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PRACTITIONER'S PERSPECTIVE

Conserving habitat for migratory ungulates: How wide is a migration corridor?

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Abstract

1. Conserving migratory ungulates relies on the analysis of GPS collar data and associated maps of migration corridors to inform management and policy actions. Current methods for identifying migratory corridors use complex statistical models designed to account for movement uncertainty rather than estimating the amount of space required by animals to migrate. Furthermore, such methods can complicate conservation efforts by producing highly variable corridor widths and non-contiguous corridors that do not fully connect seasonal ranges.
2. To remedy, we propose an intuitive line buffer approach for delineating individual migration corridors that is simple to implement and focuses on the functional corridor widths needed by migratory ungulates.
3. By buffering a line that connects successive GPS locations, we can delineate individual migration corridors with consistent widths that are robust to variable parameters (GPS fix rate, travel speed, tortuosity) and provide contiguous connection between seasonal ranges. Using a combination of expert knowledge, simulation and 10-min GPS collar data collected from mule deer (*Odocoileus hemionus*) and pronghorn (*Antilocapra americana*), we suggest 400–600 m are reasonable estimates of functional migration corridor widths for individuals of those species.
4. *Synthesis and applications*. Our line buffer approach is intended to simplify migration corridor delineation, improve transparency and encourage a broader discussion of functional corridor widths. These considerations help advance efforts to conserve habitat within migration corridors and prioritize conservation efforts within a single corridor or across multiple corridors.

KEYWORDS
connectivity, corridor conservation, GPS collar, habitat, line buffer, migration corridor, ungulate

1 | INTRODUCTION

Advances in GPS technology continue to improve our understanding of animal migration ecology (Kauffman, Aikens, et al., 2021), but can also introduce new challenges for analysing and visualizing movement data (Nathan et al., 2022). For example, fine-scale movement data are being collected from migratory taxa all over the globe (Kauffman, Cagnacci, et al., 2021; Kays et al., 2022). Yet, it remains a challenge to determine how wide of a migration corridor is needed to facilitate animal movement and ultimately, maintain connectivity between seasonal ranges. Much of the difficulty lies in the fact that the space an animal uses to move is no larger than its body dimensions, but we implicitly know that animals need more space than their actual path. Animal movement is predicated on specific habitat needs, predation risk and other factors (Beier, 2019), which together result in a broader space needed for movement, often termed functional or effective corridor width (Ford et al., 2020; Graves et al., 2007). Relatedly, when defining landscape connectivity between protected areas, connectivity is often viewed as a mix of structural habitat attributes and the propensity of animals to move through those habitats, termed functional connectivity (Abrahms et al., 2017; Carvalho et al., 2016). To date, migration corridor widths are typically estimated with methods designed to model uncertainty between successive GPS locations (Horne et al., 2008), and then used as a proxy for functional migration corridor widths (Sawyer et al., 2009).

In practice, migration corridors must have some area or width associated with them so that they (1) reflect the actual habitat needed to facilitate movement and connectivity and (2) can be translated into a spatially explicit polygon, which is necessary to be incorporated into conservation planning. The ability to easily determine and map functional corridor widths is especially important for migratory ungulates because they are a top priority for many wildlife agencies and non-governmental organizations at regional, national and international scales (Kauffman et al., 2022; Kauffman, Cagnacci, et al., 2021). This increased emphasis on migratory ungulates is due in part to their widespread declines (Bolger et al., 2008; Harris et al., 2009) and the challenges associated with transboundary management (Mason et al., 2020; Middleton et al., 2020). For example, the United States Department of the Interior issued Secretarial Order 3362 in 2018 to encourage federal agencies to support western states and their efforts to enhance migration and winter habitat for mule deer (*Odocoileus hemionus*), elk (*Cervus canadensis*) and pronghorn (*Antilocapra americana*) on federal lands (United States Department of the Interior, 2018). This federal directive provided several million dollars to western state wildlife management agencies for migration research and on-the-ground habitat improvement projects, and was followed by new executive orders (State of Colorado, 2019; State of Nevada, 2021; State of Wyoming, 2020) and legislation (State of New Mexico, 2019; State of Oregon, 2019) aimed at developing collaborative strategies to conserve ungulate migration corridors and improve landscape connectivity at the state level.

To date, the standard approach for identifying migration corridors from GPS data is the Brownian bridge movement model (BBMM; Horne et al., 2008) or similar movement models (e.g. Fleming et al., 2016), which are primarily designed to estimate uncertainty between successive GPS locations rather than functional corridor width. Furthermore, such models are highly influenced by movement parameters like speed and tortuosity as well as parameters unrelated to behaviour, such as the fix rate of the collar. As a result, current modelling practices produce highly variable corridor widths unrelated to the functional needs of an animal and often generate non-contiguous corridors that do not fully connect seasonal ranges (see some of the migration corridors in Kauffman et al., 2022). Additionally, as the resolution of GPS data continues to increase with advancing technology, uncertainty in the movement path itself will approach zero (Nathan et al., 2022). In this scenario, migration corridors estimated from these modelling approaches will produce corridors that are too small to meet the functional needs of migrating ungulates. Thus, work towards an improved rationale and guidance for determining corridor widths is needed to help inform policy, conservation and management of migratory ungulates. Here, we propose a simple and intuitive approach to delineate migration corridors that leans on the ecology and functional requirements of migratory ungulates, rather than complex statistical methods aimed at quantifying uncertainty between successive locations.

2 | DEFINING MIGRATION CORRIDOR WIDTHS AND MODELLING LIMITATIONS

The common approach for identifying migration corridors from GPS data involves at least two steps—extracting an individual migration sequence from the larger GPS dataset using net-squared displacement (Bunnefeld et al., 2011) and then using the BBMM (Horne et al., 2008) to estimate an occurrence distribution (OD) for each migration sequence (Merkle et al., 2022). The 99% contour of the individual OD is often used to identify the migration corridor (Figure 1a; Kauffman, Cagnacci, et al., 2021; Sawyer et al., 2009). To estimate migration corridors at the population level, a final step includes stacking the individual migration corridors on top of one another and determining which segments receive low, moderate and high use based on the degree of individual overlap (Merkle et al., 2022; Sawyer et al., 2009).

While this standard approach provides an objective and model-driven method to delineate the migration corridor of an individual animal, the output is strongly influenced by the Brownian motion variance (BMV), which is a key parameter of the BBMM and accounts for uncertainty between successive GPS locations (Horne et al., 2008). The BMV is largely determined by the speed and tortuosity of the moving animal, as well as the GPS fix rate and fix success of the collar (see Appendix S1). Variation in BMV can produce highly variable corridor widths ranging from 50 to >15,000 m (Appendix S1; Figure 2; Horne et al., 2008). Furthermore, the BMV can vary greatly across populations and individuals (Figure 2e), and even within the

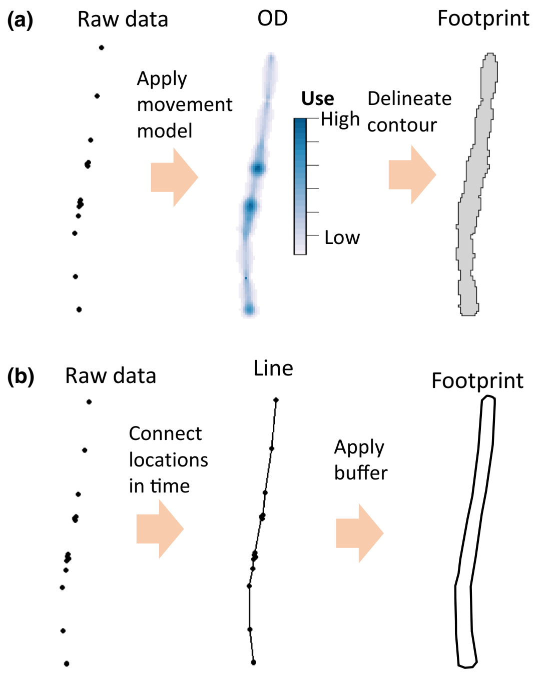

FIGURE 1 The analytical steps to create an individual migration corridor from a sequence of migration data from a GPS collared animal. The top panel (a) depicts the typical approach where a movement model (e.g. Brownian Bridge movement model; BBMM) is applied to a sequence of relocation data to create an occurrence distribution (OD). The migration corridor is then defined by calculating a contour from the OD (e.g. the 99% contour). The bottom panel (b) depicts the line buffer approach where the sequence of point data is connected by a line and then buffered by a consistent width (in this case by 250 m) to create the migration corridor. Note that the data and scale in the figure are the same, and thus, the BBMM provides a similar sized corridor to the line buffer approach, despite the simplicity of the latter.

same individual in different years (Figure 2a,b). Depending on the spatial distribution of GPS locations and the proportion of locations in a slow versus fast movement state (e.g. stopover vs. migrating), polygons from individual ODs can also break apart and not provide continuous coverage between seasonal ranges (Figure 2b).

Migration corridors estimated from BBMM have been widely used and have advanced ungulate conservation (Kauffman, Cagnacci, et al., 2021). However, several inherent limitations can thwart management application. First, estimated corridors should help identify and prioritize the areas that animals require to move between seasonal ranges. Yet, large BMV values produce corridors that are wider than biologically necessary. Furthermore, variable and artificially inflated corridor widths make it difficult to address management scenarios where prescribing a common width of a migration corridor within a population is required, such as roadway crossings or designated corridors through developed areas. Second, migratory animals require a contiguous corridor to move between their seasonal ranges. Non-contiguous coverage of the polygon from the OD leaves land planners and wildlife managers to arbitrarily fill in the missing corridor sections or delete disconnected polygons entirely. Finally, the BBMM and the associated BMV are complex analytical methods that can be difficult to implement, understand and interpret. When stakeholders do not intuitively understand the modelling process and interpret the estimated corridor(s), they may be hesitant to support corresponding conservation measures (Keeley et al., 2019).

Like other movement models, outputs from the BBMM will change as data resolution increases with advances in GPS technology. To date, most GPS data are collected at 1- to 13-h intervals. As GPS technology improves, however, collars will collect locations more frequently (e.g. every 10 min). Such frequent GPS locations will reduce the uncertainty in the movement path between GPS locations, resulting in reduced BMV estimates and in turn, narrower corridors. For example, an average width of a corridor estimated with BBMM from 2-h GPS data may be ~500 m, but the same route estimated with 10-min data may only be 50 m wide (Figure 3). Consequently, with such fine-scale data, migration corridors estimated from movement models will begin to approximate the actual trajectory walked by the animal, which is too small to account for the functional habitat needed for migratory ungulates. This problem is not necessarily a weakness of BBMM, but instead a direct result of any analytical method aimed at quantifying uncertainty associated with a movement trajectory rather than the functional width of a migration corridor.

3 | IS THERE A BETTER WAY FORWARD?

We suggest an alternative method for delineating migration corridors that is less sensitive to movement parameters such as speed and tortuosity, and sampling-based parameters such as GPS fix rate and fix success. Regardless of GPS fix rate or modelling approach, a line (either straight or estimated from a correlated random walk model; Johnson et al., 2008; Appendix S2) that connects successive GPS locations represents our best approximation of the animal movement path. Thus, we can delineate migration corridors by buffering those lines by a fixed distance (e.g. 250 m), so that corridors have consistent widths that contain adequate amounts of movement habitat, are robust to variable GPS fix rates and are fully contiguous between seasonal ranges (Figures 1b and 3).

For this approach, the width of a corridor is simply determined by the buffer distance—a fixed distance on either side of the line. The width of the buffer can be informed by expert judgement, empirical data or a combination of both. With expert judgement, corridors could be assigned widths based on local knowledge about how animals move through the landscape or disturbance levels on adjacent habitats, thus approximating how much space is needed to maintain functional connectivity of the corridor. For example, depending on the species and region, a corridor width of 500 m likely accommodates potential flight responses or zone of influence from common disturbances like roadways, energy development and recreation (Miller et al., 2020; Northrup et al., 2015; Stankowich, 2008). While narrower than the 2 km rule

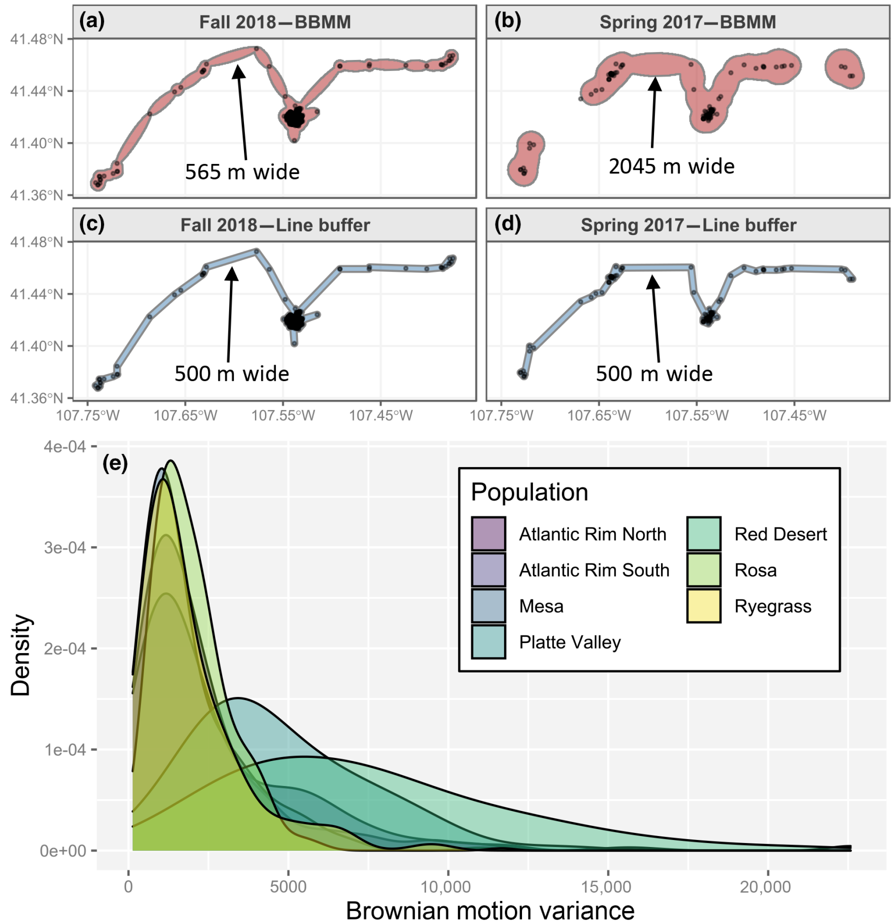

FIGURE 2 Panels (a–d) contrast migration corridors built from models designed to estimate uncertainty versus the line buffer approach which can be used to include information and knowledge about functional corridor width. Panels (a, b) Illustrate how migration corridor widths estimated from the 99% contour of a Brownian bridge movement model (BBMM) for the same individual mule deer in two different years can range from 565 to 2045 m and impact continuity between seasonal ranges. Despite the same 2-h GPS collar fix rate each year (relocations depicted by black dots), the estimated widths varied considerably because of their respective Brownian motion variance (BMV) of 561 m^2 for (a) and 2545 m^2 for (b). In contrast, panels (c, d) illustrate the line buffer approach using a 250 m buffer, where route widths are consistent across years and are fully contiguous. Panel (e) represents observed variation in the BMV estimated from >500 individual mule deer during migration (from 7 populations) marked with collars collecting GPS locations every 2 h in Wyoming, New Mexico and Colorado (from Kauffman et al., 2020). The large degree of observed variation in the BMV would result in commensurate differences in migration corridor widths.

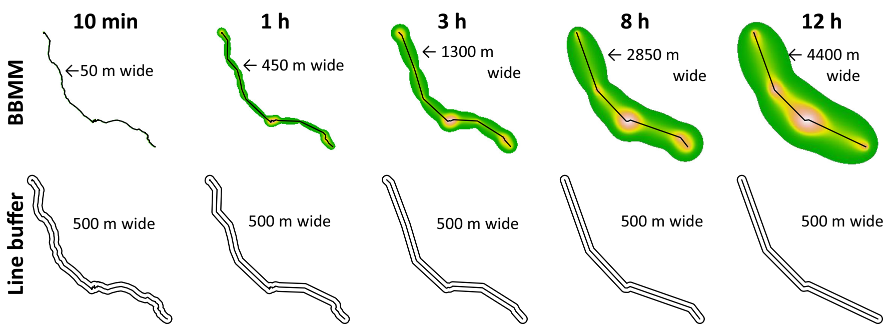

FIGURE 3 A comparison of migration corridor widths across fix rates derived from the line buffer approach (bottom row) and a Brownian Bridge movement model (BBMM) that estimates uncertainty between relocations. The top row represents the 99% contour of a BBMM, and the bottom row represents a 250-m buffer from the movement path at the sampled fix rate (denoted by the black line). With the line buffer approach, as fix rate increases, some detail in the migration corridor is lost, but the migration corridor width is consistent.

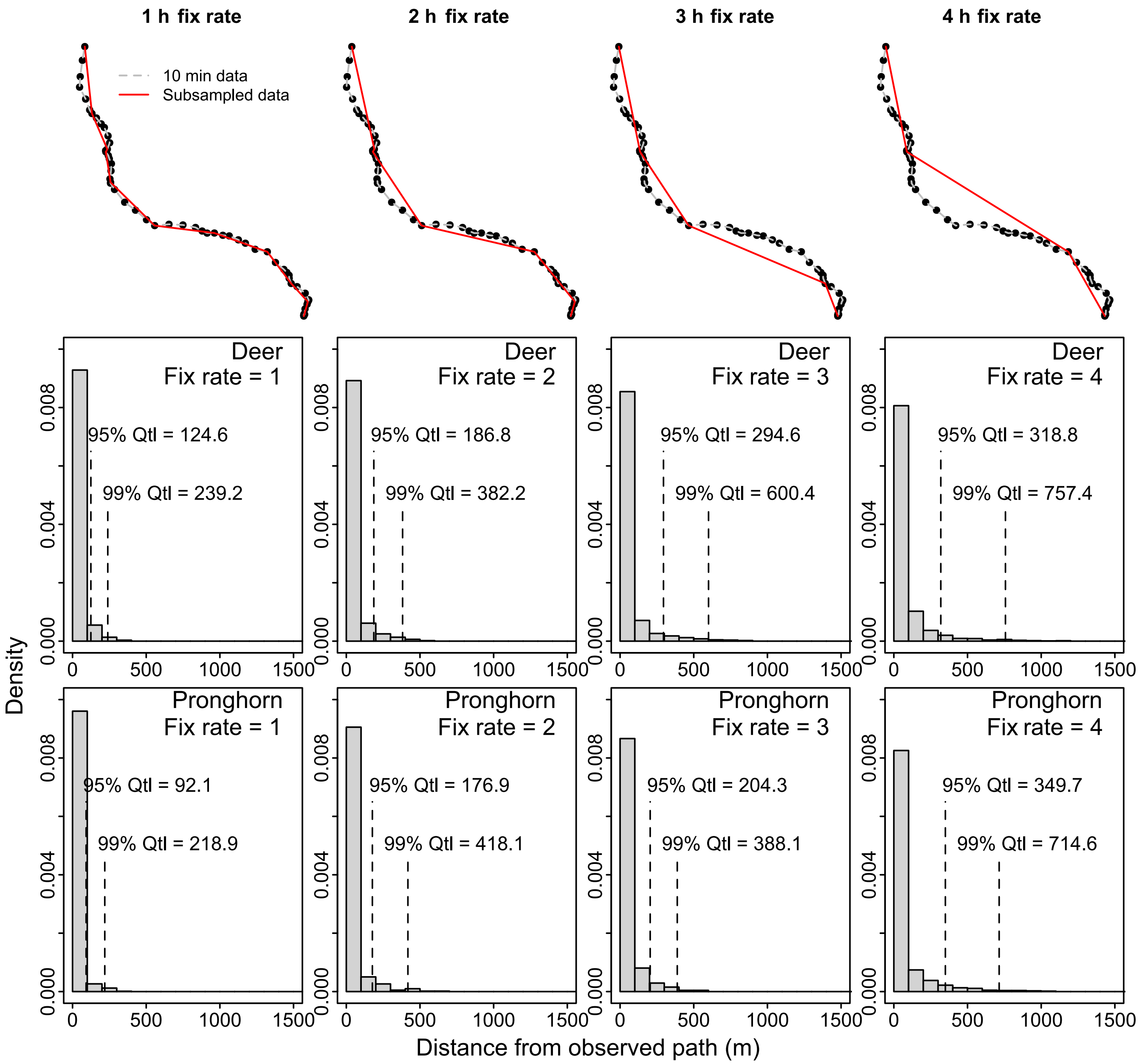

FIGURE 4 An estimation of how the line buffer approach can incorporate uncertainty associated with sampling frequency by a GPS collar. Histograms of the distance the observed path (estimated from 10 min GPS data) deviates from straight lines sampled every 1–4 h from the observed path. 95% and 99% quantiles are provided to clarify the buffer widths of sampled data that capture the majority of an animal's deviation from the observed path. Top panel provides a visual of the effect of sampling on estimates of deviation from the observed path (grey lines) from random 12-h segment of movement from a single migrating mule deer. Data were collected from two female mule deer and two female pronghorn during spring migration in 2022 in Wyoming, United States. See Appendix S3 for plots that include sampling up to 12 h.

of thumb identified for connectivity between protected areas for cross-taxa dispersal (Beier, 2019), such widths targeted specifically to ungulate migration are 5–10 times wider than the widest overpasses designed for ungulate movement over roadways (Kintsch et al., 2021; Sawyer et al., 2016; Simpson et al., 2016). Furthermore, when individual migration corridors are combined to estimate population-level corridors, the corridor width will sometimes be larger in segments used by multiple animals (Kauffman et al., 2020; Sawyer et al., 2009, 2019). Empirical data mixed with expert judgement could also be used to identify functional corridor width. In this case, a step selection analysis or other movement model paired with spatial layers of habitat patch size or width could be used to estimate thresholds of habitat area or width that begin to result in avoidance (sensu Lambert et al., 2022). However, we recognize that such empirical studies cannot be developed in every system, and expert judgement that synthesizes local knowledge with results from empirical analyses from other areas may be more practical.

The line buffer approach does not use any statistical models to account for movement uncertainty. However, we suggest that the buffer itself can provide a functional corridor width that animals need while also accounting for movement uncertainty. To illustrate, we collected 10-min data from GPS collars (model G5-D; Advanced Telemetry Systems) for a single spring migration in 2022 from two female mule deer and two female pronghorn in Wyoming, USA (Merkle et al., 2023). Animals were captured using a net gun shot from a helicopter in March 2022 following capture and handling methods approved by the University of Wyoming Animal Care and Use Committee (protocols 20200302MK00411-01 and 20210301MK00461-02) and Wyoming Department of Game and Fish (permits 33-937 and 33-1162). We then subset the 10-min data to 1- to 12-h fix frequencies (in 1-h increments) and calculated the distances between the observed 10-min locations and the straight lines connecting each of the subsampled relocations. We found that as GPS fix frequency increased, the accuracy of the straight line between sequential GPS locations increased and better matched the actual movements of the animal, as approximated by the 10-min data (Figure 4). Using a 2-h fix rate, which is common in current studies used to delineate ungulate migration corridors, we found both mule deer and pronghorn stayed within 200 m of the actual movement line 95% of the time, which suggests a 400-m corridor width would suffice for these two species (Figure 4).

We encourage more discussion and thought be given to defining functional migration corridor widths for effective conservation. Based on our analysis above, simulations of how speed, BMV and fix rate affect corridor width (Appendix S1), previous work with BBMM (Kauffman et al., 2022; Kauffman, Cagnacci, et al., 2021) and our expert judgement, we suggest functional corridor widths of 400–600 m (i.e. line buffers of 200–300 m) are reasonable starting points for individual mule deer and pronghorn migration corridors. Ultimately, the selected buffer width should (1) provide adequate space for animals to move through bottlenecks or near risky or dangerous edges (e.g. human disturbance, natural barriers), and (2) not be exceedingly large such that corridors contain areas not needed by migratory animals and thus become socially and politically unacceptable.

4 | CONCLUSION

Migratory ungulates must be able to move freely across the landscape to access seasonal forage and avoid harsh weather (Mueller & Fagan, 2008). While fine-scale GPS data and movement models have greatly improved our understanding of ungulate migration and have paved the way for conserving migratory habitat, we suggest that the analysis of GPS data and creation of actionable maps of migration corridors may benefit from simpler methods. Instead of focusing on statistical models that estimate uncertainty in movement trajectories or space use, we encourage a more biological-based discussion of how wide ungulate migration corridors need to be to encompass functional habitat that connects landscapes and provide clear maps to advance conservation efforts. The line buffer approach provides an intuitive and transparent alternative to existing methods that enables mapping of contiguous migration corridors that fully connect seasonal ranges and ensures functional corridor widths.

AUTHOR CONTRIBUTIONS

Hall Sawyer conceived the original idea, and all authors helped refine it. L. Embere Hall revised the idea critically for important intellectual content relative to wildlife management and conservation. Jerod A. Merkle and Hall Sawyer designed the methodology and analyses. Matthew J. Kauffman, Luke Wilde and Cody F. Wallace collected the data. Jerod A. Merkle and Blake Lowrey analysed the data. Jerod A. Merkle and Hall Sawyer led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

We declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.n2z34tn2h (Merkle et al., 2023).

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BIOSKETCH

Jerod A. Merkle Jerod's research foci include movement and migration ecology, fitness consequences of behavior, how cognition and innovation influence foraging behavior, and conservation and management of large mammals.

Blake Lowrey Blake works on spatial ecology topics for ungulates throughout Greater Yellowstone Ecosystem. Blake also coordinates the USGS Corridor Mapping Team describing ungulate migrations across the western U.S.

Cody F. Wallace Cody's research interests focus on cognition, memory, and learning in free-ranging migratory populations. His current work seeks to evaluating how memory and social information is used to navigate, establish, and maintain migration patterns in ungulate populations.

L. Embere Hall Embere's research interests focus on the intersection of science and resource management. In particular, she thinks about how animals respond to environmental change, and how on-the-ground management actions can facilitate population resilience.

Luke Wilde Luke researches how animal movement behaviors impact population-level responses to climate and anthropogenic stressors in addition to informing management actions to improve connectivity and phenotypic diversity.

Matthew J. Kauffman since 2006, Matt has worked as a USGS researcher and as faculty at the University of Wyoming. His research group investigates the ecology and conservation of long-distance migrations in ungulates.

Hall Sawyer Hall works with agencies and industry to conduct and communicate applied research in ways that improve management, mitigation, and planning efforts related to ungulates, with an emphasis on migration ecology and energy development.

SUPPORTING INFORMATION

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

Appendix S1. Simulation quantifying the variables that influence Brownian motion variance.

Appendix S2. Comparison of straight line versus correlated random walk model when calculating buffer widths for ungulate migration corridors.

Appendix S3. Continuation of Figure 4 to 12-h fix rates.

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