

Identifying and prioritizing ungulate migration routes for landscape-level conservation

HALL SAWYER,^{1,5} MATTHEW J. KAUFFMAN,² RYAN M. NIELSON,³ AND JON S. HORNE⁴

¹Western Ecosystems Technology, 2003 Central Avenue, Cheyenne, Wyoming 82001 USA, and Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, Wyoming 82071 USA

²United States Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, Wyoming 82071 USA

³Western Ecosystems Technology, 2003 Central Avenue, Cheyenne, Wyoming 82001 USA

⁴University of Idaho, Department of Fish and Wildlife, Moscow, Idaho 83844 USA

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 vs. 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, USA, where 2000 gas wells and 1609 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 words: Brownian bridge movement model (BBMM); global positioning system (GPS); migration; movement corridors; mule deer, *Odocoileus hemionus*; natural gas development cf. migration routes; stopover site; utilization distribution (UD); Wyoming, USA.

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 (BLM [Bureau of Land Management] 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 vs. 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, USA, 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).

Manuscript received 3 November 2008; revised 2 April 2009; accepted 28 April 2009. Corresponding Editor: J. J. Millsaugh.

⁵ E-mail: hsawyer@west-inc.com

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, Sweaner 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 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

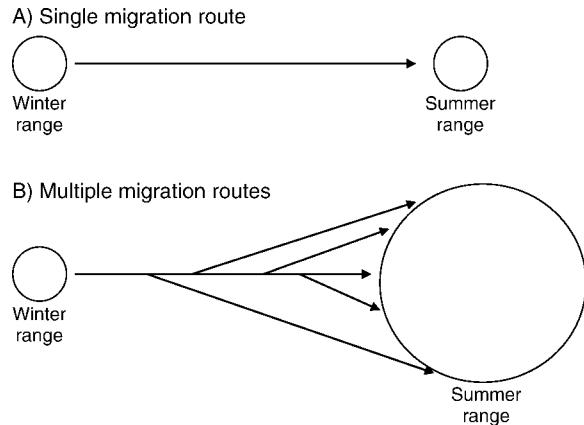


FIG. 1. Conceptual model illustrating (A) a scenario where one distinct migration route occurs between two relatively small seasonal ranges and (B) a scenario where the migration route from a small winter range splinters into multiple routes in order to access a larger summer range.

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 1093-km² 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 (*Sarcobatus vermiculatus*), Utah juniper (*Juniperus*

osteosperma), and other shrub species (*Purshia tridentata*, *Prunus virginiana*, *Amelanchier alnifolia*, *Chrysothamnus* sp., *Cercocarpus* sp.). Elevations range from 1920 m to 2530 m. The ARPA supports ~2000–3000 mule deer and contains two distinct winter ranges, locally known as Dad (40 km²) and Wild Horse (141 km²). At the time of study (2005–2006), there were approximately ~116 natural gas wells in the ARPA, but an additional 2000 wells and 1609 km of pipeline and access roads were approved for construction in 2007 (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 (Wyoming, USA) 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, Mesa, Arizona, USA) programmed to collect one location every 2.5 h. Between 10 February 2005 and 15 November 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 (Appendices A and B).

Estimating migration routes

We used the Brownian bridge movement model (BBMM; Horne et al. 2007) to estimate a utilization distribution (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 Scmieglow 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 Oriò et al. 2003). We used a grid-cell size of 50 × 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 that our locations were only 2.5 h apart, and Horne et al. (2007) successfully applied the BBMM to migratory data collected at 7-h 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; see Supplement).

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 ($n = 20$ deer), we summed the cell values of all their UD's and then re-scaled their cumulative cell values to sum to 1, 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 UD's 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 UD's 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, so that the top 25% were classified as high use and the lowest 25% were low use. Estimating population-level UD's for separate seasons (spring and fall) was not necessary because individual deer showed fidelity to their migration routes (Appendix C).

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 Mills-paugh 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

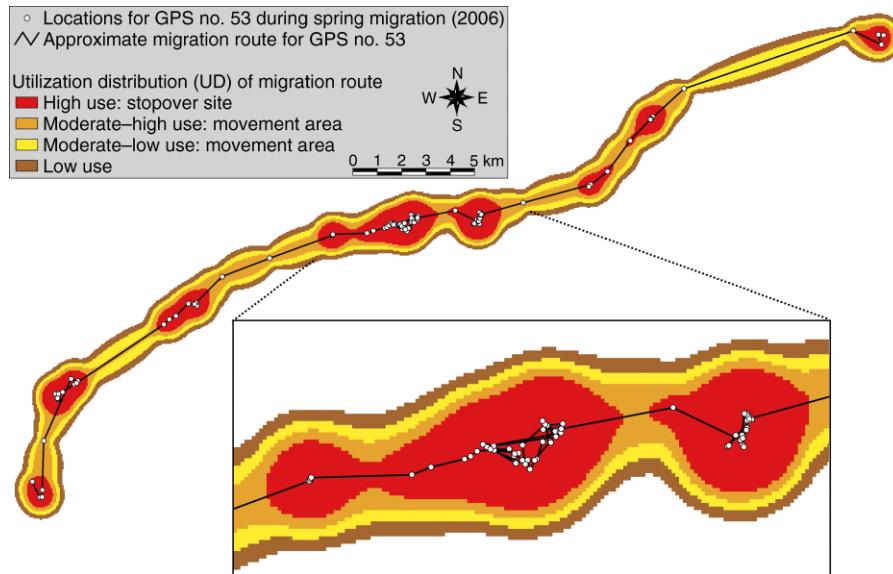


FIG. 2. Utilization distribution (UD) estimated for individual mule deer (*Odocoileus hemionus*; GPS no. 53) during spring migration of 2006. High-use areas correspond with stopover sites, where the deer spent most time (i.e., tortuous movements). Moderate-use areas located between stopover sites correspond with migratory segments through which mule deer moved quickly in one direction. Low-use areas reflect the uncertainty in the entire route.

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 make a 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-h) intervals and attempted to differentiate between two coarse-scale behavioral states (i.e., stopover vs. 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 50×50 -m cell of the estimated population-level route. Thus, cell values ranged from 1 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% criterion 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 utilization distributions (UDs) for 80 migration routes (56 spring, 24 fall) collected from 44 radio-collared deer. The Brownian motion variance (BMV) of individual migration routes in the Dad and Wild Horse winter ranges (Wyoming, USA) was $3310 \pm 685 \text{ m}^2$ (mean \pm SE; $n = 19$ migrations) and $2679 \pm 280 \text{ m}^2$ ($n = 61$ migrations), 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 and 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 km²) was nearly 3 times larger than that for the Dad population (258 km²). Proportional use of route segments within the population-level migration routes had a range of 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 and 4B) for the Wild Horse and Dad populations covered ~20% (146 km²) and 53% (137 km²) 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).

DISCUSSION

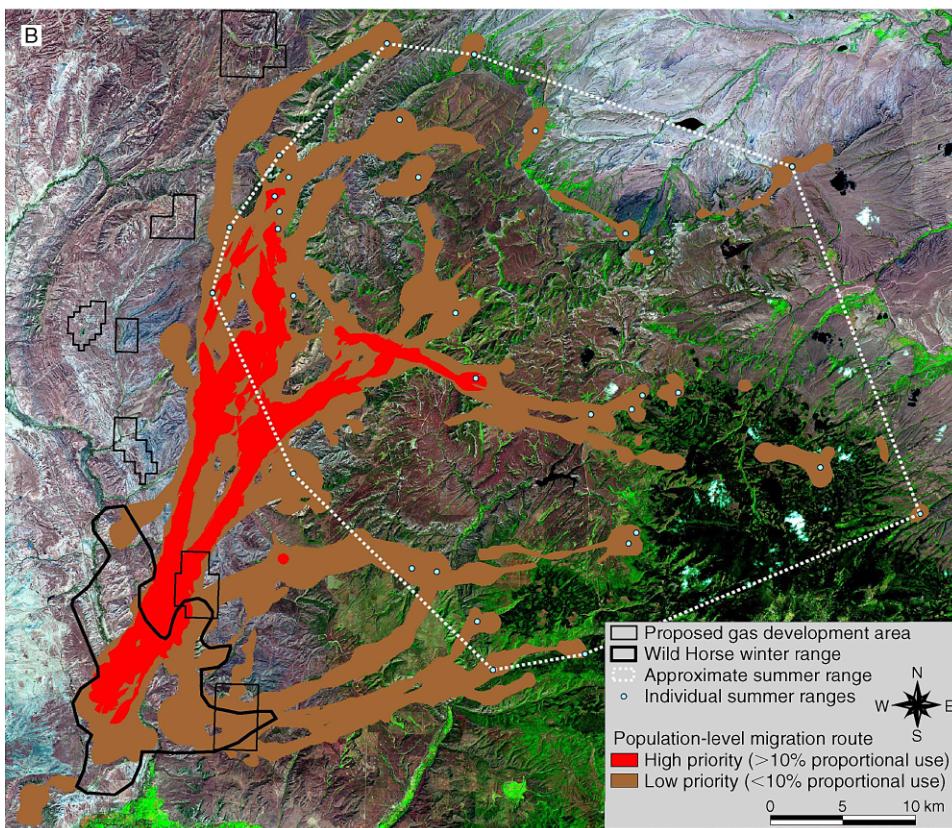
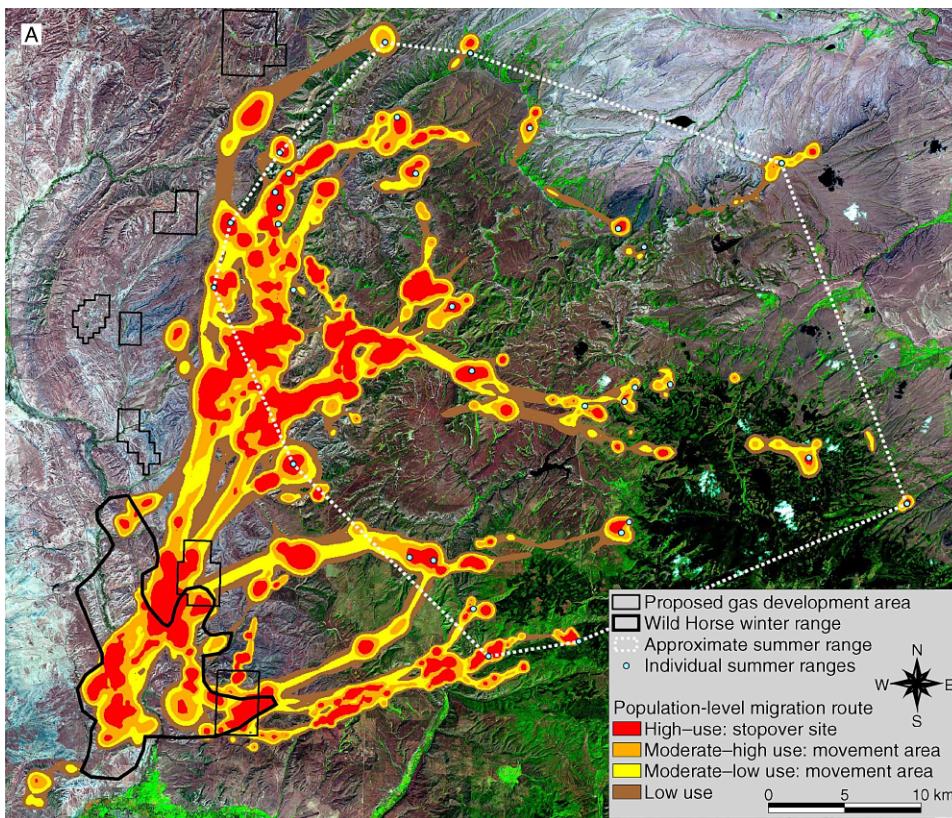
Our application of the Brownian-bridge movement model (BBMM) was successful at identifying population-level migration routes for conservation planning. Mule deer from two subpopulations in our study area used a network of migration routes, rather than one distinct route per subpopulation. We suggest 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 subpopulations 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

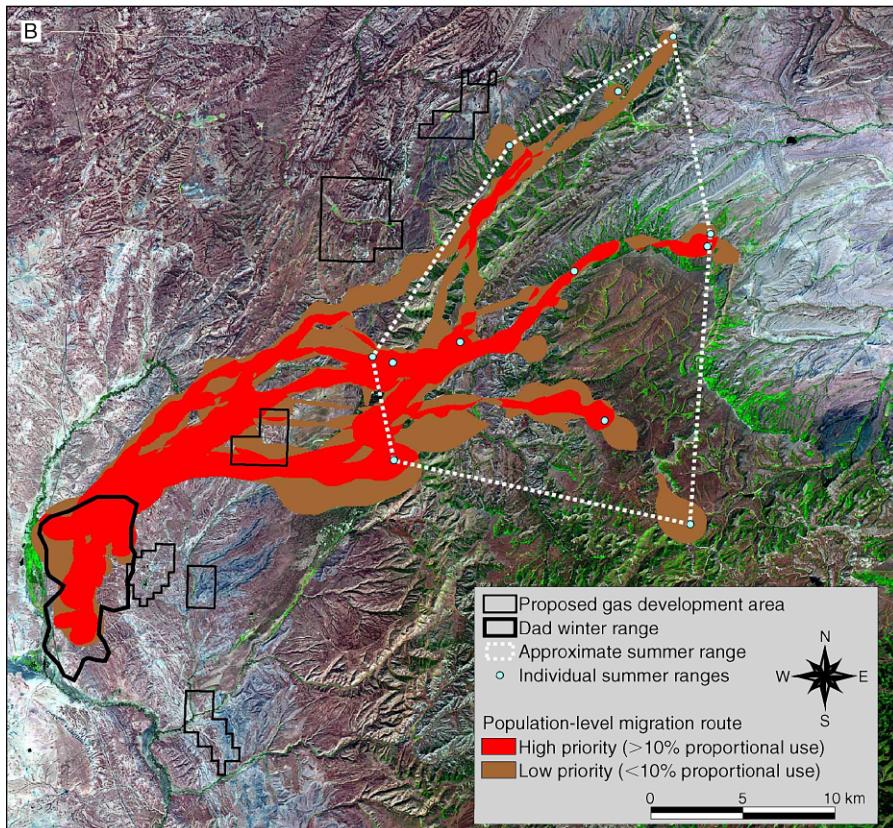
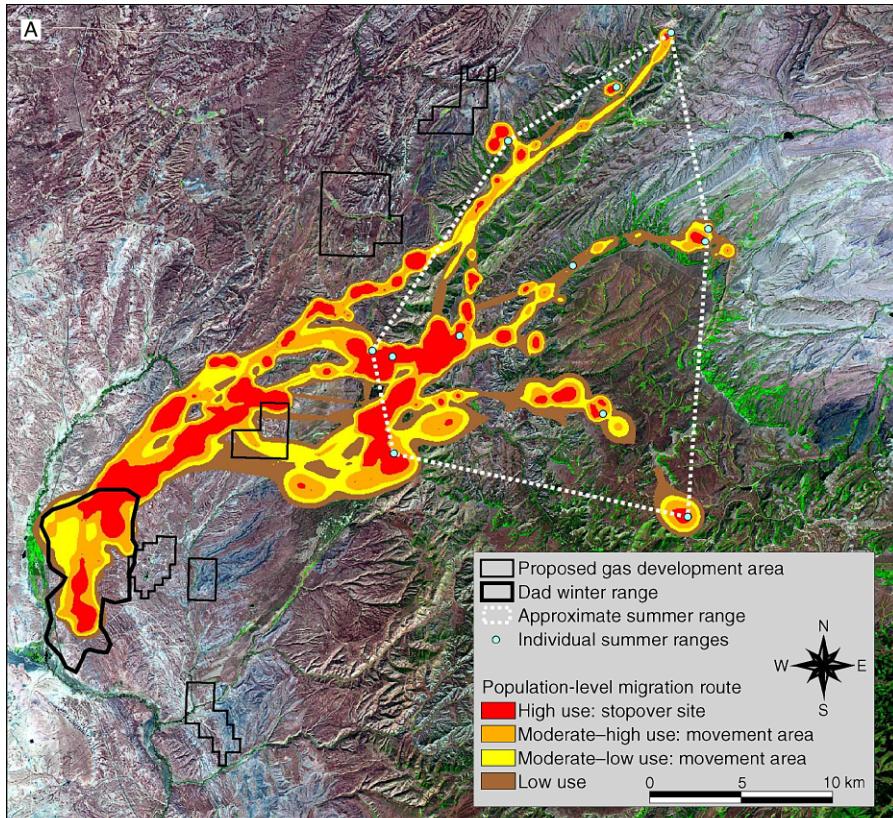
a population-level migration route provides a basis from which all migration routes may either be protected, or from which a prioritization process may be initiated to identify which routes should be targeted for conservation or management.

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 nonlinear 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 Hedenström 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 vs. 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

→
FIG. 3. (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. (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.





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 energy 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 migra-

tion 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 2000 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 1000-km² 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 vs. 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 (H. Sawyer and M. J. 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 (Wyoming, USA) experiencing unprecedented levels of energy development.

ACKNOWLEDGMENTS

We thank F. Blomquist, B. Rudd, T. Woolley, J. Rector, and D. Applegate for providing logistical support. J. Pope and W. Livingston (Leading Edge Aviation, Lewiston, Idaho, USA) provided helicopter capture services. J. Amos (SkyTruth, Sheperdstown, West Virginia, USA) provided satellite imagery. Comments from N. Korfanta, S. Buskirk, D. Doak, G. Hayward, and B. Newmark improved the manuscript. We appreciate the thorough reviews and editorial assistance provided by two anonymous reviewers. This work was supported by the Wildlife Heritage Foundation of Wyoming, the Wyoming Landscape Conservation Initiative, the Wyoming

←

FIG. 4. Mule deer migration in the Dad winter range, southwest Wyoming, USA. (A) Estimated population-level migration route and relative amounts of use for mule deer. High-use areas represent stopover sites presumably used as foraging and resting habitat, whereas moderate-use areas represent movement corridors. (B) Prioritization of migration routes based on proportion of sampled mule deer population (>10%) using routes segments across the Dad population-level migration route.

Wildlife and Natural Resource Trust, and grants provided to Western Ecosystems Technology, Inc., from Anadarko Petroleum Company, Warren Resources, and the Bureau of Land Management. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

- Albon, S. D., T. H. Clutton-Brock, and F. E. Guinness. 1987. Early development and population dynamics in red deer. II. Density-independent effects and cohort variation. *Journal of Animal Ecology* 56:69–81.
- Alerstam, T. 2001. Detours in bird migration. *Journal of Theoretical Biology* 209:319–331.
- Alerstam, T., and A. Hedenström. 1998. The development of bird migration theory. *Journal of Avian Biology* 29:343–369.
- Bailey, H., and P. Thompson. 2006. Quantitative analysis of bottlenose dolphin movement patterns and their relationship with foraging. *Journal of Applied Ecology* 75:456–465.
- Baker, R. R. 1978. *The evolutionary ecology of animal migration*. Holmes and Meier, New York, New York, USA.
- Barraquand, F., and S. Benhamou. 2008. Animal movements in heterogenous landscapes: identifying profitable places and homogenous movement bouts. *Ecology* 89:3336–3348.
- Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. *Conservation Biology* 18:320–331.
- Berger, J., S. L. Cain, and K. M. Berger. 2006. Connecting the dots: an invariant migration corridor links the Holocene to the present. *Biology Letters* 22:528–531.
- Bergman, C. M., J. A. Schaefer, and S. N. Luttich. 2000. Caribou movement as a correlated random walk. *Oecologia* 123:364–374.
- BLM [Bureau of Land Management]. 2005. Oil and gas activity on public lands in the United States and Wyoming. USDI-BLM, Wyoming State Office, Cheyenne, Wyoming, USA.
- BLM [Bureau of Land Management]. 2006. Final Environmental Impact Statement, Atlantic Rim Natural Gas Field Development Project. Bureau of Land Management, Rawlins Field Office, Rawlins, Wyoming, USA.
- Bolger, D. T., W. D. Newmark, T. A. Morrison, and D. F. Doak. 2008. The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters* 11:63–77.
- Buskirk, S. W., and J. J. Millsaugh. 2006. Metrics for studies of resource selection. *Journal of Wildlife Management* 70:358–366.
- Cameron, R. D., W. T. Smith, R. G. White, and B. Griffith. 2005. Central Arctic caribou and petroleum development: distributional, nutritional, and reproductive implications. *Arctic* 58:1–9.
- Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer–autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monographs* 155:1–61.
- Di Oriò, A. P., R. Callas, and R. J. Schaefer. 2003. Performance of two GPS telemetry collars under different habitat conditions. *Wildlife Society Bulletin* 31:372–379.
- Dyer, S. J., J. P. O'Neill, S. M. Wasel, and S. Boutin. 2001. Avoidance of industrial development by woodland caribou. *Journal of Wildlife Management* 65:531–542.
- Forester, J. D., A. R. Ives, M. G. Turner, D. P. Anderson, D. Fortin, H. L. Beyer, D. W. Smith, and M. S. Boyce. 2007. State-space models link elk movement patterns to landscape characteristics in Yellowstone National Park. *Ecological Monographs* 77:285–299.
- Frair, J. L., E. H. Merrill, H. L. Beyer, and J. M. Morales. 2008. Thresholds in landscape connectivity and mortality risks in response to growing road networks. *Journal of Applied Ecology* 45:1504–1513.
- Frair, J. L., E. H. Merrill, D. R. Visscher, D. Fortin, H. L. Beyer, and J. M. Morales. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landscape Ecology* 20:273–287.
- Franke, A., T. Caelli, and R. J. Hudson. 2004. Analysis of movements and behavior of caribou (*Rangifer tarandus*) using hidden Markov models. *Ecological Modelling* 173:259–270.
- Fryxell, J. M., J. Greever, and A. R. E. Sinclair. 1988. Why are migratory ungulates so abundant? *American Naturalist* 131:781–798.
- Fryxell, J. M., and A. R. E. Sinclair. 1988. Causes and consequences of migration by large herbivores. *Trends in Ecology and Evolution* 3:237–241.
- Hebblewhite, M., and E. H. Merrill. 2007. Multiscale wolf predation risk for elk: Does migration reduce risk? *Oecologia* 152:377–387.
- Hedenström, A. 2003. Optimal migration strategies in animals that run: a range equation and its consequences. *Animal Behaviour* 66:631–636.
- Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movements using Brownian bridges. *Ecology* 88:2354–2363.
- Johnson, C. J., K. L. Parker, D. C. Heard, and M. P. Gillingham. 2002. Movement parameters of ungulates and scale-specific responses to the environment. *Journal of Animal Ecology* 71:225–235.
- Klassen, M., S. Bauer, J. Madsen, and H. Possingham. 2008. Optimal management of a goose flyway: migrant management at minimum cost. *Journal of Applied Ecology* 45:1446–1452.
- Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the West: a large-scale analysis of anthropogenic impacts. *Ecological Applications* 18:1119–1139.
- Lindström, A. 1990. The role of predation risk in stopover habitat selection in migrating bramblings, *Fringilla montifringilla*. *Behavioral Ecology* 1:102–106.
- McCullough, D. R. 1985. Long range movements of large terrestrial animals. *Contributions in Marine Science* 27(Supplement):444–465.
- Morales, J. M., D. T. Haydon, J. Frair, K. E. Holsinger, and J. M. Fryxell. 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* 85:2436–2445.
- Nellemann, C., I. Vistnes, P. Jordhøy, O. Strand, and A. Newton. 2003. Progressive impact on piecemeal infrastructure development on wild reindeer. *Biological Conservation* 113:307–317.
- Newton, I. 2008. *The migration ecology of birds*. Elsevier, San Diego, California, USA.
- Nielson, R. M., B. F. J. Manly, L. L. McDonald, H. Sawyer, and T. L. McDonald. 2009. Estimating habitat selection when GPS fix success is less than 100%. *Ecology* 90:2956–2962.
- Patterson, T. A., L. Thomas, C. Wilcox, O. Ovaskainen, and J. Matthiopoulos. 2007. State-space models of individual animal movement. *Trends in Ecology and Evolution* 23:87–94.
- Pomeroy, A. C., R. W. Butler, and R. C. Ydenberg. 2006. Experimental evidence that migrants adjust usage at stopover site to trade off food and danger. *Behavioral Ecology* 17:1041–1045.
- R Development Core Team. 2007. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Safer, D. J., and F. K. A. Schmiegelow. 2005. Movement pathways and habitat selection by woodland caribou during spring migration. *Rangifer* 16:143–154.
- Sawyer, H., F. Lindzey, and D. McWhirter. 2005. Mule deer and pronghorn migration in western Wyoming. *Wildlife Society Bulletin* 33:1266–1273.
- Sawyer, H., R. Nielson, F. Lindzey, and L. McDonald. 2006. Winter habitat selection of mule deer before and during

- development of a natural gas field. *Journal of Wildlife Management* 70:396–403.
- Short, H. L. 1981. Nutrition and metabolism. Pages 99–127 in O. C. Wallmo, editor. *Mule and black-tailed deer of North America*. University of Nebraska Press, Lincoln, Nebraska, USA.
- Singer, F. J., A. Harting, K. K. Symonds, and M. B. Coughenour. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. *Journal of Wildlife Management* 61:12–25.
- Sweanor, P. Y., and F. Sandegren. 1988. Migratory behavior of related moose. *Holarctic Ecology* 11:190–193.
- Thirgood, S., A. Mosser, S. Tham, G. Hopcraft, E. Mwangomo, T. Mlengeya, M. Kilewo, J. Fryxell, A. R. E. Sinclair, and M. Borner. 2004. Can parks protect migratory ungulates? The case of the Serengeti wildebeest. *Animal Conservation* 7:113–120.
- White, P. J., T. L. Davis, K. K. Barnowe-Meyer, R. L. Crabtree, and R. A. Garrott. 2007. Partial migration and philopatry of Yellowstone pronghorn. *Biological Conservation* 135:502–510.

APPENDIX A

Migratory GPS locations collected from a sample of 12 adult female mule deer captured in the Dad Winter Range located in the Atlantic Rim Project Area of southwest Wyoming, USA, February 2005–November 2006 (*Ecological Archives* A019-083-A1).

APPENDIX B

Migratory GPS locations collected from a sample of 32 adult female mule deer captured in the Wild Horse Winter Range located in the Atlantic Rim Project Area of southwest Wyoming, USA, February 2005–November 2006 (*Ecological Archives* A019-083-A2).

APPENDIX C

Approximate migration routes of mule deer that had at least one spring and one fall migration recorded (*Ecological Archives* A019-083-A3).

SUPPLEMENT

R source code for the Brownian bridge movement model (BBMM) that estimates a utilization distribution (UD) for a migration route of a GPS-collared mule deer, as depicted in Fig. 2 (*Ecological Archives* A019-083-S1).