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Methods, Tools, and Technologies

Estimating ungulate migration corridors from sparse movement data

Jennifer L. McKee[1] | **Julien Fattebert**[2,3] | **Ellen O. Aikens**[4,5] | **Jodi Berg**[6] | **Scott Bergen**[7] | **Eric K. Cole**[8] | **Holly E. Copeland**[1] | **Alyson B. Courtemanch**[9] | **Sarah Dewey**[10] | **Mark Hurley**[7] | **Blake Lowrey**[11] | **Jerod A. Merkle**[12] | **Arthur D. Middleton**[13] | **Tristan A. Nuñez**[14] | **Hall Sawyer**[15] | **Matthew J. Kauffman**[16]

[1]Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming, USA

[2]School of Life Sciences, University of KwaZulu-Natal, Durban, South Africa

[3]FatBear Wildlife Science Solutions, Bière, Switzerland

[4]School of Computing, University of Wyoming, Laramie, Wyoming, USA

[5]Haub School of Environment and Natural Resources, University of Wyoming, Laramie, Wyoming, USA

[6]Alta Science & Engineering, Inc., Moscow, Idaho, USA

[7]Idaho Department of Fish and Game, Boise, Idaho, USA

[8]National Elk Refuge, U.S. Fish and Wildlife Service, Jackson, Wyoming, USA

[9]Wyoming Game and Fish Department, Jackson, Wyoming, USA

[10]National Park Service, Grand Teton National Park, Moose, Wyoming, USA

[11]U.S. Geological Survey, Northern Rocky Mountain Science Center, Bozeman, Montana, USA

[12]Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming, USA

[13]Department of Environmental Science, Policy, and Management, University of California Berkeley, Berkeley, California, USA

[14]U.S. Geological Survey, Maine Cooperative Fish and Wildlife Research Unit, Department of Wildlife, Fisheries, and Conservation Biology, University of Maine, Orono, Maine, USA

[15]Western Ecosystems Technology Inc., Laramie, Wyoming, USA

[16]U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming, USA

Correspondence
Jennifer L. McKee
Email: jennylynnmckee@gmail.com

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Abstract

Many ungulates migrate between distinct summer and winter ranges, and identifying, mapping, and conserving these migration corridors have become a focus of local, regional, and global conservation efforts. Brownian bridge movement models (BBMMs) are commonly used to empirically identify these seasonal migration corridors; however, they require location data sampled at relatively frequent intervals to obtain a robust estimate of an animal's movement path. Fitting BBMMs to sparse location data violates the assumption of conditional random movement between successive locations, overestimating

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the area (and width) of a migration corridor when creating individual and population-level occurrence distributions and precluding the use of low-frequency, or sparse, data in mapping migration corridors. In an effort to expand the utility of BBMMs to include sparse GPS data, we propose an alternative approach to model migration corridors from sparse GPS data. We demonstrate this method using GPS data collected every 2 h from four mule deer (*Odocoileus hemionus*) and four elk (*Cervus canadensis*) herds within Wyoming and Idaho. First, we used BBMMs to estimate a baseline corridor for the 2-h data. We then subsampled the 2-h data to one location every 12 h (a proxy for sparse data) and fitted BBMMs to the 12-h data using a fixed motion variance (FMV) value, instead of estimating the Brownian motion variance empirically. A range of FMV values was tested to identify the value that best approximated the baseline migration corridor. FMV values within a species-specific range (mule deer: 400–1200 m^2; elk: 600–1600 m^2) successfully delineated migration corridors similar to the 2-h baseline corridors; overall, lower values delineated narrower corridors and higher values delineated wider corridors. Optimal FMV values of 800 m^2 (mule deer) and 1000 m^2 (elk) decreased the inflation of the 12-h corridors relative to the 2-h corridors from traditional BBMMs. This FMV approach thus enables using sparse movement data to approximate realistic migration corridor dimensions, providing an important alternative when movement data are collected infrequently. This approach greatly expands the number of datasets that can be used for migration corridor mapping—a useful tool for management and conservation across the globe.

KEYWORDS

Brownian bridge movement model, Brownian motion variance, *Cervus canadensis*, conditional random walk, corridor conservation, elk, GPS collars, migration corridor, mule deer, occurrence distribution, *Odocoileus hemionus*

INTRODUCTION

Large-scale movements between discrete seasonal ranges are common across taxa (Abraham et al., 2022). In particular, many ungulate populations migrate seasonally between distinct summer and winter ranges to take advantage of spatially and temporally variable food sources (Aikens et al., 2017; Middleton et al., 2018; Mysterud et al., 2017; Sawyer & Kauffman, 2011) and to avoid threats such as predators and deep snow (Fryxell et al., 1988; Hebblewhite & Merrill, 2007; Kauffman, Aikens, et al., 2021; Monteith et al., 2018; Ortega et al., 2024). Increasingly, these migrations are threatened by an expanding human footprint (Kennedy et al., 2019; Venter et al., 2016) and associated housing developments, roads, and energy projects (Aikens et al., 2022; Reinking et al., 2019; Sawyer et al., 2020). Rapid habitat degradation (Sawyer et al., 2020; Wyckoff et al., 2018) and widespread declines in ungulate populations (Berger, 2004) have made conserving migration corridors the recent focus of global conservation efforts to ensure the persistence of migratory populations and the many ecological processes associated with these wide-ranging movements (Berger, 2004; Kaczensky et al., 2011; Kauffman, Cagnacci, et al., 2021; Middleton et al., 2020; Msoffe et al., 2019; Nandintsetseg et al., 2019).

A critical aspect of these science-based conservation efforts has been using animal movement data to identify and map migration corridors and critical foraging habitats (Kauffman, Cagnacci, et al., 2021; Sawyer et al., 2009). With advances in biologging technology in recent decades (Kays et al., 2015; Nathan et al., 2022), animal movement is now typically sampled as a series of GPS locations that can be connected sequentially to form a path of the animal's movement. However, depending on the GPS sampling frequency, a simple line connecting two successive locations may not accurately reflect the actual path used by the animal. To account for the uncertainty in the movement path between GPS locations, practitioners often use Brownian bridge movement models (BBMMs). BBMMs estimate the expected movement path between each pair of successive GPS locations under the assumption of a conditional random walk. With no known priors of an animal's movement, continuous random motion, or Brownian motion, can be used to approximate the in situ path (Horne et al., 2007; Turchin, 1998). Though many animals move using memory (Merkle et al., 2019) or external cues (e.g., environmental [Aikens et al., 2020] or from conspecifics [Jesmer et al., 2018]), models incorporating random motion are still a robust method to estimate animal movement (Börger et al., 2008; Turchin, 1998). Essentially creating a random walk that is conditioned between two points, BBMMs estimate a possible path or "Brownian bridge" between the beginning and ending points of each pair of successive GPS locations. BBMMs thus provide an estimate of the animal's intensity of space use in the form of an occurrence distribution (OD) volume (Horne et al., 2007). Provided that several animals from the same migratory population are tracked (usually ≥20 individuals), combining the two-dimensional isopleths of the individual ODs (typically the 99% contour; Kauffman et al., 2020; Sawyer et al., 2009) allows the delineation of the corridor and its intensity of use at the population level (Sawyer et al., 2009), as well as stopover sites where animals forage en route to seasonal ranges (Sawyer & Kauffman, 2011).

An important feature of the BBMM is the Brownian motion variance (BMV; in square meters), a measure of uncertainty in the movement path between two successive GPS locations, which is estimated using maximum likelihood to find the value that best predicts the path between pairs of successive GPS locations, assuming a Brownian bridge (Horne et al., 2007). Sampling frequency, rate of movement, and path tortuosity of each animal affect the distance between successive GPS locations, influencing the BMV and, in turn, the uncertainty in the movement path (Horne et al., 2007; Merkle et al., 2023). This uncertainty violates the assumption of a conditional random walk, increasing the BMV and the width of the resulting OD (Merkle et al., 2023). When individual movements are sampled at relatively frequent intervals (≤7-h intervals), a BBMM can estimate an animal's movement path between each pair of sequential relocations with relative confidence (Horne et al., 2007). However, with infrequent, or sparse, GPS data (e.g., >7-h intervals), the uncertainty in the movement path can delineate individual- and population-level corridors that are greatly inflated. The wider corridors that result from using a traditional BBMM with sparse data often extend far beyond areas actually used by a given individual or herd. Though the wider corridors simply reflect the greater uncertainty in the movement path, they are less useful for mitigating wildlife-vehicle collisions or targeting problematic fences for removal and generally have less utility in advancing management or conservation, and in some cases, delay focused conservation efforts (Kauffman et al., 2020, 2024; Kauffman, Lowrey, Beck, et al., 2022a; Kauffman, Lowrey, Berg, et al., 2022b).

While advances in GPS technology continue to allow for increasingly fine-scale GPS data collected over relatively frequent intervals, sparse data are common in older datasets, studies that focus primarily on monitoring animal survival at the expense of fine-scale movement (Curtis & Du Toit, 2017; Jung et al., 2018; Latham et al., 2015; Lowrey, Devoe, et al., 2020), or in studies tracking smaller animals that require lighter collars with smaller batteries that collect location data less frequently to conserve battery life (Kays et al., 2015). In an effort to expand the utility of the BBMM to encompass sparse GPS data, we propose using a set BMV, or fixed motion variance (FMV) value when applying BBMMs to sparse GPS data. To demonstrate this FMV approach, we used 2-h GPS data from four migratory herds of mule deer (*Odocoileus hemionus*) and four migratory herds of elk (*Cervus canadensis*) in Wyoming and Idaho. The frequency of these GPS locations allowed us to subsample them to a single location every 12 h as a proxy for sparse data and evaluate the performance of the FMV approach compared with a traditional BBMM. Though older tracking datasets, limited by available technology, may sample GPS locations less frequently (e.g., ≥24 h), the subsampled 12-h dataset is a useful representative of datasets that are sparser than recommended for BBMM use. Although the traditional BBMM (Horne et al., 2007) continues to be the most widely used technique for delineating migration corridors with fine-scale GPS data, novel approaches (e.g., Continuous-Time Movement Modeling [CTMM]; Calabrese et al., 2016; Fleming et al., 2016) that accommodate the diversity of GPS datasets globally, including sparse and high-frequency data, will further support broad-scale efforts to delineate, map, and conserve ungulate migrations.

METHODS

Study area

We used GPS datasets from eight migratory ungulate populations: four mule deer and four elk herds tracked in western Wyoming and central and east-central Idaho between 2007 and 2019. GPS collars were deployed opportunistically on mule deer and elk while on their winter ranges, before the start of the spring migration period.

This sampling scheme allowed biologists the opportunity to collar animals using the full suite of migration pathways used by the population and make inferences about each herd's population-level migration corridors. In general, these herds winter at low elevations on a mix of public and private land and follow the spring green-up (Aikens et al., 2017) as they migrate to summer ranges at higher elevations. Their migratory routes, some more than 250 km long, navigate housing developments, wind energy and gas projects, and busy highways (Kauffman et al., 2020). Climate in this region is characterized by long, cold winters and warm summers, with temperatures spanning −30 to 40°C and mean annual precipitation ranging from 10 to 150 cm. Elevation ranges from 216 to 3859 m. In central Idaho, the Batholith ecoregion is typified by steep mountains and deep canyons (Horne et al., 2019). Ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) grow at low to mid-elevations, transitioning to Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and whitebark pine (*Pinus albicaulis*) forests at higher elevations. East-central Idaho is a topographically diverse region, with rugged mountain ranges interspersed by intermontane grass, shrublands, and low-elevation stands of lodgepole pine (*Pinus contorta*). Major plant communities in northwestern Wyoming include sagebrush-steppe dominated by sagebrush (*Artemisia* spp.) at low elevations, coniferous forest dominated by lodgepole pine and fir (*Abies* spp.), interspersed with aspen (*Populus tremuloides*) at mid-elevations, and herbaceous meadows at high elevations (Kauffman et al., 2020).

Data processing and analytical workflow

GPS collars from the four herds of mule deer (135 animals) and four herds of elk (156 animals) collected location data at 2-h intervals (Table 1). We manually identified the spring and fall migratory periods for each individual by selecting migration start and end dates, which coincided with changes in the net squared displacement (NSD) curve of each animal-year using the Migration Mapper application (Bunnefeld et al., 2011; Merkle et al., 2022). After selecting the migration dates for the eight herds, data processing and analyses were performed in four sequential steps. We first estimated migration corridors using a traditional BBMM fit to the original 2-h location data (see *Estimating traditional BBMM corridors with 2-h data*). The resulting output provided our baseline migration corridors, which we used to evaluate the FMV approach. Second, we subsampled the 2-h data to one location every 12 h (hereafter, 12-h data) as a proxy for sparse data and delineated migration corridors by fitting a traditional BBMM to the 12-h data to evaluate the effects of using BBMMs on sparse data (see *Estimating traditional BBMM corridors with 12-h data*). Third, we implemented the FMV approach on the subsampled data and iteratively delineated individual- and population-level migration corridors using a range of user-defined BMV values from 200 to 3000 m^2 in increments of 200 m^2 (see *Estimating FMV corridors with 12-h data*). Finally, we performed multiple comparative assessments of the population-level corridors that evaluated the degree of overlap between (1) the baseline corridor delineated from the 2-h data and the traditional BBMM corridors delineated from the 12-h data and (2) the baseline corridor delineated from the 2-h data and the FMV corridors delineated from the 12-h data (see *Assessing the performance of traditional BBMM and FMV corridors*). The details of each step are further described in the sections below.

Estimating traditional BBMM corridors with 2-h data

We first used traditional BBMM methods to estimate a baseline corridor using the 2-h GPS data from each of the

TABLE 1 Number of individuals tracked with GPS collars that collected data every 2 h (No. ind.), and number of spring and fall migration sequences (No. mig. seq.) from four mule deer and four elk populations in Wyoming and Idaho, USA, 2007–2019.

Species	Population	Region	Years sampled	No. ind.	No. mig. seq.
Mule deer	Atlantic Rim	South-Central Wyoming	2009–2019	45	177
	Clark Forks	North-West Wyoming	2016–2018	30	82
	Dubois	North-West Wyoming	2016–2018	38	103
	Tex Creek	East-Central Idaho	2007–2009	22	27
Elk	Cody	North-West Wyoming	2014–2016	28	96
	Jackson	North-West Wyoming	2007–2018	31	57
	Lowman	Central Idaho	2008–2009	49	86
	Northfork	Central Idaho	2009–2015	48	98

four elk and four mule deer herds. For each animal-year, we fit a BBMM to each sequence of GPS locations associated with spring and fall migration using the BBMM package (Nielson et al., 2013) in the R environment for statistical computing (R Core Team, 2019). We used a 100-m resolution and 12.5 h as the maximum time interval between successive locations when building Brownian bridges (i.e., we did not build Brownian bridges between successive locations with a time gap >12.5 h). Additionally, because sequences with large BMV estimates can greatly inflate the population-level corridor (Merkle et al., 2023), we censored sequences with a BMV ≥8000 m^2 (Appendix S1: Figure S1) to avoid introducing spurious errors into our baseline corridor delineations.

Next, we applied a three-step process to delineate the population-level corridor from GPS-collared individuals, modified from Sawyer et al. (2009). First, for each individual, we averaged the spring and fall migration ODs across all years to produce a single OD for each individual, which we rescaled to sum to 1. Second, we overlaid the 99% isopleths of all individual ODs and defined levels of the intensity of corridor use (hereafter, corridor use) based on the number of individuals using a given pixel on the landscape. These levels were defined as: low (≥1 collared individual), medium (10%–<20% of collared individuals), and high (≥20% of collared individuals) following Kauffman et al. (2020). Finally, for the stopover calculation, we averaged all individual ODs to produce a single population-level OD, rescaled to sum to 1. We then defined stopovers as the ≥90th percentile of the population level OD (i.e., where ≥10% of collared individuals stopped over).

Estimating traditional BBMM corridors with 12-h data

As a proxy for sparse GPS data, we subsampled the 2-h data to one location every 12 h, simulating a programmed GPS collar sampling scheme that collected two GPS locations per day: one location at ~00 h00 or 01 h00 Mountain Time and then another location at 12 h00 or 13 h00 Mountain Time (depending on the GPS collar). If one of the GPS locations was missing from the original 2-h data, it was subsequently also missing in the 12-h data. As with the 2-h data above, we used 12.5 h as the maximum time interval between successive locations when building Brownian bridges (i.e., we did not build Brownian bridges between successive locations with a time gap >12.5 h). We then fit a traditional BBMM to the 12-h data (using the BBMM package [Nielson et al., 2013]), with BMV estimated empirically, to assess the effect of violating the BBMM assumptions of a conditional random walk by fitting the model to sparse data. As we did for the baseline data (in *Estimating traditional BBMM corridors with 2-h data*), we applied the three-step procedure to delineate the population-level migration corridors.

Estimating FMV corridors with 12-h data

Using the 12-h data, we implemented the FMV approach to estimate population-level migration corridors. Rather than estimating the BMV for each migration sequence empirically as in the traditional BBMM, we provided a user-defined value of the motion variance ranging from 200 to 3000 m^2 in increments of 200 m^2. These values were within the first three quartiles of the distribution of BMV values estimated empirically when fitting traditional BBMMs to the 2-h data (median: 1755 m^2; Appendix S1: Figure S1) and are similar to the BMV values derived from other elk and mule deer with 2-h GPS data in the Western United States (Kauffman et al., 2020, 2024; Kauffman, Lowrey, Beck, et al., 2022a; Kauffman, Lowrey, Berg, et al., 2022b). As we did for the baseline data (in *Estimating traditional BBMM corridors with 2-h data*), we applied the three-step procedure to delineate the population-level migration corridors for each FMV value.

Assessing the performance of traditional BBMM and FMV corridors

Last, we evaluated the degree of overlap between the traditional BBMM corridors delineated with the 12-h (sparse) and the 2-h (baseline) data and also compared the FMV corridors delineated from the sparse data with the baseline corridor delineated from the 2-h data. These comparisons helped to highlight the issue of inflated corridors when using traditional BBMM methods with sparse data and evaluate the performance of the FMV approach. We compared the degree of overlap between the migration corridors delineated with baseline and sparse datasets using a traditional BBMM. Additionally, for each level of corridor use (low, medium, and high) and the stopover areas, we assessed how the FMV corridors and the traditional BBMM corridors with the 12-h data compared with the extent of the baseline corridor using two metrics. For both sets of comparisons, we calculated two different metrics: (1) "corridor area ratio" and (2) "overlap ratio." The corridor area ratio was defined as the ratio of the area (in square kilometers) of the corridor delineated from 12-h data (either using a traditional BBMM or FMV) to the area (in square kilometers) of the baseline corridor. The corridor area ratio is <1 when the corridor delineated from 12-h data is smaller than the baseline corridor, and >1 when the corridor delineated from 12-h data is larger compared with the baseline corridor. The corridor area ratio, however, does not indicate how much of the baseline corridor surface is covered by the corresponding corridor delineated from 12-h data. Therefore, we also calculated the overlap ratio, defined as the proportion of the baseline corridor that overlaps the corridor delineated from 12-h data (range: 0–1). The overlap ratio equals 1 when the corridor delineated from 12-h data perfectly matches the extent of the baseline corridor. We calculated these metrics for each of the FMV values that were tested (e.g., 200–3000 m^2 in increments of 200 m^2). We then identified the optimal FMV value that best matched the spatial characteristics of the baseline corridor, by maximizing the overlap of the baseline corridor by the FMV corridor (precision) while minimizing the area beyond the extent of the baseline corridor (accuracy). Then for mule deer and elk, separately, we calculated the overall optimal FMV value as the mean of these optimal FMV values across all levels of corridor use and stopover area.

RESULTS

Comparison of traditional BBMM corridors estimated with 2- and 12-h data

The BMV estimated empirically from BBMMs fitted to the 12-h data was more than twice (2.2 times higher) the BMV from BBMMs fitted to the 2-h (hereafter, baseline) data for mule deer, and nearly double (1.8 times higher) for elk. When fitting BBMMs to the baseline data, the empirically estimated BMV was 2453 ± 1855 m^2 (mean ± SD; range: 198–7935 m^2) for mule deer and 2114 ± 1548 m^2 (81–7998 m^2) for elk (Appendix S1: Figure S1). When fitting BBMMs to the 12-h data, BMV averaged 5392 ± 7071 m^2 (129–87,900 m^2) for mule deer and 3780 ± 4358 m^2 (33–29,722 m^2) for elk (Appendix S1: Figure S2).

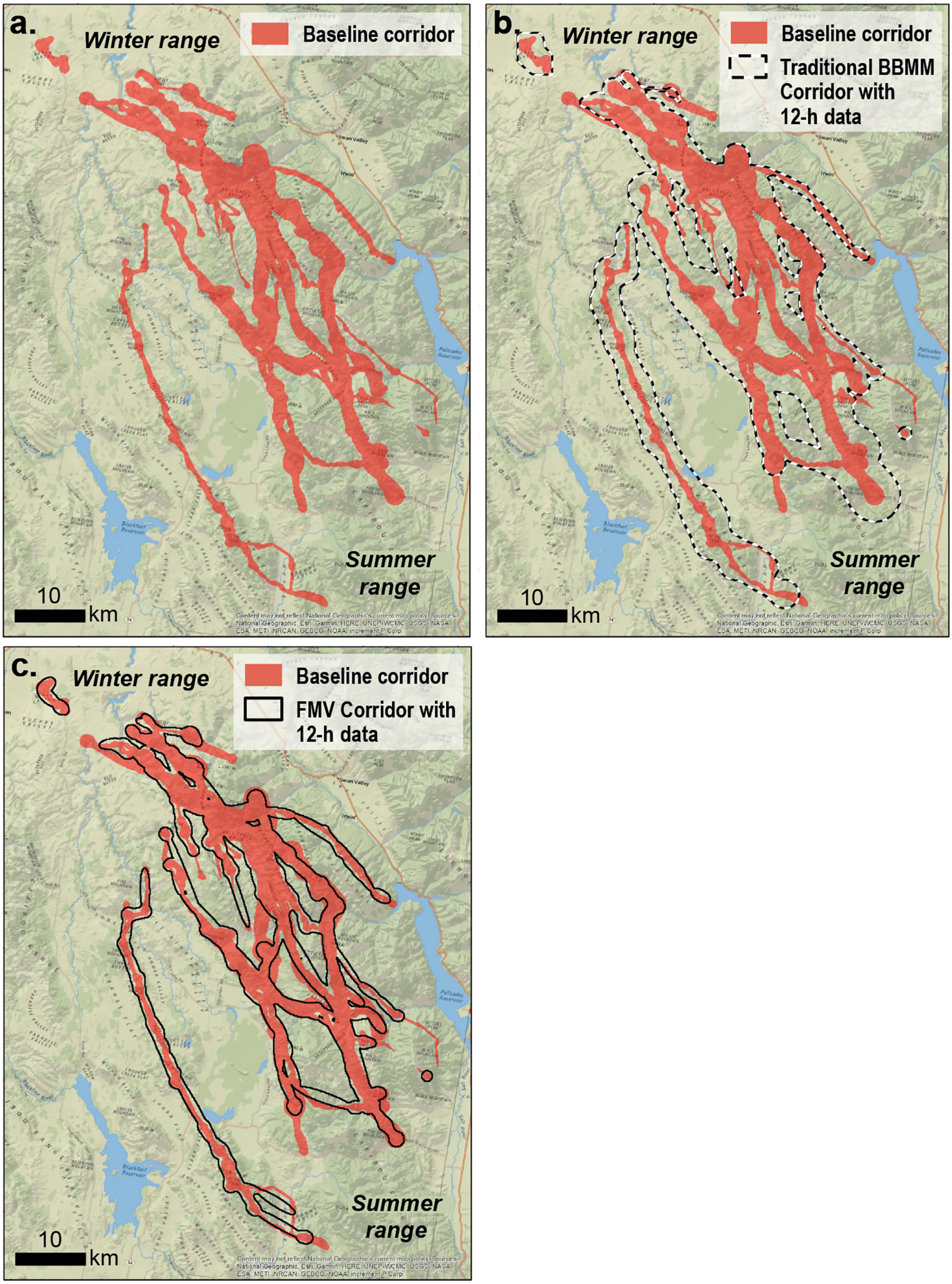
Corresponding with the large inflation in BMV, the BBMMs fitted to the subsampled 12-h data increased the area of the corridors and the stopovers compared with the corresponding baseline corridors and stopovers in all eight herds (Figures 1 and 2). Area inflation increased with increasing corridor use (low to high) in both species (Figure 2a,c). In mule deer, the 12-h/baseline corridor area ratio was, on average, 1.76 ± 1.21 SD (range: 1.50–1.97) for low-use corridors, 2.53 ± 1.34 (2.22–3.02) for medium-use corridors, 4.12 ± 2.12 (2.75–5.38) for high-use corridors, and 1.75 ± 1.24 (1.47–2.01) for stopovers (Figure 2a). In elk, the 12-h/baseline area ratio was 1.48 ± 1.19 (1.27–1.73) for low-use corridors, 1.68 ± 1.32 (1.36–2.04) for medium-use corridors, 2.07 ± 1.69 (1.46–2.81) for high-use corridors, and 1.47 ± 1.21 (1.26–1.77) for stopovers (Figure 2c). We found high overlap of the baseline corridors and stopovers across herds in both species: The average overlap area ratio of the baseline corridors by each corresponding corridor (low, medium, and high use) delineated from the 12-h data was 0.96 ± 0.05 (0.83–1.00) for corridors and 0.85 ± 0.05 (0.79–0.92) for stopovers in mule deer (Figure 2b), and 0.90 ± 0.15 (0.46–1.00) for corridors and 0.83 ± 0.03 (0.79–0.87) for stopovers in elk (Figure 2d).

Evaluating the FMV approach

Applying the FMV approach to the 12-h data minimized inflation of the corridor area, while providing high overlap with the baseline corridor (Figure 1c; Appendix S1: Figure S3). Small FMV values (e.g., 200 m^2) estimated smaller corridors than the baseline corridors, and overlapped only a fraction of the baseline corridors (Figures 3 and 4). Contrastingly, large FMV values (e.g., 3000 m^2) estimated larger corridors compared with the baseline corridors and had high overlap (Figures 3 and 4). The FMV corridors delineated from large FMV values were similar to those using a traditional BBMM with the 12-h data (Figure 1b; Appendix S1: Figure S3).

Compared with the baseline corridors, FMV corridors estimated from intermediate values of FMV had the best balance of accuracy and precision, minimizing corridor inflation while maximizing overlap with the baseline corridors. Across levels of corridor use, the optimal FMV value (mean of the optimal FMV values across all levels of corridor use and stopover area) for mule deer was 800 ± 300 m^2 (range: 400–1200 m^2; Table 2, Figure 3). For elk, the optimal FMV value was 1000 ± 300 m^2 (range: 600–1600 m^2; Table 2, Figure 4).

For the optimal value in mule deer (FMV = 800 m^2), the FMV/baseline corridor area ratio was 1.05 ± 1.12 (range: 0.96–1.22) for low-use corridors, 1.09 ± 1.17 (0.97–1.35) for medium-use corridors, 1.24 ± 1.32 (0.97–1.64) for high-use corridors, and 1.03 ± 1.13 (−0.94–1.21) for stopovers (Figure 5a). For the optimal value in elk (FMV = 1000 m^2), the FMV/baseline corridor area ratio was 1.09 ± 1.15 (0.89–1.26) for low-use corridors, 1.17 ± 1.29 (0.90–1.56) for medium-use corridors, 1.25 ± 1.54 (0.88–2.05) for high-use corridors, and 1.06 ± 1.14 (0.89–1.22) for stopovers (Figure 5c).



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We found high overlap of the baseline corridors and stopovers in both species: The average overlap area ratio of the baseline corridors by the corresponding FMV corridors was 0.82 ± 0.11 (0.62–0.98) for corridors and 0.80 ± 0.07 (0.74–0.90) for stopovers in mule deer and 0.80 ± 0.12 (0.51–0.90) for corridors

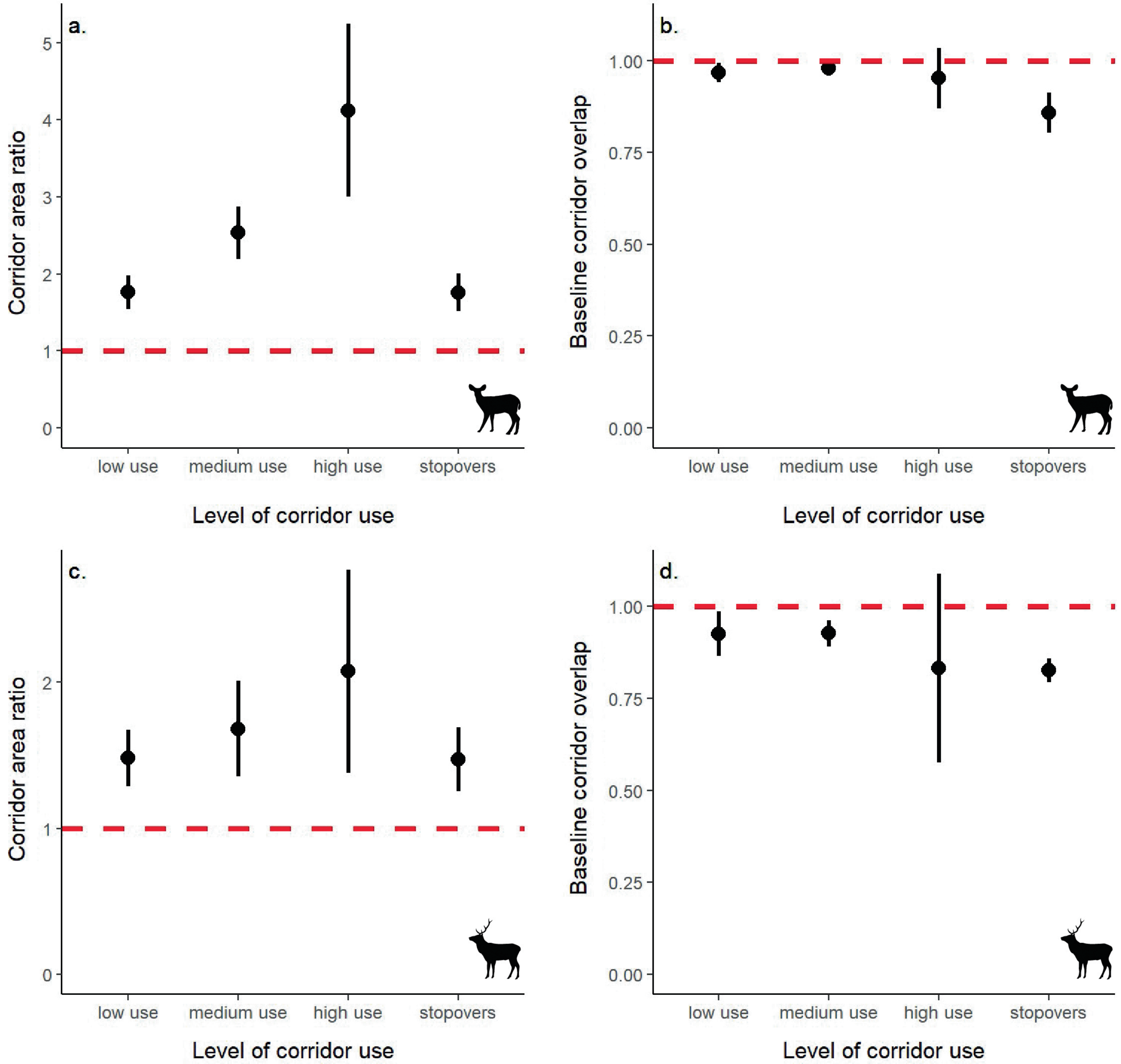
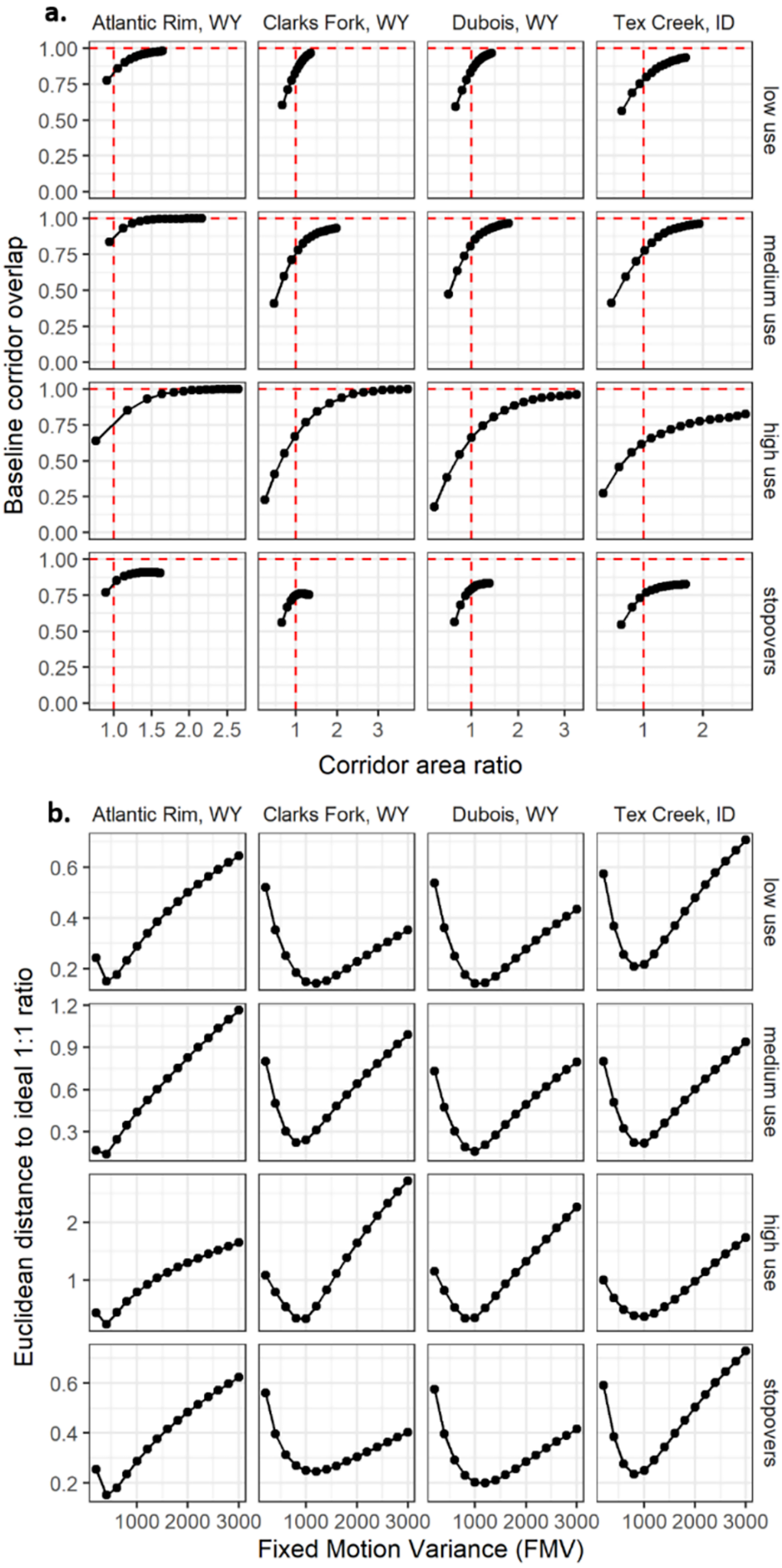


FIGURE 2 Inflation in area of the Brownian bridge movement model (BBMM) corridors fitted to the subsampled 12-h datasets compared with the corresponding BBMM fitted to the 2-h baseline datasets in (a) four populations of mule deer, and (c) four populations of elk in Wyoming and Idaho, USA, 2007–2019 (mean ± SD). Mean overlap of the 2-h baseline BBMM corridors by the corresponding BBMM corridors fitted to the 12-h datasets for each level of corridor use in (b) mule deer and (d) elk. The red dashed lines mark the ratio of 1, corresponding to a theoretical perfect match between the 12-h and the 2-h baseline BBMM corridors.

FIGURE 1 Effect of sparse data on corridor area estimation using a Brownian bridge movement model (BBMM), and the application of fixed motion variance (FMV) to constrain the corridor width on data from Tex Creek mule deer in Idaho. (a) A baseline corridor is delineated using a BBMM fitted to data collected every 2 h. (b) Fitting a BBMM to the dataset subsampled to 12-h intervals as a proxy for sparse movement datasets overestimated the corridor area by an average 76%. (c) Fitting a BBMM using FMV on subsampled 12-h data constrained the width of the corridor so that it overlaps the baseline corridor by 81%, without overestimating its surface area.



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and 0.77 ± 0.04 (0.72–0.81) for stopovers in elk (Figure 5b,d).

DISCUSSION

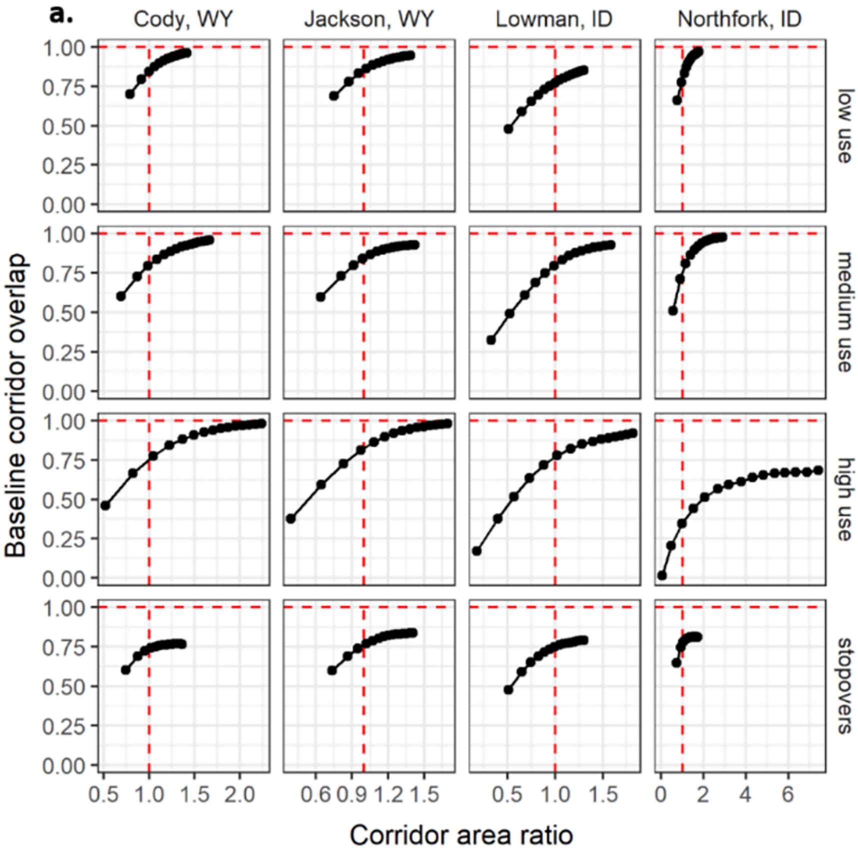
Recent efforts to conserve ungulate migrations rely on mapped migration corridors using GPS data. Because of the analytical limitations of using traditional BBMMs with location data collected infrequently, we aimed to provide an alternative method to delineate migration corridors from sparse GPS data. Here, we demonstrated an approach for modeling migration corridors from sparse data (locations collected every 12 h) using FMV values. With the 12-h data, the FMV method performed better compared with the traditional BBMM and empirically estimated BMV, which resulted in much wider migration corridors than corridors delineated using 2-h data and the traditional BBMM (Figure 1b). Our analyses suggest that the FMV method—essentially a modified BBMM—fit to the 12-h data closely approximated the spatial extent of the baseline corridors delineated from the GPS data collected every 2 h (Figure 1c). Thus, the FMV approach we describe here offers a practical option to delineate migration corridors using sparse location data by optimizing the trade-off between maximizing overlap of a migration corridor (precision) and minimizing inflation in the area of a corridor modeled from sparse data (accuracy; Figures 3 and 4).

Although BBMMs are the standard approach for mapping ungulate corridors (Kauffman et al., 2020, 2024; Kauffman, Lowrey, Beck, et al., 2022a; Kauffman, Lowrey, Berg, et al., 2022b), corridor width is strongly influenced by BMV and the GPS sampling frequency. For example, Merkle et al. (2023) subsampled a 10-min GPS dataset from mule deer to create 1-, 3-, 8-, and 12-h relocation datasets and delineated an individual migration corridor using the traditional BBMM methods for each of the 10-min and subsampled datasets. The resulting width of the corridor created with the 12-h data was nearly 90 times wider than the corridor created from the original 10-min data and 10 times wider than the corridor created from data subsampled to 1-h intervals. BBMMs, with empirically estimated BMV, can still generate migration corridors from sparse data, but they are largely inflated compared with the corridors delineated from more frequent sampling (Merkle et al., 2023; Figure 1b). These inflated corridors from sparse data do not allow the accurate identification of migratory habitats or stopover sites because they potentially encompass areas that the animals do not, or cannot, use (Horne et al., 2007) due to human development (e.g., Sawyer et al., 2020) or other geographic boundaries such as roads or water bodies. Thus, inflated corridors prevent accurately assessing barriers to animal movement or the impact of habitat disturbance on migration corridors (Gigliotti et al., 2022; Sawyer et al., 2009; Wyckoff et al., 2018), requiring an alternative method to inform the design of mitigation measures for anthropogenic activities (Beier, 2019).

The FMV method described here can be successfully applied to delineate migration corridors for sparse animal tracking datasets across the globe. Indeed, as global migration mapping efforts increase (Kauffman, Cagnacci, et al., 2021), an array of analytical methodologies will be needed to accommodate the varied datasets that may be available to inform regional conservation and management efforts. Our results showed interspecific variation of the optimal FMV value that best matched the baseline corridor for each population (800 m^2 for mule deer and 1000 m^2 for elk). An FMV of 800 m^2 in mule deer decreased the inflation of the 12-h corridor relative to the baseline corridor by 57%, while still overlapping the baseline corridor by 81%. In elk, using an FMV value of 1000 m^2 decreased the inflation of the 12-h corridors by 34%, while overlapping the baseline corridor by 79%. Wildlife managers and researchers can use FMV to identify and map corridors of sparse movement data that otherwise would estimate excessively wide corridors, or preclude the sparse dataset's use in conservation applications. Additionally, FMV grants managers the flexibility to apply the method to the entire herd's dataset, or only as necessary to specific individuals for which data were collected infrequently (e.g., older GPS collars or missing locations).

The FMV approach provides a useful alternative to traditional BBMMs to create migration corridors with

FIGURE 3 Fixed motion variance (FMV) diagnostic plots for four herds of mule deer in Wyoming and Idaho, USA, 2007–2019. (a) For different values of FMV between 200 and 3000 m^2, we calculated the ratio of the area (in square kilometers) of the 12-h corridor to the area (in square kilometers) of the baseline corridor: this "corridor area ratio" (*x*-axis) is <1 when the 12-h corridor was smaller in area than the 2-h baseline, and >1 when the 12-h corridor was inflated in area compared with the baseline. We also calculated the "overlap ratio" or baseline corridor overlap (*y*-axis), which approaches 1 when the corridor fit to the subsampled 12-h data covers most of the 2-h baseline corridor. (b) The optimal FMV value that best approximates the baseline corridor is the value that minimizes the corridor area ratio, while maximizing the overlap of the baseline by the 12-h corridor (i.e., the FMV value for which the 12-h corridor covers most of the baseline corridor, without being overly inflated).



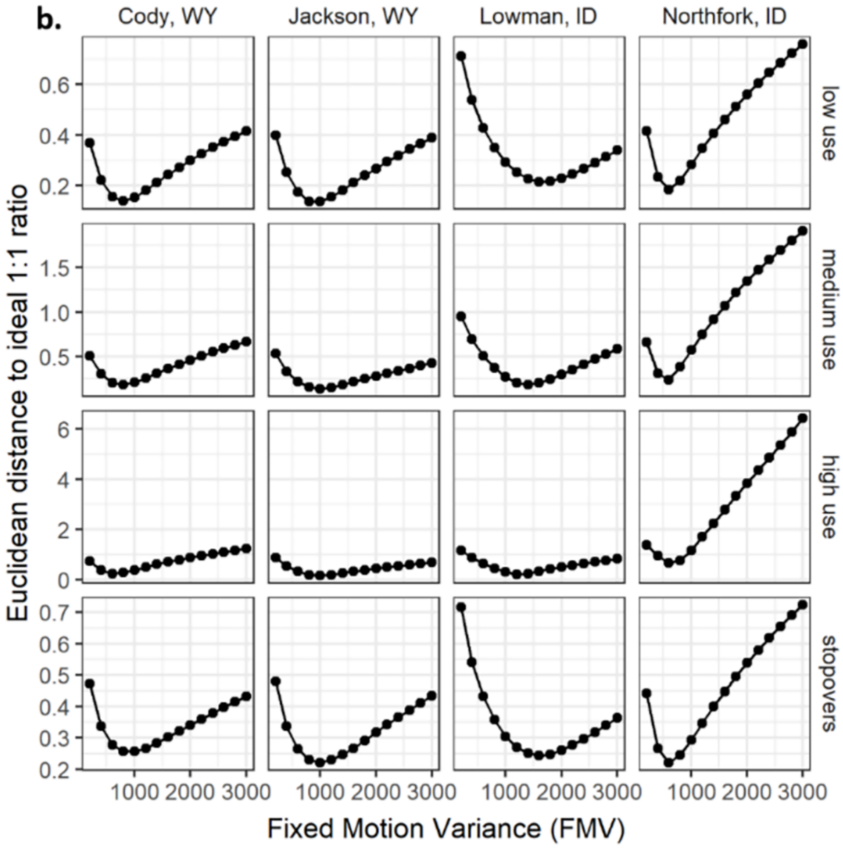


FIGURE 4 Legend on next page.

sparse data, provided some cautionary steps are taken. As with traditional BBMMs, the ultimate goal with the FMV method is to create a population-level migration corridor that is representative of the entire population's behavior (Sawyer et al., 2009). In practice, the sample size required to infer this population-level migration corridor is unknown and will vary by species and herd. In situations where all individuals follow a common migration route, a modest sample size of collared individuals (e.g., 20) may reasonably describe population-level patterns. However, in systems where topography (Kie et al., 2005), management histories (Lowrey, McWhirter, et al., 2020), sex (Rodgers et al., 2021), or individual personalities (Found et al., 2019) result in diverse migratory movements, a larger sample size may be needed. As with any sampling effort, practitioners should assess the population-level inference that can be made from the sampled members of the population when mapping migrations (Anderson, 2008). However, it is also important to acknowledge the empirical data that have been collected, even if limited, because migration corridors or seasonal ranges delineated from these data can still be highly informative for managers; this can be especially true for sensitive or highly threatened species, where important conservation decisions may hinge on limited empirical data. Initial migration corridors delineated from small sample sizes can also be updated as additional GPS data are collected. For example, population-level migration corridors for the Arizona San Francisco Peaks mule deer herd were originally delineated from only four individuals as part of a highway and wildlife-vehicle collision study (Dodd et al., 2012; Kauffman et al., 2020), but population-level corridors and the resulting maps were further refined with data from 20 more individuals (Kauffman, Lowrey, Beck, et al., 2022a).

When applying the FMV method to sparse datasets, FMV values within the range of interspecific variation we identified in our study (400–1200 m^2 for mule deer, and 600–1600 m^2 for elk) are useful starting points for an analysis. However, populations of elk and mule deer in other landscapes might show different movement rates or directionality (e.g., with regard to topography [Kie et al., 2005] or landscape structure [Lendrum et al., 2013]), so values of FMV outside the range we suggest could possibly delineate a more biologically realistic corridor, or one more appropriate for conservation planning (Beier, 2019). For other species whose migration ecology differs from mule deer or elk, or that do not show strong, directional movement—at least seasonally—a careful review of the model outputs may be warranted. In practice, a smaller FMV value would delineate a narrower corridor (Figure 1c) that might be too conservative and overlook important migration habitats at the margins, while a larger FMV value would delineate a wider corridor, potentially encompassing habitats that

TABLE 2 Optimal fixed motion variance (FMV) values (in square meters) for each level of corridor use for four mule deer and four elk herds in Wyoming and Idaho, USA, 2007–2019.

Species	Herd	Low use	Medium use	High use	Stopover
Mule deer	Atlantic Rim, WY	400	400	400	400
	Clarks Fork, WY	1200	800	1000	1200
	Dubois, WY	1000	1000	800	1200
	Tex Creek, ID	800	1000	1000	800
Elk	Cody, WY	800	800	600	1000
	Jackson, WY	1000	1000	1000	1000
	Lowman, ID	1600	1400	1200	1600
	Northfork, ID	600	600	600	600

Note: The optimal FMV value constrained the corridor width of the Brownian bridge movement model (BBMM) fitted to the 12-h data so that it overlaps with most of the baseline BBMM corridor, while minimizing the surface area inflation.

FIGURE 4 Fixed motion variance (FMV) diagnostic plots for four herds of elk in Wyoming and Idaho, USA, 2007–2019. (a) For different values of FMV between 200 and 3000 m^2, we calculated the ratio of the area (in square kilometers) of the 12-h corridor to the area (in square kilometers) of the baseline corridor: This "corridor area ratio" (*x*-axis) is <1 when the 12-h corridor was smaller in area than the 2-h baseline, and >1 when the 12-h corridor was inflated in area compared with the baseline. We also calculated the "overlap ratio" or baseline corridor overlap (*y*-axis), which approaches 1 when the corridor fitted to the subsampled 12-h data covers most of the 2-h baseline corridor. (b) The optimal FMV that best approximates the baseline corridor is the value that minimizes the corridor area ratio, while maximizing the overlap of the baseline by the 12-h corridor (i.e., the FMV value for which the 12-h corridor covers most of the baseline corridor, without being overly inflated).

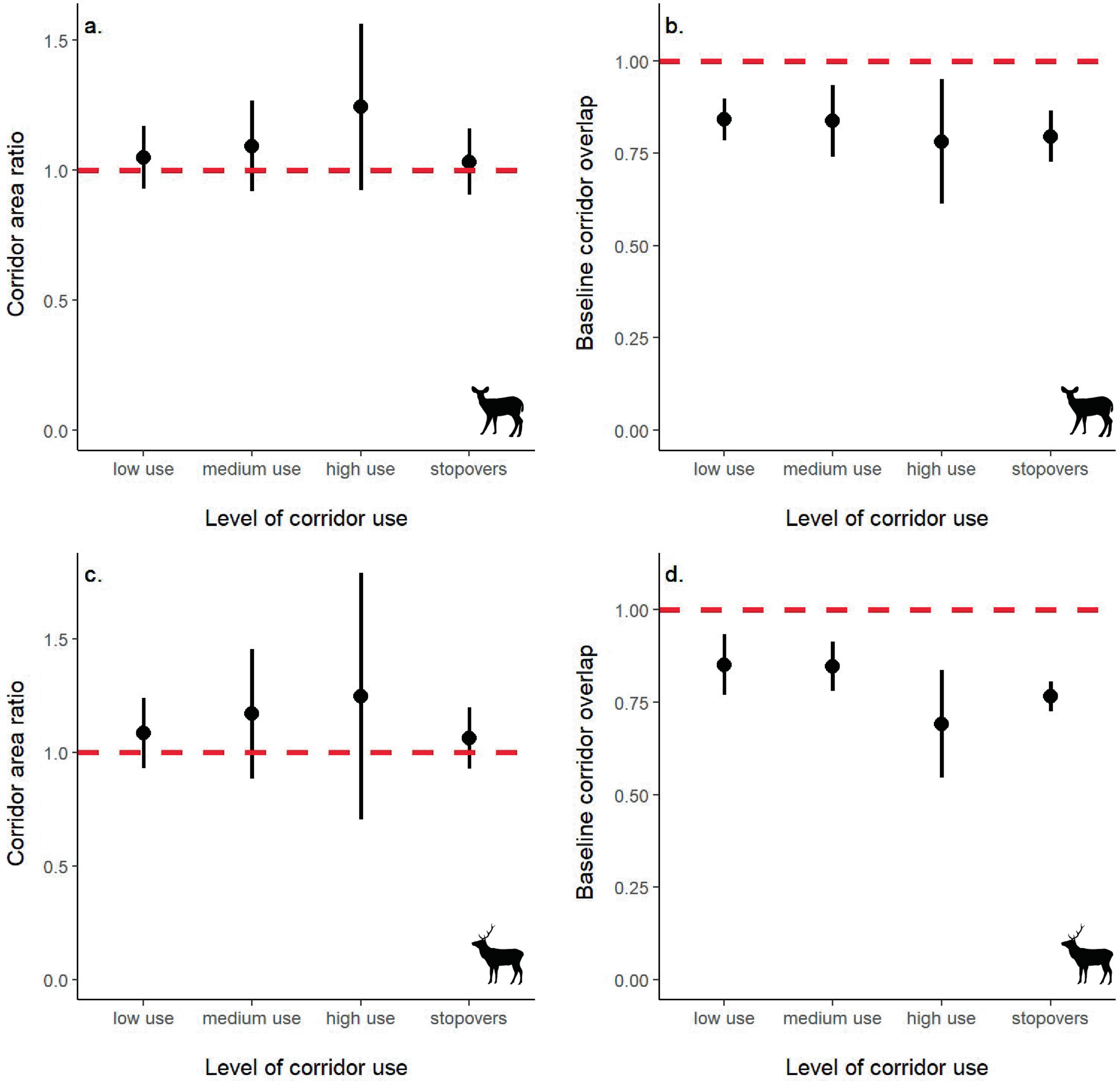


FIGURE 5 Inflation in area of the Brownian bridge movement model (BBMM) corridors fitted with an optimal fixed motion variance (FMV) value to the subsampled 12-h datasets compared with the corresponding BBMM fitted to the 2-h baseline datasets in (a) four mule deer herds and (c) four elk herds in Wyoming and Idaho, USA, 2007–2019 (mean ± SD). Mean overlap of the 2-h baseline BBMM corridors by the corresponding BBMM corridors fitted with an optimal FMV to the 12-h datasets for each level of corridor use in (b) mule deer and (d) elk. The red dashed lines mark the ratio of 1, corresponding to a theoretical perfect match between the 12-h and the 2-h baseline BBMM corridors. An optimal FMV value of 800 m^2 in mule deer decreased the inflation of the 12-h corridor relative to the 2-h baseline corridor (Figure 2) by 57%, while still overlapping the different levels of the 2-h baseline corridor by 81% on average. In elk, using an FMV value of 1000 m^2 decreased the inflation of the 12-h corridors (Figure 2) by 34%, while overlapping the 2-h baseline corridor by 79% on average.

ungulates are known to avoid, such as urban environments. It is also possible that excessively wide corridors may not be acceptable to other stakeholders where migrations traverse multiple-use landscapes. If feasible, it may also be worth validating the FMV values by repeating this analysis in other regions and with additional species. Practitioners may choose to test several FMV values through iteration and visual inspection with field personnel familiar with the herd's movements. When possible, consider incorporating local knowledge of the population and its migration path, which might influence the selection of the appropriate FMV value. Practitioners could also reconcile the delineation of the final corridor with their knowledge of the animals' behavioral response to local landscape features. In particular, paying special attention to the minimum corridor width required such that animal movement and corridor use is not impaired by disturbance (e.g., Sawyer et al., 2020), may be valuable. For situations where existing data are too sparse for delineating corridors with the proposed FMV method or traditional BBMM, other methods, like buffering the line by a set distance, may be more practical (Merkle et al., 2023). However, the line buffer method is limited in only delineating migration corridors; it does not identify stopovers along a migration corridor, which can be critical areas for ungulates to seek forage and replenish energetic reserves en route to seasonal ranges (Sawyer & Kauffman, 2011). To effectively delineate stopovers using sparse data, the FMV method provides practitioners with a robust alternative to the traditional BBMM.

CONCLUSION

Although BBMMs are currently the standard approach to delineate migration corridors from movement data, they estimate excessively wide corridors when used with sparse datasets. These wide corridors can be problematic for conservation efforts, particularly when traversing multiple-use landscapes with varied stakeholders. Providing alternative methods to delineate more realistic migration corridors can improve relevancy with all stakeholders and advance conservation. Here, we demonstrated that an alternative FMV method successfully used sparse data to approximate the dimensions of population-level migration corridors estimated from more frequent GPS data collected at 2-h intervals. FMV values within a species-specific range (mule deer: 400–1200 m^2; elk: 600–1600 m^2) successfully delineated migration corridors similar to the baseline corridors; overall, lower values delineated narrower corridors and higher values delineated wider corridors. FMV values of 800 m^2 (mule deer) and 1000 m^2 (elk) decreased the inflation of the 12-h corridors relative to the 2-h baseline corridors. The FMV approach enables practitioners to make use of sparse datasets to delineate migration corridors that otherwise would require using more frequent location data. The success of this approach enables leveraging the many existing sparse GPS datasets that may have been previously deemed unsuitable for movement modeling and corridor mapping. Thus, the FMV modification to a traditional BBMM expands the methodological tools available to accommodate the diversity of GPS datasets globally, which could lead to new corridor mapping and improve science-based conservation.

AUTHOR CONTRIBUTIONS

Julien Fattebert and Matthew J. Kauffman conceived the study. Jodi Berg, Eric K. Cole, Alyson B. Courtemanch, Sarah Dewey, Mark Hurley, Scott Bergen, Arthur D. Middleton, Matthew J. Kauffman, and Hall Sawyer contributed data. Ellen O. Aikens, Tristan A. Nuñez, Holly E. Copeland, and Jerod A. Merkle contributed to analysis. Jennifer L. McKee, Julien Fattebert, and Blake Lowrey wrote the initial manuscript drafts. All authors commented on and edited manuscript drafts.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (McKee et al., 2024) for analyses of the Atlantic Rim mule deer, Clarks Fork mule deer, Dubois mule deer, and Jackson elk herds in Wyoming are available from Dryad: https://doi.org/10.5061/dryad.15dv41p51. Data for analyses of the Cody elk in Wyoming are available upon request from Arthur D. Middleton (amiddleton@berkeley.edu) from University of California, Berkeley. Data for analyses of the Tex Creek mule deer, Lowman elk, and Northfork elk herds in Idaho are available upon request from Idaho Department of Fish and Game, Idaho Fish and Wildlife Information System, 600 S. Walnut Street, Boise, ID 83703 (idfgdatarequests@idfg.idaho.gov).

ORCID

Jennifer L. McKee https://orcid.org/0000-0002-9195-2650
Julien Fattebert https://orcid.org/0000-0001-5510-6804
Ellen O. Aikens https://orcid.org/0000-0003-0827-3006

Alyson B. Courtemanch https://orcid.org/0000-0001-7405-7657
Blake Lowrey https://orcid.org/0000-0002-4994-2117
Jerod A. Merkle https://orcid.org/0000-0003-0100-1833
Tristan A. Nuñez https://orcid.org/0000-0002-1776-1442

REFERENCES

Abraham, J. O., N. S. Upham, A. Damian-Serrano, and B. R. Jesmer. 2022. "Evolutionary Causes and Consequences of Ungulate Migration." *Nature Ecology & Evolution* 6: 998–1006.

Aikens, E. O., M. J. Kauffman, J. A. Merkle, S. P. H. Dwinnell, G. L. Fralick, and K. L. Monteith. 2017. "The Greenscape Shapes Surfing of Resource Waves in a Large Migratory Herbivore." *Ecology Letters* 20: 741–750.

Aikens, E. O., A. Mysterud, J. A. Merkle, F. Cagnacci, I. M. Rivrud, M. Hebblewhite, M. A. Hurley, et al. 2020. "Wave-Like Patterns of Plant Phenology Determine Ungulate Movement Tactics." *Current Biology* 30: 3444–3449.e4.

Aikens, E. O., T. B. Wyckoff, H. Sawyer, and M. J. Kauffman. 2022. "Industrial Energy Development Decouples Ungulate Migration from the Green Wave." *Nature Ecology & Evolution* 6: 1733–41.

Anderson, D. R. 2008. *Model Based Inference in the Life Sciences: A Primer on Evidence*. London: Springer New York.

Beier, P. 2019. "A Rule of Thumb for Widths of Conservation Corridors." *Conservation Biology* 33: 976–78.

Berger, J. 2004. "The Last Mile: How to Sustain Long-Distance Migration in Mammals." *Conservation Biology* 18: 320–331.

Börger, L., B. D. Dalziel, and J. M. Fryxell. 2008. "Are There General Mechanisms of Animal Home Range Behaviour? A Review and Prospects for Future Research." *Ecology Letters* 11: 637–650.

Bunnefeld, N., L. Börger, B. Van Moorter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. "A Model-Driven Approach to Quantify Migration Patterns: Individual, Regional and Yearly Differences." *Journal of Animal Ecology* 80: 466–476.

Calabrese, J. M., C. H. Fleming, and E. Gurarie. 2016. "ctmm: An R Package for Analyzing Animal Relocation Data as a Continuous-Time Stochastic Process." *Methods in Ecology and Evolution* 7: 1124–32.

Curtis, A. M., and J. T. Du Toit. 2017. "Efficacy of Travel Management Areas for Reducing Disturbance to Mule Deer during Hunting Seasons." *Wildlife Society Bulletin* 41: 309–312.

Dodd, N. L., J. W. Gagnon, S. Sprague, S. Boe, and R. E. Schweinsburg. 2012. *Wildlife Accident Reduction Study and Monitoring: Arizona State Route 64* 118. Phoenix, AZ: Department of Transportation Research Center.

Fleming, C. H., W. F. Fagan, T. Mueller, K. A. Olson, P. Leimgruber, and J. M. Calabrese. 2016. "Estimating Where and How Animals Travel: An Optimal Framework for Path Reconstruction from Autocorrelated Tracking Data." *Ecology* 97: 576–582.

Found, R., and C. C. St. Clair. 2019. "Influences of Personality on Ungulate Migration and Management." *Frontiers in Ecology and Evolution* 7: 438.

Fryxell, J. M., J. Greever, and A. R. E. Sinclair. 1988. "Why Are Migratory Ungulates So Abundant?" *The American Naturalist* 131: 781–798.

Gigliotti, L. C., W. Xu, G. R. Zuckerman, M. P. Atwood, E. K. Cole, A. Courtemanch, S. Dewey, et al. 2022. "Wildlife Migrations Highlight Importance of Both Private Lands and Protected Areas in the Greater Yellowstone Ecosystem." *Biological Conservation* 275: 109752.

Hebblewhite, M., and E. H. Merrill. 2007. "Multiscale Wolf Predation Risk for Elk: Does Migration Reduce Risk?" *Oecologia* 152: 377–387.

Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. "Analyzing Animal Movements Using Brownian Bridges." *Ecology* 88: 2354–63.

Horne, J. S., M. A. Hurley, C. G. White, and J. Rachael. 2019. "Effects of Wolf Pack Size and Winter Conditions on Elk Mortality." *Journal of Wildlife Management* 83: 1103–16.

Jesmer, B. R., J. A. Merkle, J. R. Goheen, E. O. Aikens, J. L. Beck, A. B. Courtemanch, M. A. Hurley, et al. 2018. "Is Ungulate Migration Culturally Transmitted? Evidence of Social Learning from Translocated Animals." *Science* 361: 1023–25.

Jung, T. S., T. M. Hegel, T. W. Bentzen, K. Egli, L. Jessup, M. Kienzler, K. Kuba, et al. 2018. "Accuracy and Performance of Low-Feature GPS Collars Deployed on Bison *Bison bison* and Caribou *Rangifer tarandus*." *Wildlife Biology* 2018: 1–11.

Kaczensky, P., R. Kuehn, B. Lhagvasuren, S. Pietsch, W. Yang, and C. Walzer. 2011. "Connectivity of the Asiatic Wild Ass Population in the Mongolian Gobi." *Biological Conservation* 144: 920–29.

Kauffman, M., B. Lowrey, C. Beaupre, S. Bergen, S. Bergh, K. Blecha, S. Bundick, et al. 2024. "Ungulate Migrations of the Western United States, Volume 4." U.S. Geological Survey Scientific Investigations Report 2024–5006: 1–86.

Kauffman, M., B. Lowrey, J. Beck, J. Berg, S. Bergen, J. Berger, J. W. Cain, III, et al. 2022a. "Ungulate Migrations of the Western United States, Volume 2." U.S. Geological Survey Scientific Investigations Report 2022–5008: 1–160. https://doi.org/10.3133/sir20225008

Kauffman, M., B. Lowrey, J. Berg, S. Bergen, D. Brimeyer, P. Burke, T. Cufaude, et al. 2022b. "Ungulate Migrations of the Western United States, Volume 3." U.S. Geological Survey Scientific Investigations Report 2022–5088: 1–114. https://doi.org/10.3133/sir20225088

Kauffman, M. J., E. O. Aikens, S. Esmaeili, P. Kaczensky, A. Middleton, K. L. Monteith, T. A. Morrison, T. Mueller, H. Sawyer, and J. R. Goheen. 2021. "Causes, Consequences, and Conservation of Ungulate Migration." *Annual Review of Ecology, Evolution, and Systematics* 52: 453–478.

Kauffman, M. J., F. Cagnacci, S. Chamaillé-Jammes, M. Hebblewhite, J. G. C. Hopcraft, J. A. Merkle, T. Mueller, et al. 2021. "Mapping Out a Future for Ungulate Migrations." *Science* 372: 566–69.

Kauffman, M. J., H. E. Copeland, J. Berg, S. Bergen, E. K. Cole, M. Cuzzocreo, S. Dewey, et al. 2020. *"Ungulate Migrations of the Western United States*, Volume 1." U.S. Geological Survey Scientific Investigations Report 2020–5101: 1–119. https://doi.org/10.3133/sir20205101

Kays, R., M. C. Crofoot, W. Jetz, and M. Wikelski. 2015. "Terrestrial Animal Tracking as an Eye on Life and Planet." *Science* 348: aaa2478.

Kennedy, C. M., J. R. Oakleaf, D. M. Theobald, S. Baruch-Mordo, and J. Kiesecker. 2019. “Managing the Middle: A Shift in Conservation Priorities Based on the Global Human Modification Gradient.” *Global Change Biology* 25: 811–826.

Kie, J. G., A. A. Ager, and R. T. Bowyer. 2005. “Landscape-Level Movements of North American Elk (*Cervus elaphus*): Effects of Habitat Patch Structure and Topography.” *Landscape Ecology* 20: 289–300.

Latham, A. D. M., M. C. Latham, D. P. Anderson, J. Cruz, D. Herries, and M. Hebblewhite. 2015. “The GPS Craze: Six Questions to Address before Deciding to Deploy GPS Technology on Wildlife.” *New Zealand Journal of Ecology* 39: 143–152.

Lendrum, P. E., C. R. Anderson, K. L. Monteith, J. A. Jenks, and R. T. Bowyer. 2013. “Migrating Mule Deer: Effects of Anthropogenically Altered Landscapes.” *PLoS One* 8: e64548.

Lowrey, B., J. Devoe, K. M. Proffitt, and R. A. Garrott. 2020. “Hiding without Cover? Defining Elk Security in a Beetle-Killed Forest.” *Journal of Wildlife Management* 84: 138–149.

Lowrey, B., D. E. McWhirter, K. M. Proffitt, K. L. Monteith, A. B. Courtemanch, P. J. White, J. T. Paterson, S. R. Dewey, and R. A. Garrott. 2020. “Individual Variation Creates Diverse Migratory Portfolios in Native Populations of a Mountain Ungulate.” *Ecological Applications* 30: e2106.

McKee, J. L., J. Fattebert, E. O. Aikens, J. Berg, S. Bergen, E. K. Cole, H. E. Copeland, et al. 2024. “Data From: Estimating Ungulate Migration Corridors from Sparse Movement Data [Dataset].” Dryad. https://doi.org/10.5061/dryad.15dv41p51.

Merkle, J. A., J. Gage, H. Sawyer, B. Lowrey, and M. J. Kauffman. 2022. “Migration Mapper: Identifying Movement Corridors and Seasonal Ranges for Large Mammal Conservation.” *Methods in Ecology and Evolution* 13: 2397–2403.

Merkle, J. A., B. Lowrey, C. F. Wallace, L. E. Hall, L. Wilde, M. J. Kauffman, and H. Sawyer. 2023. “Conserving Habitat for Migratory Ungulates: How Wide Is a Migration Corridor?” *Journal of Applied Ecology* 60: 1763–70.

Merkle, J. A., H. Sawyer, K. L. Monteith, S. P. H. Dwinnell, G. L. Fralick, and M. J. Kauffman. 2019. “Spatial Memory Shapes Migration and Its Benefits: Evidence from a Large Herbivore.” *Ecology Letters* 22: 1797–1805.

Middleton, A. D., J. A. Merkle, D. E. McWhirter, J. G. Cook, R. C. Cook, P. J. White, and M. J. Kauffman. 2018. “Green-Wave Surfing Increases Fat Gain in a Migratory Ungulate.” *Oikos* 127: 1060–68.

Middleton, A. D., H. Sawyer, J. A. Merkle, M. J. Kauffman, E. K. Cole, S. R. Dewey, J. A. Gude, et al. 2020. “Conserving Transboundary Wildlife Migrations: Recent Insights from the Greater Yellowstone Ecosystem.” *Frontiers in Ecology and the Environment* 18: 83–91.

Monteith, K. L., M. M. Hayes, M. J. Kauffman, H. E. Copeland, and H. Sawyer. 2018. “Functional Attributes of Ungulate Migration: Landscape Features Facilitate Movement and Access to Forage.” *Ecological Applications* 28: 2153–64.

Msoffe, F. U., J. O. Ogutu, M. Y. Said, and C. Shem. 2019. “Wildebeest Migration in East Africa: Status, Threats and Conservation Measures.” bioRxiv.

Mysterud, A., B. K. Vike, E. L. Meisingset, and I. M. Rivrud. 2017. “The Role of Landscape Characteristics for Forage Maturation and Nutritional Benefits of Migration in Red Deer.” *Ecology and Evolution* 7: 4448–55.

Nandintsetseg, D., C. Bracis, K. A. Olson, K. Böhning-Gaese, J. M. Calabrese, B. Chimeddorj, W. F. Fagan, et al. 2019. “Challenges in the Conservation of Wide-Ranging Nomadic Species.” *Journal of Applied Ecology* 56: 1916–26.

Nathan, R., C. T. Monk, R. Arlinghaus, T. Adam, J. Alós, M. Assaf, H. Baktoft, et al. 2022. “Big-Data Approaches Lead to an Increased Understanding of the Ecology of Animal Movement.” *Science* 375: eabg1780.

Nielson, R. M., H. Sawyer, and T. L. McDonald. 2013. “BBMM: Brownian Bridge Movement Model.” R Package Version 3.0. https://CRAN.R-project.org/package=BBMM.

Ortega, A. C., J. A. Merkle, H. Sawyer, K. L. Monteith, P. Lionberger, M. Valdez, and M. J. Kauffman. 2024. “A Test of the Frost Wave Hypothesis in a Temperate Ungulate.” *Ecology* 105: e4238.

R Core Team. 2019. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/.

Reinking, A. K., K. T. Smith, T. W. Mong, M. J. Read, and J. L. Beck. 2019. “Across Scales, Pronghorn Select Sagebrush, Avoid Fences, and Show Negative Responses to Anthropogenic Features in Winter.” *Ecosphere* 10: e02722.

Rodgers, P. A., H. Sawyer, T. W. Mong, S. Stephens, and M. J. Kauffman. 2021. “Sex-Specific Migratory Behaviors in a Temperate Ungulate.” *Ecosphere* 12: e03424.

Sawyer, H., and M. J. Kauffman. 2011. “Stopover Ecology of a Migratory Ungulate.” *Journal of Animal Ecology* 80: 1078–87.

Sawyer, H., M. J. Kauffman, R. M. Nielson, and J. S. Horne. 2009. “Identifying and Prioritizing Ungulate Migration Routes for Landscape-Level Conservation.” *Ecological Applications* 19: 2016–25.

Sawyer, H., M. S. Lambert, and J. A. Merkle. 2020. “Migratory Disturbance Thresholds with Mule Deer and Energy Development.” *Journal of Wildlife Management* 84: 1–8.

Turchin, P. 1998. *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sunderland, MA: Sinauer Associates.

Venter, O., E. W. Sanderson, A. Magrach, J. R. Allan, J. Beher, K. R. Jones, H. P. Possingham, et al. 2016. “Global Terrestrial Human Footprint Maps for 1993 and 2009.” *Scientific Data* 3: 160067.

Wyckoff, T. B., H. Sawyer, S. E. Albeke, S. L. Garman, and M. J. Kauffman. 2018. “Evaluating the Influence of Energy and Residential Development on the Migratory Behavior of Mule Deer.” *Ecosphere* 9: e02113.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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