phenology has important implications for why ungulates migrate (Albon and Langvatn 1992, Hebblewhite et al. 2008, Holdo et al. 2009). If ungulate migration is driven by the selection of high-quality forage, then the duration of altitudinal migrations should correspond with the delayed phenology associated with elevation gradients. For example, given a phenology delay of 50 days for every 1000-m increase in

elevation (Hebblewhite et al. 2008), we would expect a 420-m elevation gain in the average 21-day migration period observed in our study. Consistent with this prediction, the average elevation gain for deer in our study was 324 ± 60 m (mean ± 95% CI). Accordingly, we propose that stopover use is the mechanism that allows temperate ungulates to take full advantage of the forage quality gradient created by phenological delays associated with elevation. We know ungulates are capable of moving long distances in short periods of time (20-50 km/day; Thomas and Irby 1990, Berger et al. 2006), yet deer migrations we observed across multiple years and distances took several weeks to complete. This pattern is consistent with a migration strategy designed to exploit nutritional gradients associated with elevation. If a phenology gradient did not exist along the migration route, we would expect ungulates to complete their migrations more quickly. This ecological role of stopovers also fits well with the seasonal life cycle of temperate ungulates. During the spring migration, stopover use allows ungulates to move off of winter range as soon as plant phenology permits and maintain diets of high quality forage by matching their foraging with plants at a nutritious phenological state. During the fall migration, stopover use allows ungulates to benefit from higher quality forage at mid-elevation stopovers and delay their arrival to winter ranges where forage quality is lower. Overall, stopover use facilitates a strategy that effectively reduces the amount of time spent on winter range and presumably allows individuals to recover body condition earlier in the spring and maintain it longer in the fall.

The conservation of stopover habitat has become a clear goal of agencies and non-governmental organizations tasked with sustaining migratory bird populations (Mehlman et al. 2005). The protection of stopover sites is an effective conservation strategy in large part because

many birds follow very similar or identical migration routes between years (Alerstam et al. 2006) and return to known stopover sites year after year (Åkesson 2003). Our results indicate mule deer showed fidelity to stopovers across seasons and years. Accordingly, the protection of stopover sites may provide an effective conservation strategy for migratory ungulates, particularly in areas where migration routes overlap with anthropogenic disturbances. Based on the presumed function of stopovers (i.e., foraging habitat) and movement corridors (i.e., travel), Sawyer et al. (2009) suggested that different management strategies may be warranted for the two types of migration segments. Specifically, they recommended that stopovers be managed to minimize habitat loss and anthropogenic disturbance, whereas movement corridors be managed to maintain connectivity. Full protection of a migration route is always preferable to protection of a series of migratory segments; however, this is unlikely to occur in landscapes with high potential for agricultural, housing, or energy development. A conservation strategy focused on stopovers may allow limited amounts of development to occur in migratory segments not used as stopover habitats, so long as the development does not impede animal movement. Stepping stone corridors, similar to those created by stopovers, can provide effective movement corridors in terrestrial systems, as long as the intervening matrix is highly permeable (Baum et al. 2004).

Of particular ecological and conservation concern is the demographic consequences of habitat loss at stopover sites. Disturbance to stopover sites can have population-level effects in birds (Newton 2008), but the potential effects of habitat loss are more difficult to quantify within the network of stopover sites. Weber et al. (1999) found habitat loss at stopovers close to the breeding grounds had greater reproductive costs for birds because there were fewer opportunities for compensation in the later stages of the migratory journey. For temperate ungulates, migration

routes typically radiate from a common winter range to a much larger summer range, such that stopover sites close to winter range are used by a larger proportion of the population than those far from winter range (Sawyer et al. 2009). Thus, habitat loss at stopovers close to winter range may be most detrimental to the population. Additional research is needed to reveal how or if ungulate demography is influenced by habitat loss or disturbance at stopover sites. Identifying the habitat characteristics of stopovers will be an important first step towards understanding their influence on animal fitness and identifying potential mitigation opportunities. Future work should also focus on identifying development thresholds (e.g., road densities) at which movement corridors no longer provide connectivity between stopovers (e.g. Frair et al. 2008). Also of interest is predicting how climate change may affect stopover use and associated migration patterns (e.g., Post et al. 2008), and whether stopovers play a prominent role in ungulate migrations that do not follow elevation gradients, i.e., lateral migrants (McCullough 1985).

ACKNOWLEDGEMENTS

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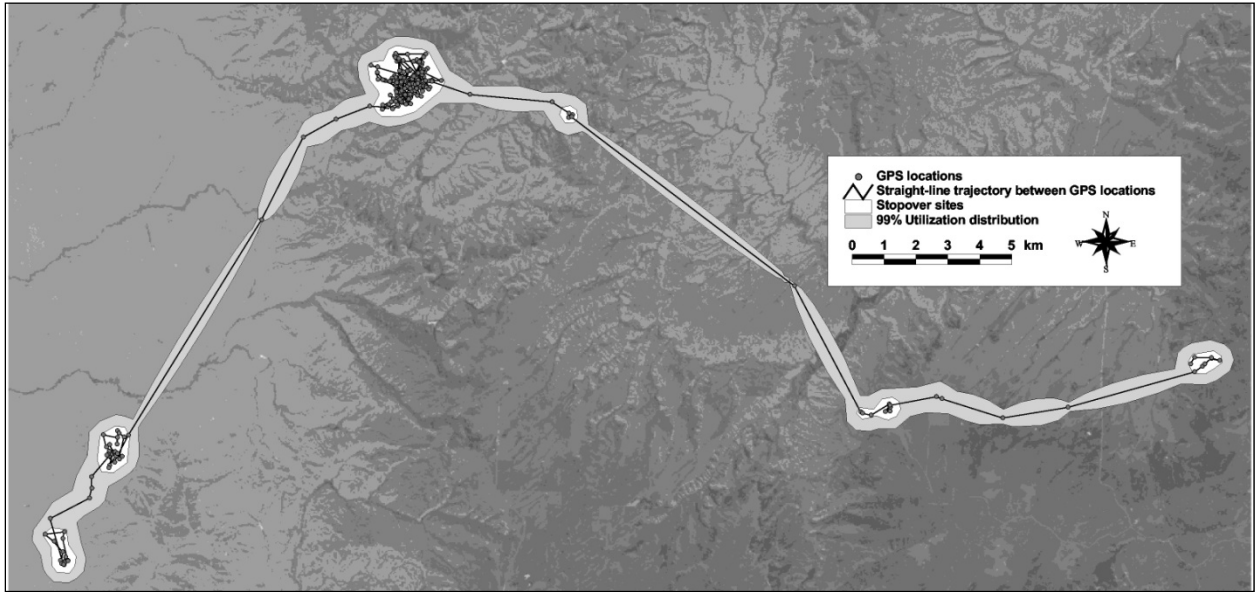
Fig. 1. Six stopover sites and 99% utilization distribution estimated for an individual mule deer (GPS no. 10) during spring migration of 2005. Migration route is overlaid on the Normalized Difference Vegetation Index (NDVI) estimated during the spring 2005 migration.
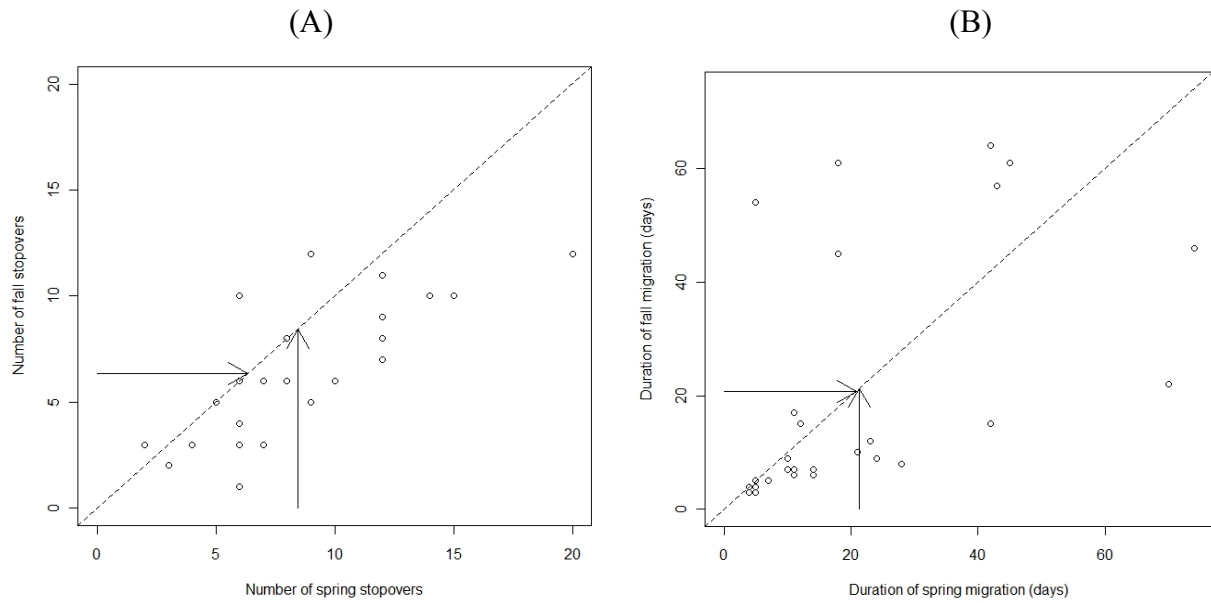
Fig. 2. (A) Number of stopovers in the spring and fall migrations of mule deer ($n = 27$) for which both spring and fall migrations were documented. (B) Duration (days) of spring and fall migrations mule deer ($n = 27$) that had data collected for both spring and fall migrations. Diagonal line represents 1:1 relationship between X and Y axis. Arrows depict the mean values for each axis.
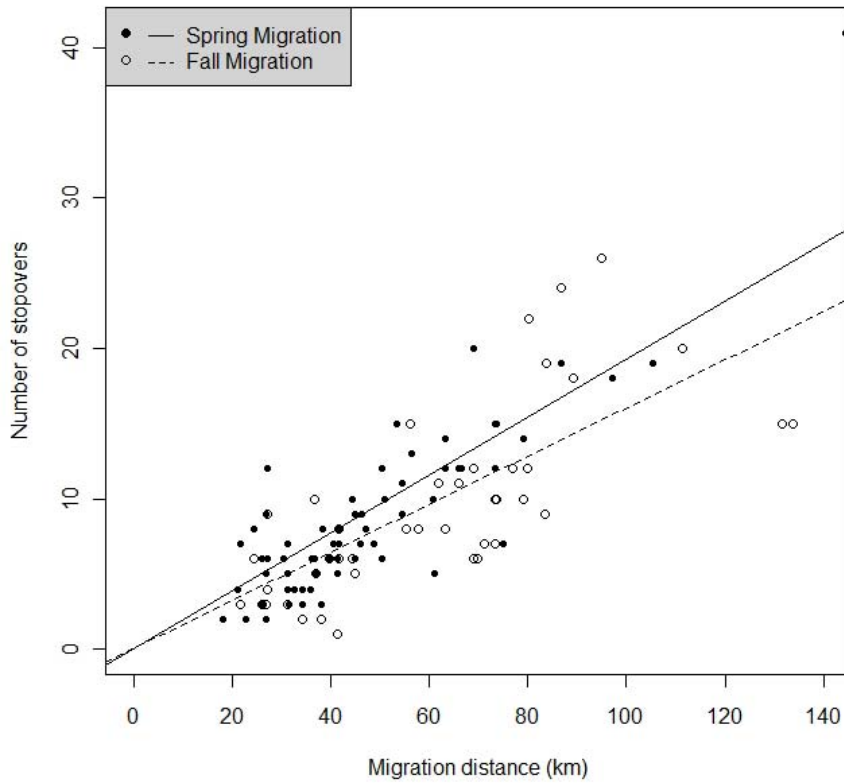
Fig. 3. Number of mule deer stopovers plotted as a function of migration distance (km) during spring ($n = 65$) and fall ($n = 44$) migrations. Fitted lines are based on regression analysis for spring ($B_1 = 0.19$) and fall ($B_1 = 0.15$).
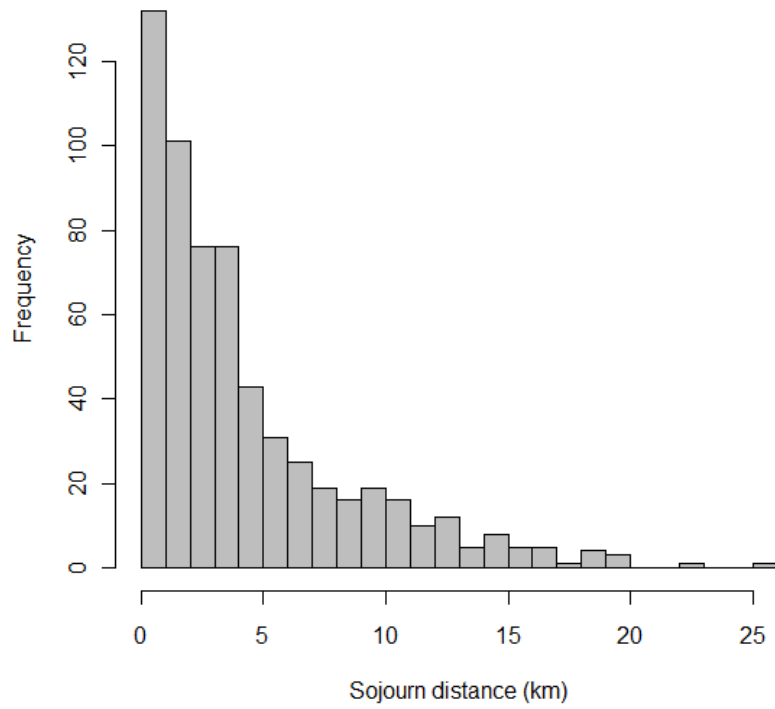
Fig. 4. Histogram of sojourn distances ($n = 609$) measured from mule deer migration routes ($n = 66$) that had at least 6 stopovers.
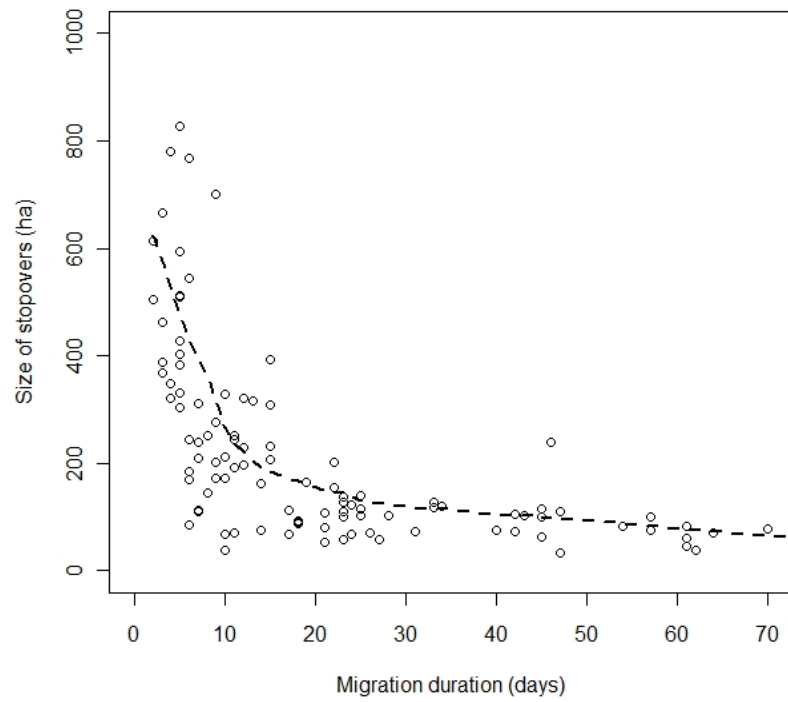
Fig. 5. Relationship between the temporal length (days) of migration and the average size (ha) of stopover size within a migration route. Dashed line represents smoothed scatterplot line.
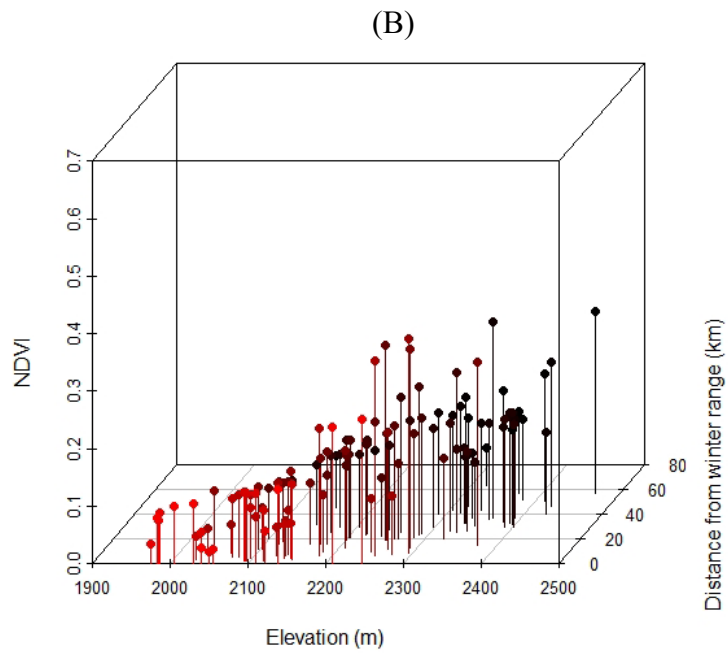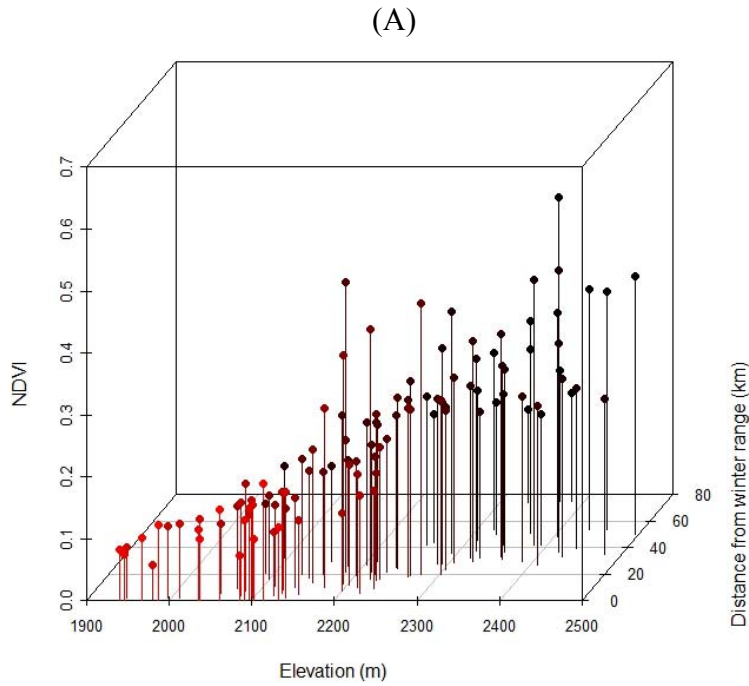
Fig. 6. Mean NDVI value of stopovers from 15 mule deer, plotted as a function of mean

elevation (m) and distance from winter range (km) in 2005 (A) and 2006 (B).

CHAPTER FIVE

Discussion

The current level of natural gas and wind energy development across the Intermountain West is unprecedented (BLM 2005). As energy development becomes more widespread, wildlife and development conflicts will be inevitable. Recognizing how mule deer respond to different development strategies and traffic regimes can improve the ability of agencies and industry to estimate cumulative effects and quantify indirect habitat losses associated with different development scenarios (e.g., clustered development; Theobald et al. 1997). My results from Chapter 2 showed that mule deer avoided all types of natural gas well pads (i.e., active drilling, producing with liquids gathering system [LGS], producing without LGS) but tended to select areas farther from well pads with higher levels of traffic. Indirect habitat loss associated with active drilling pads was much higher than that at producing well pads; however, active drill pads were used for directional drilling, which is generally a short-term (6 months-2 yr) disturbance, whereas producing well pads represent a long-term (i.e., decades) disturbance. The reduced behavioral response of mule deer to low traffic levels suggests that impacts of gas development on mule deer may be reduced by technology and planning that minimizes the number of well pads (e.g., directional drilling) and the level of traffic associated with them (e.g., LGS). When condensate products were collected in LGS pipelines rather than being stored at well pads and removed via tanker trucks, traffic was reduced from 7 to 3 vehicles per day and associated indirect habitat loss to mule deer was reduced by 38-63%. The LGS appeared to be an effective means for reducing long-term (i.e., production phase) indirect habitat loss to wintering mule

deer, whereas drilling in crucial winter range created a short-term (i.e., drilling phase) increase in deer disturbance and indirect habitat loss (Sawyer et al. 2009*a*).

Given that > 90% of mule deer in western Wyoming are migratory (Sawyer et al. 2005), providing managers with the tools to identify and prioritize migration routes is needed to ensure that development plans are designed to minimize potential impacts to mule deer populations. Recent advances in GPS technology have improved our ability to study ungulate movements; however, identifying migration routes from discrete location data has remained problematic. Specifically, it is difficult to account for the uncertainty in animal movements between known locations (Horne et al. 2007, Patterson et al. 2007) and it has been unclear how to combine migration routes of individuals to make population-level inference. For example, the method of connecting the dots between GPS locations of marked animals (Sawyer et al. 2005, Berger et al. 2006) has improved our understanding of ungulate migrations, including the timing, distances traveled, and movement rates. Yet, such approaches ignore the uncertainty in both the locations and the trajectory of movement, thereby producing a line with no associated area or error (e.g., is the route 10 m or 1 km wide?) and no means of combining individual routes to characterize the population-level route network.

The quantitative framework I developed in Chapter 3 accounts for these shortcomings. My results demonstrate how the Brownian bridge movement model (BBMM; Horne et al. 2007) can be used to estimate relative amounts of use along a migration route. Additionally, this study provides a method for combining multiple individual routes into a population-level estimate of migration corridors. The ability to quantify and visualize population-level migration routes represents a significant advancement in terms of studying migration routes and incorporating

them into land-use planning. My results also show that the BBMM may be a useful tool for distinguishing between areas associated with different behavioral states (e.g., stopover or movement), as others have done with non-linear curve-fitting (Johnson et al. 2002), state-space models (Forester et al. 2007), Markov models (Franke et al. 2004), random walks (Morales et al. 2004), and first-passage-time approaches (Bailey and Thompson 2006). Interestingly, mule deer migration routes were characterized by a series of stopover sites, where deer spent most of their time and moved slowly, connected by movement corridors through which they moved quickly. These findings suggest management strategies that differentiate between stopover sites and movement corridors may be warranted, and because some migration routes were used by more mule deer than others, proportional level of use may provide a reasonable metric by which routes can be prioritized for conservation. In short, delineation of the population-level migration route provides a basis for conserving all routes or prioritizing which routes should be targeted for conservation or management.

A key finding from Chapter 3 was the fact that mule deer used stopover sites along their migration routes (Sawyer et al. 2009*b*). The study and conservation of stopover habitat has become a clear goal of agencies and non-governmental organizations tasked with sustaining migratory bird populations (Moore 2000, Mehlman et al. 2005). The protection of stopover sites is an effective conservation strategy in large part because many birds follow very similar or identical migration routes between years and return to known stopover sites year after year (Alerstam et al. 2006). In contrast, the winter ranges of migratory ungulates are often afforded some level of protection, but their migration routes are rarely considered in management or land-use plans. Recent studies have identified where ungulate migration routes occur and emphasized

the conservation value of narrow bottleneck regions believed to be vulnerable to anthropogenic disturbance (Sawyer et al. 2005, Berger et al. 2006, 2008). Yet, despite the global attention that migratory ungulate conservation has received (Berger 2004, Thirgood et al. 2004, Berger et al. 2008, Bolger et al. 2008, Harris et al. 2009), stopover ecology and its potential conservation benefits have yet to be considered. My results from Chapter 4 suggest the benefits of stopover ecology are not limited to avian taxa. Rather, stopovers likely play a key role in the altitudinal migrations of mule deer and other temperate ungulates that complete long-distance migrations along traditional routes. Mule deer utilized a series of stopover sites along their seasonal migrations routes, which they appeared to use year after year. Deer spent 95% of their migration time in stopovers, and the number of stopovers increased linearly with migration distance. Stopovers had higher forage quality compared to the movement corridors that connected them and their forage quality improved as elevation and distance from winter range increased. Assuming that the general strategy of migratory ungulates is to follow the most nutritious vegetation in order to maximize energy intake during the growing season (Albon and Langvatn 1992, Fryxell et al. 2004, Holdo et al. 2009), my findings suggest that stopover use may be a key behavioral mechanism that allows migratory ungulates to exploit nutritional gradients associated with altitudinal migrations. The protection of stopover sites has provided an effective conservation strategy for birds (Mehlman et al. 2005) and, given their importance to mule deer, my results suggest stopover protection may also benefit migratory ungulate populations, particularly in areas where migration routes overlap with anthropogenic disturbances.

<div align="center">Literature Cited</div>

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